Systematics, Biogeography and Conservation of Bald Uakaris (*Cacajao* Lesson, 1840)

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Bald uakaris: (A) *C. calvus*, (B) *C. rubicundus*, (C) *C. ucayalii*, (D) *Cacajao novaesi*.
Photos: Amanda Lelis (A), Marcelo I. Santana (B and D), Mark Bowler (C).

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LIST OF ABBREVIATIONS

IUCN	International Union for Conservation of Nature
SDR	Sustainable Development Reserve
ES	Ecological Station
ER	Extractive Reserve
NP	National Park
VU	Vulnerable
EN	Endangered
LC	Least Concern
DD	Data Deficient
EOO	Extent of Occurrence
JJES	Juami-Japurá Ecological Station
BJER	Baixo Juruá Extractive Reserve
USDR	Uacari Sustainable Development Reserve
MJER	Médio Juruá Extractive Reserve
DIL	Deni Indigenous Land
KJIL	Kanamari do Juruá Indigenous Land
RGER	Rio Gregório Extractive Reserve
RLER	Riozinho da Liberdade Extractive Reserve
SDNP	Serra do Divisor National Park
MUZUSP	Museu de Zoologia da Universidade de São Paulo
MPEG	Museu Paraense Emílio Goeldi
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro
IDSM	Instituto de Desenvolvimento Sustentável Mamirauá
FMNH	Field Museum of Natural History
INPA	Instituto Nacional de Pesquisas da Amazonia
UFPA	Universidade Federal do Pará
RADseq	restriction site-associated DNA sequencing
ddRADseq	Double-digest restriction site-associated DNA sequencing
LUC	Land Use/Cover
IPCC	Intergovernmental Panel on Climate Change
GCM	General Circulation Models
RCP	Representative Concentration Pathways
Pas	Protected Areas
Ils	Indigenous Land
BAU	Business-as-usual
ENM	Ecological Niche Modelling
ROC	receiver operating characteristic
AUC	Area under the curve
MAXENT	Maximum entropy
BIOCLIM	Bioclimatic
PCR	Polymerase Chain Reaction
mtDNA	Mitochondrial DNA

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ABSTRACT

Uakaris, genus *Cacajao*, possess adaptations to their unripe seed-focused diet and habitat preference for Amazonian flooded forest habitats. These include large procumbent canines (shared by the other 2 Pitheciinae, *Chiropotes* and *Pithecia*, large home ranges, and large group sizes). The diversity, evolution and phylogenetics of Pitheciinae are limited to few studies and their geographic distribution to a few records and localities. The overall goal of this study is to investigate the phylogenetic relationship of bald uakaris, genus *Cacajao*, using molecular data, and to get new information on its genetic diversity and geographic distribution to assess their taxonomic classification. The molecular analysis of the mitochondrial DNA supports the origin of the ancestral of *Cacajao* in the Western Amazon with the sister genus *Chiropotes* expanding to the Guiana and Brazilian shields during the Pleistocene. Therefore, the genus *Cacajao* had its diversification influenced by the formation of the flooded forests of Western Amazon during the process of drainage of the Pebas Lake. The ddRAD analysis supported the reciprocal monophyly of bald uakaris, with all clades including only individuals with exclusive diagnostic characters. Therefore, bald uakaris can be classified as follow: *Cacajao calvus* (I. Geoffroy, 1847), *C. rubicundus* (I. Geoffroy and Deville, 1848), *C. ucayalii* (Thomas, 1928), and *C. novaesi* (Hershkovitz, 1987). I provide an update of the geographic distribution of each species of bald uakari and how the predicted scenarios of deforestation and climate change can affect the four species by 2050. *Cacajao novaesi* has the more restricted geographic distribution occurring only between Gregorio and Tarauacá rivers. All other bald uakaris occur in a patchy distribution. The synergistic effects of climate change and deforestation will imply in habitat loss in the future scenarios, and along with hunting of *C. ucayalii* and *C. novaesi*, will result in a population decrease. Studies on the feeding ecology in different field sites and the population status for each taxon are the priorities for the research of bald uakaris.

Chapter 1. Introduction

1.1 Neotropical Primates: Diversity, Evolution, and Conservation

Primates are an order of placental mammals that includes two groups: the suborders Strepsirrhini, and Haplorrhini. The first, Strepsirrhini, has a rhinarium (moist tip of the nose), *tapetum lucidum* (a tissue layer behind the retina), and the epitheliochorial placenta (maternal and fetal vascular system separated by several cellular layers), and include the lemurs, lorises and galagos (bushbabies)(Groves 2018). Haplorrhini, however, does not possess the rhinarium and *tapetum lucidum* and have a haemochorial placenta (fetal-maternal bloodstream in contact). New World monkeys, Old World monkeys, apes and humans are Haplorrhini (Groves 2018).

Non-human primates (hereafter, primates) occur mainly in the equatorial regions of Central and South America (Neotropics), Africa and Asia. These areas harbour the main tropical forests and a primate diversity that includes 516 species classified in 79 genera (PSG 2020a). Primates are intrinsically related to tropical rainforest in a sophisticated ecological and evolutionary way (Sussman 1995; Chapman and Onderdonk 1998; Estrada et al. 2017). Both forest structure and productivity are essential for the primate richness in tropical rainforests (Kay et al. 1997; Gouveia et al. 2014). A range of characteristics in their feeding ecology is associated with critical ecological functions (Marshall and Wich 2016).

This co-dependency between primates and tropical rainforests can be seen in the many adaptations in plants and primates. For example, the evolution of colour vision in primates is suggested to confer foraging advantages in finding ripe coloured fruits against the greenish forest background (Melin et al. 2009, 2014; Kawamura 2016). At the same time, the evolution of fruit colour is associated with mutualistic interactions with seed dispersers (Valenta et al. 2017, 2018).

Several studies reveal the importance of primates as seed dispersers, with some plants depending on primates to increase the success in the seed germination (e.g. Dew and Wright 1998; Canale et al. 2016; Fuzessy et al. 2016; Albert-Daviaud et al. 2018; Andresen et al. 2018; Tsuji and Su 2018; Gestich et al. 2019). Consequently, those forest patches where primates were locally extinct will probably have their structures impoverished. The overhunting, for instance, negatively affected those plants that rely on primates for seed dispersal and recruitment (Chapman and Onderdonk 1998; Nuñez-Iturril and Howe 2007; Nuñez-Iturril et al. 2008; Fuzessy et al. 2016).

Although seed dispersal is one of the most studied ecological function, many other critical roles that primates have in the ecosystem remains overlooked. For example, primates with a specialized diet (frugivorous or seed predators) are important to regulate the diversity of plant species by frequently seeking a similar targeted resource (Norconk et al. 1998; Marshall and Wich 2016). Primate is frequently reported as prey for felines, eagles, and heavy-bodied snakes, but this predator/prey relationship is mostly limited to anecdotal cases (Luna et al. 2010; Barnett et al. 2011; Quintino and Bicca-Marques 2013; but see Bidner 2014; Isbell et al. 2018).

A range of ecological and behavioural strategies are reported in primates to optimize the use of resources and compensate for the downside of a potential intra and interspecific competition. Some of these strategies are possible due to the evolution of phenotypical adaptations such as the coloured vision, masticatory and digestor system adapted to a specific diet, body size, and vocalization (Cunha and Byrne 2009; Melin et al. 2009; Norconk et al. 2009; Snodderly et al. 2019)

New World monkeys (Neotropical primates) are one such case where the adaptative radiation led to the evolution of several ecological, behavioural, and morphological adaptations in their 21 genera with the body size ranging from ~100g (*Cebuella*) to >10kg (*Brachyteles*) (Rylands and Mittermeier 2014; Buckner et al. 2015; Rylands et al. 2016; Lynch-Alfaro 2017; Byrne et al. 2018). They have their origin traced back to a single common ancestral population from 24 to 19 Ma (Lynch-Alfaro 2017) and with a species-level diversification occurring from 5 to 10 Ma or even more recently (Buckner et al. 2015; Lynch-Alfaro et al. 2015; Lynch-Alfaro 2017; Byrne et al. 2018; dos Reis et al. 2018).

1.1.1. ON THE SPECIES CONCEPTS AND THE TAXONOMIC CLASSIFICATION OF NEOTROPICAL PRIMATES

Although the adaptative radiation of Neotropical primates implied in a relatively rapid diversification, our interpretation of this diversity in terms of the number of species is still controversial. In the late ’70s and '80s, the renowned taxonomist Philip Hershkovitz published several reviews based on the detailed study of pelage colouration and morphometrics of museum specimens for many groups (Hershkovitz 1977- Callithrichidae;

1983 - *Aotus*; 1984 - *Saimiri;* 1987a - *Cacajao*; 1987b - *Pithecia*; 1990 - *Callicebus*). These proposals were widely accepted by the scientific community and considered the foundation of Neotropical primate taxonomic classification until the late 90s when new species were described – especially in Amazon Rainforest – and the Phylogenetic Species Concept began to be adopted by many primatologists.

Hershkovitz brought together an impressive set of information from zoological collections around the world. He presented taxonomical proposals for groups that were limited to a few specimens collected by the naturalists of the 19th and early 20th centuries. Hershkovitz used the pattern of pelage colouration to identify the diagnostic characters in most of his proposals and considered a polytypic species framework, using the subspecies rank. However, he never mentioned if he was following a particular species concept (Groves 2014a).

The species concept is one of the most fervent debates in evolutionary biology. Different criteria are used to define the more than 20 species concepts (Mayden 1997). The reader will find a prolific discussion for and against these concepts in the scientific literature, although there is no consensus on which one would be “the best”. Taxonomists will follow the precepts of a species concepts according to the characteristics of the group of organisms they are studying but, as we can see in the more than hundred years of debate, there is no consensus – even among specialists of each taxonomic group.

The different species concept can be broadly defined as theoretical or operational (Branham 2008). Theoretical concepts focus on the definition of what is a species; therefore, they are process-oriented in their conceptual framework. The Hennigian Species Concept (Meier and Willmann 2000), the Evolutionary Species Concept (Simpson 1961; Wiley 1978; Wiley and Mayden 2000), and the Biological Species Concept (Mayr 2000) are examples of theoretical concepts (Branham 2008). The many variants of the Phylogenetic Species Concept – although based on precepts of Hennig’s Phylogenetic Systematics – are focused on different criteria to identify species; therefore, they are considered operational concepts. Here, I will discuss some aspects of the Biological Species Concept (BSC) and Phylogenetic Species Concept (PSC) – which are more relevant in the context of this research.

1.1.2. REPRODUCTIVE ISOLATION AND THE BIOLOGICAL SPECIES CONCEPT (BSC)

The main criteria to define a species under the BSC is reproductive isolation. Ernst Mayr, one of the leading advocates of this concept, defined species as follow:

"Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1969, p. 26).

Interbreeding, in this case, includes not only those groups of natural populations where sexual reproduction can be, indeed, verified, but refers much more to a <u>propensity</u> of geographically isolated populations to do so if they were in contact (i.e. inference of interbreeding) (Mayr 2000). Herein lies one of the main criticisms to the BSC: whether two geographically isolated populations can reproduce is difficult to test in most situations. Reproductive isolation, according to Mayr (1969), is the mechanism by which two species will maintain their gene pool well-structured and, thus, prevent the interbreeding. Consequently, these two species will accrue differences in the phenotype that can be inferred as evidence of reproductive isolation. The "amount of difference", however, is an arbitrary decision that the taxonomist will take according to the available material – in many situations, a few specimens – and on the set of evidence used.

Under the BSC, the subspecies rank is warrantable if the evidence of reproductive isolation among the allopatric populations were ambiguous. Therefore, subspecies suggest that reproductive isolation has not fully evolved:

"..*Subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of species*" (Mayr 1969, p. 41).

Two aspects are important to consider in the subspecies concept: "(1) closest relationship and (2) allopatry" (Mayr 1969, p. 197). A subspecies, therefore, includes those populations that are similar but phenotypically and genetically different from each other populations from the same species; thus, these populations are taxonomically distinct (Mayr 1969). They are geographically separated from each other (allopatric), but as they belong to the same species, they can interbreed in contact zones. When the BSC began to be widely adopted by taxonomists, many populations previously holding a species status – based on any variation within local populations in what Mayr refers as Typological Species Concept (Mayr 2000) – were lumped in a single polytypic species (Wilson and Brown 1953).

However, molecular evidence was decisive to show that gene flow occurs not only in contact zones but also between sympatric species and is an essential component in the diversification process (Whittemore and Schaal 1991; Patton et al. 1996; Via 2001; Groves 2012; Martin et al. 2013; Yoder 2014). Mayr (2000) himself mentioned that, in many cases, the inference of reproductive isolation is difficult, even when using molecular evidence:

> *“Molecular biology, of course, has given us far more evidence on which to base our conclusions than the purely morphological evidence previously available to a taxonomist. The greatest practical difficulty encountered by the investigator is the occurrence of mosaic evolution. Populations may acquire reproductive isolation but only minimal morphological difference (resulting in sibling species), whereas other populations may acquire conspicuously different morphologies but no isolating mechanisms. Equally, rates of molecular divergence and the acquisition of niche specializations vary independently of the acquisition of reproductive isolation.”* (Mayr 2000, p.25-26)

Where draw the line to assign the species or subspecies status will depend on the inference that a taxonomist does about how reproductively isolated two populations (or group of populations) are in fact – and this is an arbitrary decision. In addition, while different species may be indeed reproductively isolated, there are many other properties involved in speciation (see de Queiroz 2007). Consequently, many systematists challenged the role of biological species (“species” under the BSC) as a unit of evolution and the view of species as a lineage gained strength (Simpson 1961; Wiley 1978; Cracraft 1983; Donoghue 1985; Wheeler and Meier 2000).

1.1.3. SPECIES AS LINEAGES AND THE PHYLOGENETIC SPECIES CONCEPT (PSC)

When considering species as lineages, the temporal component is essential to understand the speciation. Time and shared derived characters (synapomorphies) were in the foundation of the Phylogenetic Systematics proposed by Willi Hennig (Hennig 1965; Williams and Ebach 2008). In Hennig’s proposal, species are reproductive communities, and the evolution of genetic isolation mechanisms is the core factor of speciation (Hennig 1965). The ancestry would, thus, define the phylogenetic relationship:

> *…all species (reproductive communities) which exist together at a given time, e.g., the present, have originated by the splitting of older homogeneous reproductive communities. On this fact is based the definition of the concept, "phylogenetic relationship": under such concept, species, B, is more nearly related to species, C, than to another species,*

A, when B has at least one ancestral species source in common with species C which is not the ancestral source of species A (Hennig 1965, p. 97) (see Figure *1.1* below)

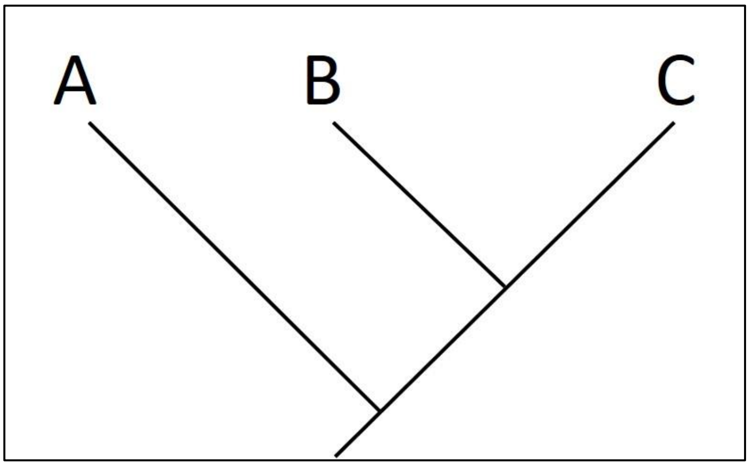

Figure 1.1 The essential phylogenetic relationship scheme depicting an ancestry-descent arrangement

Accordingly, the reproductive isolation separates the members of two species originated from a common ancestor, and the time would be the boundary of a biological species between two successive speciation events (Willmann 1986; Meier and Willmann 2000). Meier and Willmann (2000) also highlighted the secondary role of characters in the species definition in what became known as the Hennigian Species Concept:

> *"…Hennigian Species Concept is identical to the Biological Species Concept if absolute isolation is adopted as the criterion for contemporaneous populations and the origin of the isolation of two sister species is used to delineate species boundaries in time. In any case, it is important to stress that neither the Hennigian nor the Biological Species Concept is character related. Characters merely provide evidence as to where species boundaries are and can never be definitive species criteria. It is the detection of reproductive gaps that is decisive, and that avoids arbitrary species boundaries and the "creation" of arbitrary species based on arbitrarily chosen sets of characters."* (Meier and Willmann 2000, p. 38)

Although Hennig has put the speciation in a temporal perspective and the synapomorphy as the foundation of a phylogenetic relationship, the HSC took the reproductive isolation to an even more restrictive level. For this reason, it has been criticised for also not offer a testable approach to identify species (see Wheeler and Meier 2000). The essential problem here is that interbreeding is considered a plesiomorphic condition and as such will not contribute to unveil the phylogenetic relationship, which is based on synapomorphy (Rosen 1978; Bremer and Wanntorp 1979; Lidén and Oxelman 1989; Pinna 1999; Mishler and Theriot 2000).

Hennig's Phylogenetic Systematics brought the theoretical concept of species-as-lineage, and several concepts are deriving from this thread. The Phylogenetic Species Concept (PSC) is one of them and, at least, three versions are discussed in the literature. Two criteria are essential in these versions: diagnosability and monophyly (Mayden 1997).

The first criteria of the PSC, diagnosability, is essential to identify species according to the intrinsic traits of a population or group of populations. These intrinsic traits characterise these populations since they have inheritable and genetic properties; therefore, are considered diagnostic characters (Cracraft 1983; Mayden 1997; Dubois 2017). It was referred as the diagnosable version of the PSC (see Mayden 1997), and it emphasizes the pattern behind the species evolution (Nelson and Platnick 1981; Cracraft 1983; Nixon and Wheeler 1990; Mayden 1997; Pinna 1999; Wheeler and Platnick 2000). Thus, "*A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent*" (Cracraft 1983, p.170). This concept, unlike the BSC and HSC, emphasizes the importance of identifying the diagnostic characters as a proxy of the phylogenetic relationship among taxa and delimit the smallest diagnosable units (i.e. species).

The second criteria underlining the PSC is monophyly, which is inferred from the analysis of the unique derived characters (autapomorphies) (Rosen 1978, 1979). Accordingly, species should be monophyletic as any other supraspecific taxa and the character analysis will define the smallest clusters possessing the autapomorphies that qualifies them as species (Rosen 1978, 1979; Donoghue 1985; Mayden 1997; Mishler and Theriot 2000). Both criteria, when considered separately, present drawbacks. For example, in many situations only a few samples from few localities are available for taxonomic analysis and a variation across populations from different localities can be identified as diagnostic characters – which could be an incorrect interpretation due to the lack of material available for a detailed assessment (Gutiérrez and Garbino 2018). In addition, a species may encompass many monophyletic groups, but representing different populations since individuals from the same populations will probably share similar morphological and genetic characters and may have been geographically isolated only recently (Gutiérrez and Garbino 2018). Here lies the third version of the PSC, which required both diagnosability and monophyly as criteria to delimit species (Mckitrick and Zink 1988; Mayden 1997). According to this version, a species is "*the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent*" (Mayden 1997, p. 407).

The PSC came into play with a great deal of controversy and discussions on its application in mammalian taxonomy. Along with the philosophical discussion on the "species problem", the adoption of the PSC implied in an increase in the number of species. Under the PSC, species is the unit of evolution. The use of subspecies is, therefore, a taxonomic convenience to identify populations that are "sufficiently distinguishable" from each other. However, for many of the PSC adherents, subspecies is an unnecessary taxonomic rank. If a population is diagnosable and monophyletic, then it is "*the smallest diagnosable cluster of individual organisms forming a monophyletic group*" and can be placed at the species level. The subjectivity of subspecies, therefore, would hinder the interpretation of the diversity (Cracraft 1983; Donoghue 1985; Groves 2012). As such, Cracraft (1983) argue that a polytypic species does not convey an evolutionary and operational perspective under the PSC; therefore, it has no ontological status:

> *A polytypic "biological species" cannot logically constitute the lowest- level taxonomic "unit of evolution" because these "species" may be composed of a variable number of evolutionary units, each possessing their own geographic, phenotypic, and (presumably) genetic integrity.* (Cracraft 1983, p. 165)

1.1.4. THE PHYLOGENETIC SPECIES CONCEPT AND THE NEOTROPICAL PRIMATES TAXONOMY

The adoption of the PSC in Primates taxonomy was largely a consequence of the extensive mammals' taxonomic revisions by Collin Groves, in what became referred as the "Groves' Effect" (Behie and Oxenham 2015; Pilbrow and Rylands 2019). After Groves' seminal review of Primates taxonomy (Groves 2001), the number of valid species increased in a ripple effect of the application of the PSC criteria (**Error! Reference source not found.**). Indeed, the identification of different diagnosable units encouraged researchers to raise to species level those populations that were previously classified as subspecies. Some researchers, however, have condemned this trend. They accuse what they call 'splitters' to cause undesirable taxonomical inflation and a flurry debate on the pros and cons of the PSC reveals that "the species problem" is far from obsolete (Gippoliti and Amori 2007; Gippoliti and Groves 2012; Rosenberger 2012; Zachos and Lovari 2013; Groves 2013, 2014b, Zachos et al. 2013, 2019, Zachos 2015, 2018, 2019; Taylor et al. 2019; Gippoliti 2019).

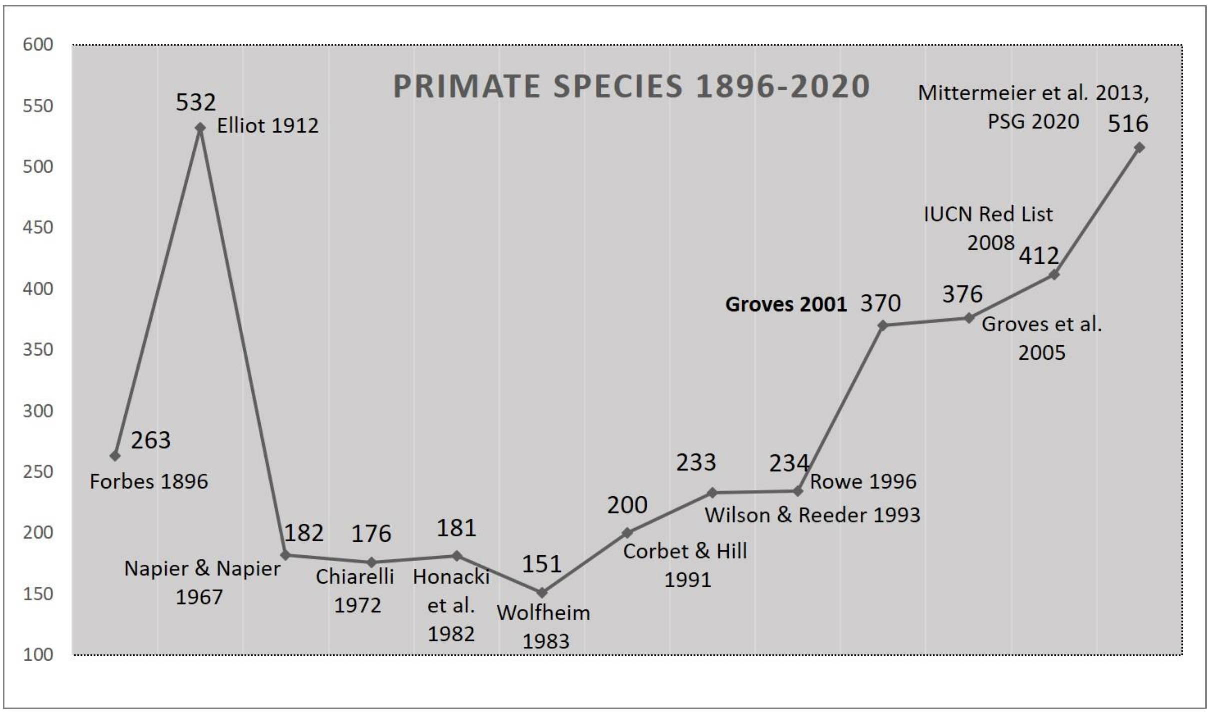

Figure 1.2 Number of primate species according to different authors (Forbes 1896; Elliot 1912; Napier and Napier 1967; Chiarelli 1972; Honacki et al. 1982; Wolfheim 1983; Corbet et al. 1991; Wilson and Reeder 1993; Rowe 1996; Groves 2001; Groves et al. 2005; Mittermeier et al. 2013; PSG 2020b). Number of primate species according to different compilations. Note that after Groves 2001, the number of primate species continued to increase. Modified, with permission, from Rylands and Mittermeier 2014.

In the case of the New World Monkey, Hershkovitz compiled in his revisions much essential information on the pelage colouration, morphometry, and geographic distribution that were the start point for many other researches (including this one). The use of diagnostic characters under the PSC brought an operational criterion to delimit species. In Neotropical Primates, this approach was remarkable in the taxonomic revision of *Callithrix* of the Brazilian Taxonomist Dr Mario de Vivo (Vivo 1991). The author applied the binomial nomenclature to different diagnosable units (i.e. species) when in the absence of evidence of intergradation. Therefore, the paradigm change in the taxonomic classification of Neotropical Primates can be traced back to the monography of Vivo (1991) and to the subsequent taxonomic reassessment proposed by Rylands et al. (2000) and Groves (2001), with a profound influence on how we understand the Neotropical Primate diversity today.

However, along with the adoption of the PSC, the increasing number of species recognized, and new species descriptions are also due to two other factors. The first is the use of technologies that were not available in the ’80s or ’90s facilitated access to remote areas. For example, the use of Geographic Information System (GIS) allows researchers to plan the main routes to reach remote areas, to check the accessibility during rainy or dry seasons, and to get detailed maps on the terrain and vegetation that can be downloaded to many mobile devices. Another example is the use of camera traps to inventory arboreal mammals – a powerful method to assess the species richness and occupancy in tropical forests (Bowler et al. 2016; Mills et al. 2016; Whitworth et al. 2016). Consequently, field expeditions to remote areas provided an opportunity to collect new information and significantly improve our knowledge on the occurrence and distribution of many primate species (Vermeer et al. 2013; Rabelo et al. 2014, 2018; Vermeer and Tello-alvarado 2015; Silva et al. 2018d, c).

The second important factor to influence the increasing number of primate species is the use of molecular data. The protocols are becoming more streamlined, costs are lowering, and higher computing power is allowing for unprecedented analysis of massive data as the type generated by Next Generation Sequencing (NGS). Therefore, the molecular phylogeny is allowing many researchers – including non-primatologists and non-taxonomists – to re-evaluate objectively earlier taxonomical hypothesis. For example, several recent studies have presented a reassessment of the taxonomy of different Neotropical Primate genera based on new data from the field, and on the use of molecular analysis combined with the systematic adoption of the PSC (Boubli et al. 2008; Lynch-Alfaro et al. 2012a; Morales-Jimenez et al. 2015a; Buckner et al. 2015; Mercês et al. 2015; Byrne et al. 2016; Rylands et al. 2016). In some cases, these studies are updating the taxonomic proposals of Hershkovitz, either by supporting the validity of some taxa and the classification schemes or rejecting and amending it by presenting new evidence.

1.1.5. THE MOLECULAR ERA: TOWARDS AN INTEGRATIVE TAXONOMY

Molecular biology has revolutionized the study of biodiversity with its increasingly sophisticated and novel approaches to investigate the phylogenetic relationships between species. It has contributed to the field of taxonomy by adding one more line of evidence in the reassessment of existing taxonomical hypothesis for several different taxa for which classification had been based mostly on morphology (Gaubert et al. 2004; Outlaw and Voelker 2006; Boubli et al. 2012; Cortés-Ortiz et al. 2015; Baird et al. 2015, 2018; Byrne et al. 2016). Consequently, the combination of different lines of evidence (e.g. morphology, molecular genetics, ecology) in species delimitation has been a practice in recent taxonomic revisions – a practice that some authors refer to as “integrative taxonomy” (Dayrat 2005; Padial et al. 2010; Schlick-Steiner et al. 2010). Integrative taxonomy seeks robust evidence for species delimitation providing solid ground for naming new species (Dayrat 2005).

The first studies on phylogenetic analysis using molecular data for Neotropical Primates were published in the 1990s (e.g. Schneider et al. 1993, 1996) and they represented the first contribution to understanding the phylogenetic relationship of the main groups of NWP: Pithecidae, Atelidae and Cebidae. These first molecular approaches were also important to raise other questions on the taxonomic classification within these groups (Schneider and Sampaio 2015).

It was only in the 2000s that the increasing development of technology and decreasing costs of DNA sequencing enabled the use of multi markers for molecular analysis. These new pieces of evidence supported the monophyly of the three Families of Neotropical Primates (Cebidae, Atelidae and Pithecidae) (Ray et al. 2005; Opazo et al. 2006; Osterholz et al. 2009), although with some controversy in the position of some genera (e.g.: *Aotus*). The supermatrix approach came on the scene when Wildman et al. (2009) published the first “fully resolved” genus-level phylogeny of Neotropical Primates using a concatenated data matrix with 17,809bp x 17 taxa (Wildman et al. 2009). This paper and the two subsequent publications (Perelman et al. 2011; Perez et al. 2012) used for the first time a molecular dataset consisting of a large number of genes or markers to support the three Families of Neotropical Primates, allowing researchers to turn their attention to genus and species level phylogenies.

Indeed, molecular data has unveiled a much greater diversity of lineages than initially suspected. In the Neotropical Primates, the lineages delimitation implied in new taxonomic proposals notably in two levels. First, the genus-level classification, previously strictly defined by morphological characters, has been revised as molecular and biogeographic data were considered. Examples of these reassessments include the capuchins (Lynch-Alfaro et al. 2012b), titis (Byrne et al. 2016), and tamarins (Buckner et al. 2015; Rylands et al. 2016). Secondly, the diversity and phylogenetic relationship within the genera have been elucidated in recent studies that combine nuclear and mitochondrial markers (Boubli et al. 2012, 2018; Morales-Jimenez et al. 2015a; Mercês et al. 2015; Carneiro et al. 2016).

Following the unprecedented moment in the molecular studies driven by the development of different sequencing platforms, the Next Generation Sequencing (NGS) enabled the sequencing of millions of fragments of DNA in parallel (reads), allowing to get different portions and sizes of the genome (Behjati and Tarpey 2013). Recent studies applied these techniques to unveil the diversity of Amazonian Primates (Boubli et al. 2018, 2019; Lima et al. 2018; Costa-Araújo et al. 2019). Therefore, the NGS is a powerful tool to scrutinise the species level relationship and the population structure, providing an excellent opportunity to review the primate diversity in Amazon Rainforest, either in the number of species formally proposed, or in the lineages identified as units of Conservation (e.g. Evolutionary Significant Units - ESU - Casacci et al., 2014; Coates et al., 2018; Moritz, 1994)

However, for most Neotropical Primate genera, sampling gaps hinder the assessment of the diversity, especially for Amazonian Primates where we are still discovering new species and where necessary information on the geographic distribution is yet required. Some taxa are particularly poorly represented in scientific collections with voucher specimens collected many decades ago from few localities. A good example is the uakari monkeys, genus *Cacajao*.

1.2 Primate Conservation and the Amazon Rainforest

The Amazon Rainforest harbours the greatest diversity of Primates in the world. In the last assessment of the Global Primate Diversity, the IUCN Primate Specialist Group recognised 146 species and subspecies in 17 genera living in the Amazon Rainforest (PSG, 2018). Since then, three species were described (Costa-Araújo et al. 2019; Gusmão et al. 2019; Boubli et al. 2019). Also, recent taxonomic revisions based on morphological and/or molecular analysis have been discussed for different groups. Furthermore, taxonomic revisions based on molecular and/or morphological analysis has been published for different groups (Marsh 2014; Byrne et al. 2016; Rylands et al. 2016; Serrano-Villavicencio et al. 2019).

Although a species is a taxonomic hypothesis, when new proposals are published without substantial evidence from molecular, geographical and morphological data, it likely hampers the work of conservationists. It creates taxonomical instability due to the short-lived fate of these “new species”, and the list of species that are assessed by policymakers, and organisations will continuously change. This situation may hinder the implementation of effective actions for conservation, which, for the most part, are focused on species. The Neotropical Primates have many such cases, especially those species description based on the pelage colouration of few individuals and without precise information on the type localities (Alperin 1993; van Roosmalen et al. 2000; Pontes et al. 2006; Marsh 2014). The advance in the DNA sequencing technology and the new methods and approaches proposed to delimitate species will also contribute to getting species lists based on a more integrative and stable taxonomy, which in turn will help the conservation decisions for Amazonian primates.

For example, the essential information in the management plans of Protected Areas (PA) is the species list. However, many of these documents are outdated or containing misidentified taxa, or the PAs were not inventoried, and the information on the species diversity is unknown. In Brazil, a significant effort to improve the information on the primate diversity in PAs was led by the Chico Mendes Institute for Biodiversity Conservation, an administrative sector of the Brazilian Ministry of the Environment, in 2017. In this initiative, a call for the special issue of their electronic journal (Revista BioBrasil) on the Primates in

Protected Areas in Amazon Rainforest had the contribution of 44 researchers in 14 articles updating the species list of 12 Protected Areas (Azevedo 2015; Buss et al. 2017; Rossato et al. 2017; Santos Júnior et al. 2017; Silva et al. 2017) – besides the information on the population, ecology, and conservation. Many of the species listed in these articles followed the recent changes in the taxonomy of Neotropical Primates.

While new studies continue to improve our knowledge on the diversity of primates in Amazon Rainforest (species delimitation, new species, list of species), other two crucial information to any conservation action has been presented in recent studies: the update on the geographic distribution, and the assessment of the species' conservation status. Recent field surveys are significantly contributing to refine the information on the geographic distribution of many primates, which also improve the accuracy of the species list in PAs (Vermeer et al. 2013; Nunes and Orsini 2016; dos Santos-Filho et al. 2017; Printes et al. 2018; Rabelo et al. 2018; Silva et al. 2018d, c). Also, the Species Distribution Modelling has been used to improve the information on the geographic distribution of Amazonian primates (Ochoa-Quintero et al. 2017; Rabelo et al. 2018; Silva et al. 2018c; Cavalcante et al. 2020).

In practice, these studies provide a baseline to reassess the conservation status of those species. By defining the species' Extent of Occurrence (EOO) and Area of Occupancy (AOO) (IUCN 2018) it is possible to estimate what was already deforested within these areas in the last decades using data from PRODES project – a deforestation monitoring program in the Brazilian Amazon via satellite (PRODES 2018). Additionally, using the information on the predicted deforestation in the Amazon Rainforest for the next decades (Soares-Filho et al. 2006), it is possible to crop the analysis to the species' EOO – and, therefore, to estimate of the amount of habitat that the species will lose in the future. By determining the deforestation for the Amazon Rainforest, some authors are providing evidence to assess the conservation status of Amazonian primates according to the categories proposed by the IUCN Red List (Ochoa-Quintero et al. 2017; Rabelo et al. 2018; Silva et al. 2018d, c; Boubli et al. 2019).

1.3 Why Evolutionary history, Systematics and Conservation of bald uakaris?

Cacajao is the largest in body size among the Pitheciinae and the only Neotropical primate with a short tail (Hershkovitz 1987a). Along with *Chiropotes* and *Pithecia*, they comprise the Pitheciinae, the only Neotropical primate group sharing the morphological adaptations in mandibular muscle and dentition for the predation of seeds of hard-shelled fruits that are usually at an immature stage – their main food item (Ayres and Johns 1987; Liedigk et al. 2012; Ayres and Prance 2013). Some studies considered uakaris as opportunistic seed predators, according to the seasonal abundance of key resources (Boubli 1999; Bowler and Bodmer 2011). Within the Pithecinae, uakaris seem to take this adaption further including a preference for flooded forests which contain high densities of trees of the Lecythidaceae, their preferred plant family (Ayres and Prance 2013).

Cacajao occurs over a wide region in the Western Amazonia (Figure *1.3*). The Western Amazonia harbours forests that are flooded by regular annual cycles of rivers, according to the rainy and dry season. These rivers are classified according to chemical, sedimentological, and fertility parameters (Junk et al. 2011). Whitewater rivers transport nutrient-rich sediments from the Andes and present a highly productive forest, locally known as *várzea* (Junk et al. 2011). Blackwater rivers, on the other hand, transport a low amount of nutrients, originally drained from the Precambrian Guiana shield, and their forests are of low fertility – also known as *igapó* (Junk et al. 2011). Bald uakaris occur mainly in *várzea* forests of Ucayali-Solimões-Juruá river basins. In contrast, black-backed uakaris occur in the *igapó* forests of Negro-Orinoco river basins (Silva-Júnior et al. 2013) (Figure *1.3*).

Especially for bald uakaris, their pattern of distribution throughout this area is poorly known with new and isolated populations recorded in Brazil and Peru (Silva Jr et al. 1999; Vermeer and Tello-alvarado 2015; McHugh et al. 2019). Available data suggest that they have a patchy distribution along the rivers, but do not occupy the most central regions of the interfluves (Silva-Júnior et al. 2013) – at least not regularly as found for many Amazonian Primates. It is unknown what are the main factors behind the patchy and disjunct distribution of bald uakaris and how the dynamic geomorphological changes in the

Western Amazonia during the Neogene could have influenced the current distribution of bald uakaris populations.

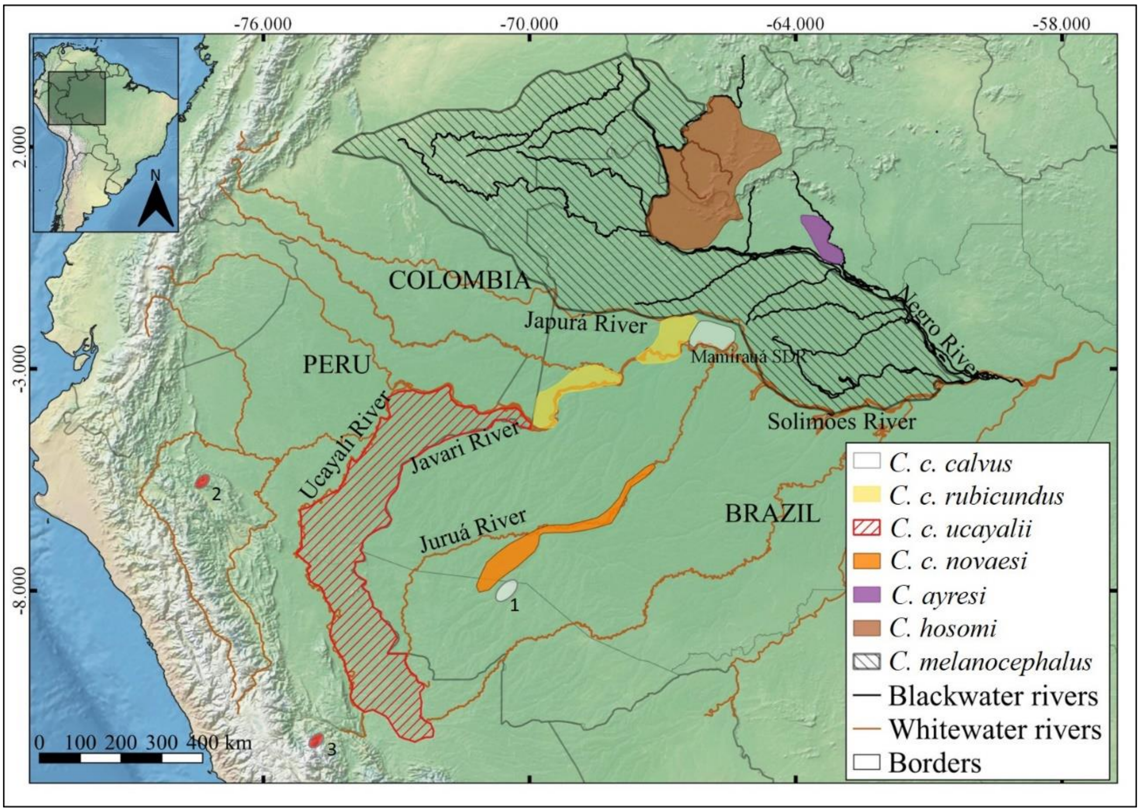

Figure 1.3 The geographic distribution of *Cacajao*. Adapted from Silva Jr. et al. (2013) and Boubli et al. (2008). [1] Isolated population of *C. c. calvus* reported by Silva Jr and Martins (1999). Isolated population of *C. ucayalii* reported by [2]Vermeer et al. (2013) and [3]McHugh et al. (2019). Blackwater and whitewater rivers classification follows Junk et al. (2011).

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1.3.1 A BRIEF BACKGROUND ON THE TAXONOMIC CLASSIFICATION OF CACAJAO

The genus includes two main groups: the black uakaris, which are uniformly hirsute with blackish forehead occupying the forests of the north bank of Japurá and Negro rivers; and the bald uakaris, which have the bare red face – a characteristic caused by a complex vascular system in the facial skin – and inhabit mostly the forests of the south bank of Japurá and Solimoes rivers and the *Ucayalii*-Javari interfluve. Hershkovitz (1987a) reviewed the taxonomy of the genus *Cacajao* and proposed the following arrangement:

1. ***Cacajao melanocephalus***
    a. *Cacajao m. melanocephalus* (Humboldt, 1811)
    b. *Cacajao m. ouakari* (Spix, 1823)

2. *Cacajao calvus*

a. *Cacajao c. calvus* (Geoffroy, 1847)
b. *Cacajao c. rubicundus* (Geoffroy and Deville, 1848)
c. *Cacajao c. ukayalii* (Thomas, 1928)
d. *Cacajao c. novaesi* Hershkovitz, 1987

The first uakari species were described based on voucher specimens collected by the 19th century's naturalists. The golden-brown uakari, *Simia melanocephala*, was described based on a specimen that was not stored in a scientific collection and without precise information on its locality (Hershkovitz 1987a; Boubli et al. 2008). In 1823, the naturalist Johann Baptist von Spix described a second species, *Brachyurus ouakari*, assigning a genus name for the uakari monkeys. However, the *Brachyurus* Spix 1823 was considered a junior synonym of *Brachyurus* Fisher, 1813, a rodent genus, and the *Cacajao* Lesson, 1840 became the genus name used for uakari monkeys. When Spix described *ouakari*, the author also mentioned the type locality as "Rio Içá at the Rio Solimões" (Hershkovitz, 1987a), where this taxon does not occur; therefore, the precise locality where this voucher was collected is also unknown. Due to the inaccuracy on the type localities of these taxa, their validity has been debated (Boubli et al. 2008; Ferrari et al. 2014).

The Hershkovitz' taxonomic proposal maintained the arrangement suggested by Hernández-Camacho, J. & Cooper (1976), which recognised the Humboldt's and Spix's black uakaris into two subspecies: *Cacajao melanocephalus melanocephalus* and *C. m. ouakari*. This taxonomic proposal for black-headed uakaris was followed for two decades when Boubli et al. (2008) reviewed the diversity of this group based on molecular analysis of cytochrome *b* gene and their pelage colouration. The authors also used new evidence on the ecology and on geographic distribution to support a new classification scheme for black-headed uakaris. They reviewed the historical information on the type localities and holotypes used for the two subspecies of black-headed uakaris and argued that the *C. m. ouakari* Spix, 1823 is a junior synonym of *C. m. melanocephalus* Humboldt, 1811.

Therefore, *Cacajao melanocephalus* was restricted to the golden-brown individuals from south of the Rio Negro (golden-backed uakaris) and a new specific name was provided for black uakaris from Pico da Neblina region, *Cacajao hosomi*. A third species was described for the uakaris from Aracá River as *Cacajao ayresi*. According to the taxonomic review presented by Boubli et al. (2008), the black-headed uakaris sets as follows (Figure *1.4*):

1. ***Cacajao melanocephalus*** (Humboldt 1811): extending to a wide area from de La Macarena Mountain and Apaporis River (Colombia) west, and Guaviare River (Colombia) to Orinoco River and Cassiquiari channel (Venezuela) north. In Brazil, the species is limited by the Negro River and Cassiquiari channel in the north, with a southern distribution in Solimões and Japurá rivers.
2. ***Cacajao hosomi*** Boubli, Silva, Amado, Hrbek, Pontual, and Farias 2008: delimited to the south and west by the Negro River (Brazil, Venezuela), and by the Cassiquiare Channel and Orinoco River to the north (Venezuela).
3. ***Cacajao ayresi*** Boubli, Silva, Amado, Hrbek, Pontual, and Farias 2008: occurring in a small region that encompasses the Curuduri River basin and adjacent areas, left bank (north) of Negro River.

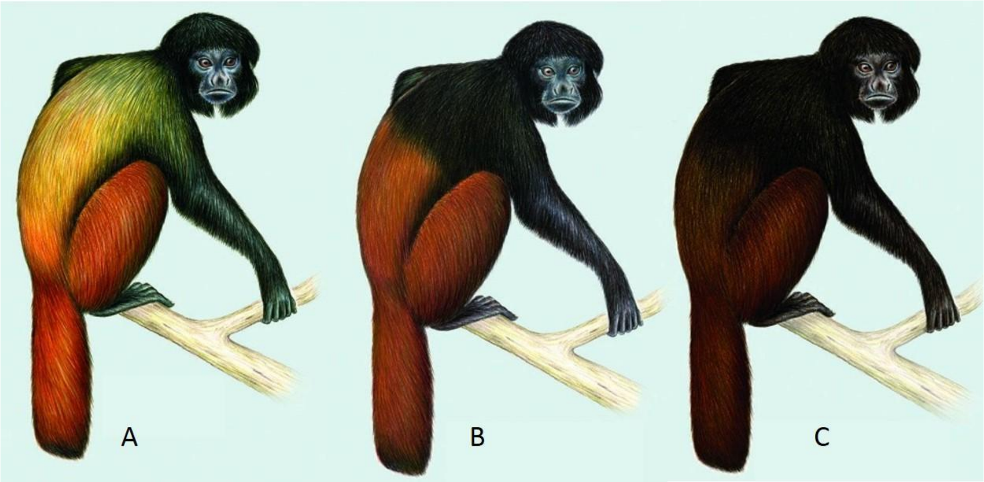


Figure 1.4 The black-headed uakaris following the classification proposed by Boubli et al. (2008). A) *Cacajao melanocephalus*; B) *Cacajao hosomi*; C) *Cacajao ayresi*. Drawing by Stephen Nash

This taxonomic arrangement for black uakaris, however, was contested by Ferrari et al. (2014). Among the main points that these authors argued against Boubli et al. (2008) is the level of diversification between the two forms of the north bank of Negro River. Ferrari et al. (2014) argue that, while the differentiation of the northern and southern clade is well supported in the molecular analysis, the genetic variability between the two northern forms is low for a species-level differentiation and the use of a single mitochondrial DNA marker to define the genetic divergence can be premature. Although Ferrari et al. (2014) agree with the Negro River as the main barrier to separate the two species of black-headed uakaris, the authors proposed that the two forms from the north bank of Negro River should be classified as subspecies.

While the taxonomic classification of black uakaris has been debated in Boubli et al. (2008) and Ferrari et al. (2014), the taxonomic status of the bald uakaris remains overlooked. The same problems with type localities occur with the first species descriptions of bald uakaries. The French Naturalist Isidore Geoffroy Saint-Hilaire was the first to describe a bald uakari, the white uakari (*Brachyurus calvus*) (Geoffroy 1847). The author's description was based on a specimen donated to the Muséum National d'Histoire Naturelle, Paris, but the type locality is not precise and only indicated as "province de Pará" (Geoffroy 1847, 1852) – possibly a reference to the former province of Grão-Pará, an administrative territory from the colonial period that included a vast area in the north of Brazil. Geoffroy (1852) examined two other specimens with the same general characteristics of "*Brachuyrus calvus*", but their locality is also uncertain and described as upper Amazonas River, Peru, nearby Fonte Boa municipality:

"C'est du Para, comme je l'ai dit plus haut, qu'est venu le type de cette espèce. Les individus que le Muséum a reçus, quelques mois plus tard, de MM. de Castelnau et Deville, viennent du Pérou, Haut-Amazone, environs de Fonteboa. Malgré la différence des localités, les mêmes caractères se retrouvent presque exacte ment chez tous." (Geoffroy 1852, p. 564)

"It is Para, as I said above, that the type of this species has come. The individuals whom the Museum received a few months later from MM. from Castelnau and Deville, come from Peru, Haut-Amazon, near Fonteboa. In spite of the difference of the localities, the same characters are found almost exactly in all." (Geoffroy 1852, p. 564)

A year after the description of the first bald uakari monkey, Geoffroy and Deville (1848) described the second species, "*Brachyurus rubicundus*", based on the material collected by Catelneau and Deville in their expedition to South America (Geoffroy and Deville 1848). The type specimen was collected nearby the territory of São Paulo de Olivença municipality (*Le Brésil, Haut-Amazone, près Saint-Paul*). However, it is not clear if it was collected in the right (south) or left (north) bank of Solimões River. By sharing the findings of his expedition to the Ucayali River, Peru, Thomas (1928) proposed the Peruvian uakaris as a new subspecies, *Cacajao rubicundus ucayalii* (Thomas 1928).

When Hershkovitz (1987a) reviewed the taxonomy of *Cacajao,* he proposed the classification of bald uakaris as subspecies of *Cacajao calvus*. He also described the form from Gregório – Tarauacá interfluve as a new one, *Cacajao calvus novaesi.* The classification scheme proposed by Hershkovitz (1987a) was entirely based on pelage colouration, and the use of subspecies was probably a decision made from the geographic variation in the coat colour. The author explains this variation using the biological principle of metachromism, a term he used to describe the evolutionary variation in hair, skin and eye colours (Hershkovitz 1968). According to the author:

"The archetypal monochromic pheomelanic C. calvus bleached to albinotic C. c. calvus through successively paler tones represented by such forms as C. ucayalii or C. rubicundus, and C. c. novaesi" (Hershkovitz 1987a, pp. 22) (Figure *1.5*)

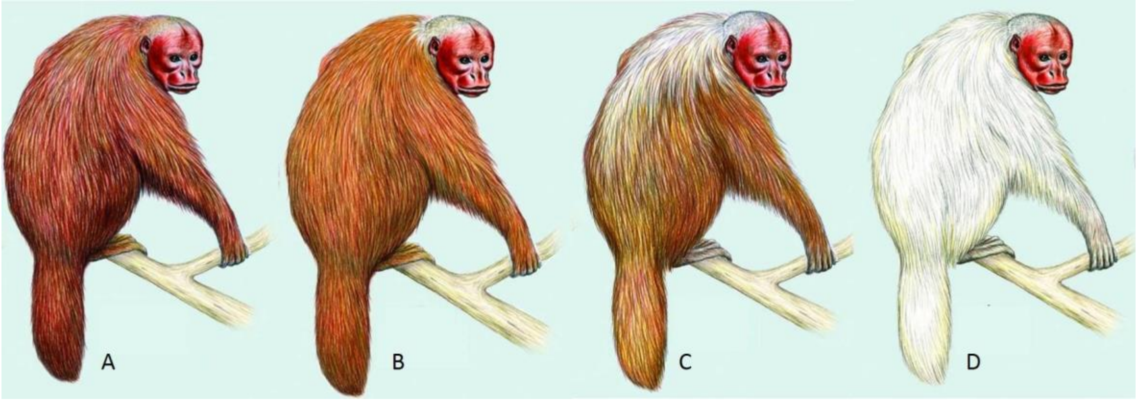


Figure 1.5 The bald uakaris following the classification proposed by Hershkovitz (1987). A) *Cacajao calvus ucayalii*; B) *Cacajao c. rubicundus*; C) *Cacajao c. novaesi*; D) *Cacajao c*. *calvus*. Drawing by Stephen Nash.

In a molecular analysis that included most species and subspecies of both bald and black-headed uakaris, Figueiredo-Ready et al. (2013) used the mitochondrial marker cytochrome *b* (Figueiredo-Ready et al. 2013) and found that both groups diverged around 5.8 Mya. The phylogeny presented by the authors showed a division in two main clades for bald uakaris and other two clades for black-headed uakaris. Although the analysis presented in Figueiredo-Ready et al. (2013) seems to overlook the shallower relationships in the phylogenetic tree of uakaris, cytochrome *b* may still be a valuable option to address questions on the evolutionary history of the genus *Cacajao*. Cytochrome *b* sequences are available in repositories for most of *Cacajao* taxa. Therefore, biogeographical patterns behind the evolution of the genus in the Western Amazonia can be identified by increasing the number of sequences (from different populations) rather than the number of base pairs in the analysis.

Indeed, mitochondrial DNA (mtDNA) markers are widely used in molecular studies, and several papers are discussing the pros and cons for phylogenetic and phylogeographic analysis, (Rubinoff and Holland 2005; Song et al. 2008; Galtier et al. 2009; Near and Keck 2013). For Primates, mtDNA still provides valuable insights and is particularly useful because it can be extracted from different sources such as faeces and museum vouchers and can be compared to sequences available in repositories. Therefore, several recent publications have shown that the mtDNA can provide an insight on the evolutionary history of poorly studied Primates (Botero et al. 2015; Di Fiore et al. 2015; Morales-Jimenez et al. 2015a, b; Mercês et al. 2015; Hoyos et al. 2016; Fan et al. 2017; Munds et al. 2018).

However, for some groups, the use of one single marker can hinder the phylogenetic analysis in lineages recently diverged, or with incomplete lineage sorting, or when the biogeographic dynamic allows successive gene flow between the populations. Therefore, identify lineages in these cases can be hindered using a single mtDNA. All these scenarios may be behind the evolutionary history of *Cacajao* and the dataset used to analyse the molecular phylogeny can profoundly impact the results and, consequently, the interpretation. A robust molecular analysis using the most recent techniques, such as NGS, can provide an essential view on the number of lineages in the genus *Cacajao* and its phylogenetic relationship. As a practical implication, the taxonomic classification of bald uakaris can significantly benefit from the latest methods on molecular analysis by adding new lines of evidence to identify the main lineages in an integrative approach – an essential step to consistently support other studies and to allow a more assertive assessment of the conservation status of each taxon defined.

1.3.2 Overall Dissertation Goal

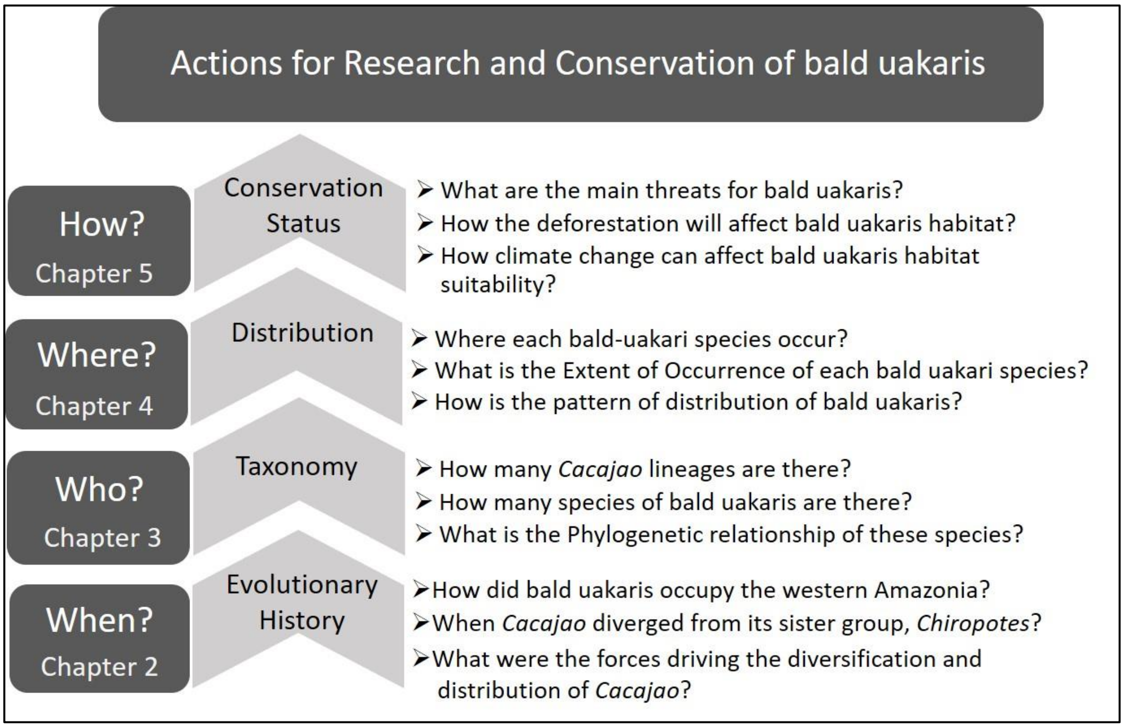
The bald uakaris are a flagship species for Conservation in Brazil and Peru. One of the most remarkable examples is the creation of the Mamirauá Sustainable Development Reserve (Mamirauá SDR) located at the confluence of the Solimões and Japurá Rivers, in Brazilian Amazon Rainforest. Mamirauá SDR is a vast area of flooded forest that was specifically designed in the ’90s to protect the white uakari, *Cacajao calvus calvus* (Alves 2011; Queiroz 2011). The pioneering study on the ecology and behaviour of the white uakaris (*C. c. calvus*), conducted by the Brazilian Primatologist Dr Márcio Ayres, was the first step for the creation of this new Protected Area of 1,124,000ha that encompasses a large part of the geographic range of the species (Alves 2011; Queiroz 2011). The unique red face, striking orange or white coat colour, and the remarkable evolutionary uniqueness of their ecology and behaviour (e.g. use of space, group size, adaptation for seed predation) make them noticeable primates that are easily recognised by locals in any forest. Therefore, a robust phylogeny of *Cacajao* and a taxonomic classification that reflects the evolutionary history of the genus is essential for the identification of the units for conservation.

This dissertation is structured in four data chapters where I am addressing four main aspects of bald uakaris: Evolutionary history (Chapter 2), Molecular Phylogeny and Taxonomic classification (Chapter 3), Geographic Distribution (Chapter 4), and Conservation (Chapter 5) (Figure *1.6*). In Chapter 2, I used 91 cytochrome *b* sequences (58 from the Genebank and 33 newly generated) including all Pithecidae genera and all *Cacajao* taxa to get a calibrated time tree. I applied the statistical phylogeographic analysis to investigate how the *Cacajao* occupied the Western Amazonia, providing insights into its evolutionary history and diversification.

In Chapter 3, I use ddRAD analysis to investigate the population structure of bald uakaris and to reconstruct a phylogenomic tree, including all *Cacajao* taxa. Although I am primarily focusing on bald uakaris, I include the black uakaris in some analysis to verify the consistency of the phylogenetic relationship of the lineages throughout the genus *Cacajao.* I tested how different parameter settings influence the results, and I discuss the importance of the parametrisation for phylogenomic analysis using ddRADseq. Finally, I present a taxonomic proposal for the bald uakaris according to the phylogenetic relationship of the main lineages and the morphological diagnostic characters presented by Hershkovitz (1987a) – therefore, considering the monophyly and diagnosability, according to the Phylogenetic Species Concept.

In Chapter 4, I present an update on the geographic distribution of bald uakaris according to the new taxonomic proposal. In addition, I used new evidence of fieldwork and from different databases to update the Extent of Occurrence of each species, identify gaps in its distribution as well as the priority areas for further surveys. In Chapter 5, I use Ecological Niche Modelling to predict the habitat suitability for bald uakaris and the amount of habitat each species is expected to lose according to different deforestation scenarios by 2050.

These chapters fill some of the primary gaps in our knowledge of uakaris and show the next steps in the research and conservation of this unique group of Amazonian primates. The chapters are structured to consolidate the fundamental aspects of the bald uakaris (Evolutionary history, Taxonomy, Distribution, and Conservation) using the most updated information. Taken together, these chapters can provide a baseline for future researches initiatives for uakaris and can be a framework to be followed for other poorly studied groups in Amazon Rainforest. The priorities for research and conservation of biodiversity in the Amazon Forest include several lines of evidence (population status, genetics, evolutionary history, threats, geographic distribution). This evidence must be brought together in collaborative efforts to allow the assessment of the species conservation status and the implementation of effective strategies to reduce the biodiversity loss due to increasing deforestation, especially in Brazil (base-year 2020).



Actions for Research and Conservation of bald uakaris

How? Chapter 5 — Conservation Status

- What are the main threats for bald uakaris?
- How the deforestation will affect bald uakaris habitat?
- How climate change can affect bald uakaris habitat suitability?

Where? Chapter 4 — Distribution

- Where each bald-uakari species occur?
- What is the Extent of Occurrence of each bald uakari species?
- How is the pattern of distribution of bald uakaris?

Who? Chapter 3 — Taxonomy

- How many *Cacajao* lineages are there?
- How many species of bald uakaris are there?
- What is the Phylogenetic relationship of these species?

When? Chapter 2 — Evolutionary History

- How did bald uakaris occupy the western Amazonia?
- When *Cacajao* diverged from its sister group, *Chiropotes*?
- What were the forces driving the diversification and distribution of *Cacajao*?

Figure 1.6 The framework used in this dissertation. Each aspect is addressed in separated hierarchical chapters and will provide a baseline for future researches and actions for bald uakaris Conservation.

Chapter 2. Molecular phylogeny and phylogeography of uakaris (*Cacajao* Lesson, 1840): identifying lineages and understanding the evolutionary history of a flooded forest specialist.

2.1 Introduction

The Amazon system is a primary source of diversity that evolved from a network of geomorphological events. Recent studies have significantly contributed to understand the Amazonian drainage evolution and to support that the west region of Amazon was a vast area of freshwater wetlands known as Pebas Lake, which existed until the Pliocene (Wesselingh et al. 2002; Hoorn et al. 2010). Accordingly, the Andean mountain formation catalysed significant changes in the adjoining lowlands, including the establishment of the Amazon River basin and its transcontinental drainage (Horn et al. 2010). However, the dating of these geological events from stratigraphic and palynological data is controversial (Rossetti et al. 2005; Campbell et al. 2006; Hoorn et al. 2010; Latrubesse et al. 2010; Ribas et al. 2012; Lynch-Alfaro 2017). Some studies suggest that the Amazon River was originated more recently, in the Plio-Pleistocene, with the Amazon River formation at 3–2 Mya and the principal tributaries formation up to 1 Mya (Campbell et al. 2006, Latrubesse et al. 2010, Ribas et al. 2012, see also Lynch-Alfaro 2017). However, a comprehensive study on the dynamic of the Andean uplift and the landscape evolution in Amazon estimated the formation of the transcontinental drainage at ~11-9 Mya (Horn et al. 2010).

The drying up of the Pebas Lake and the formation of wetland environments (*várzea* and *igapó*) may have been an essential factor in the diversification of several groups, especially for those who are associated with the flooded forests in some level. Therefore, this different estimation has significant consequences for our interpretation of the speciation and evolution of the Amazonia biota. While the geomorphological and paleogeographic studies shed light on the time when the main landscape events happened, the molecular analyses provide a valuable tool to estimate the divergence time of the main lineages. In this sense, recent studies have put together these elements to investigate the evolutionary history of different taxonomic groups. Therefore, classical biogeographical models and questions such as the riverine barrier hypothesis, refugia, and centre of origin have been tested using different taxa as a model.

For example, a study on the biogeography of Amazonian birds found that the lineages associated with seasonally flooded forests had their evolutionary history linked with the western Amazonia, where the landscape was historically shaped by the dynamic changes caused by the drainage of Pebas Lake and the formation of the main rivers (Aleixo and Rossetti, 2007 - Fig. 1a). Conversely, those lineages with their distributions on the Brazilian and Guianan shields only dispersed to the western Amazonian lowlands after the drainage of the Pebas Lake, when the upland forests of this region became established in that region, therefore following a pattern for upland forest species (Aleixo and Rossetti, 2007 - Fig. 1b). By using molecular and geological data to investigate the evolutionary history of different lineages of Amazonian birds, the analysis presented in Aleixo and Rossetti (2007) shed light on an interesting pattern of evolution and diversification that could be applied to other vertebrates with a widespread geographic distribution throughout the Amazon Rainforest.

The order Primates has some such cases. New information on the DNA sequences and species localities for some genera has allowed addressing these questions. For example, Lynch Alfaro et al. (2015) used mitochondrial DNA to test the biogeographical hypotheses behind the evolution of the squirrel monkeys, genus *Saimiri*, a widespread Amazonian primate. Beside infer the correlation between the main Amazonian rivers and the distribution and diversification of the main lineages, the authors tested whether *Saimiri* was initially a lowland lake-affiliated or upland forest taxa. The biogeographic analysis presented in Lynch Alfaro et al. (2015) support the genus *Saimiri* as a western Amazonian lowland taxon that spread throughout the Amazon. Being a group associated with seasonally flooded forests, the main *Saimiri* lineages only occupied the areas of Brazilian (Pará and Belém centres of vertebrate endemism) and Guiana shields more recently with the availability of floodplain forest and lowland riverine habitat in these areas, which follows the scenario for floodplain forest species (Aleixo and de Fátima Rossetti, 2007 - Fig. 1a).

The pattern found by Lynch-Alfaro et al. (2015) for *Saimiri* differs, however, from what was for titi monkeys (Byrne et al. 2018). Byrne et al. (2018) used the vertebrate centres of endemism in Amazon Rainforest (Cracraft 1985) and a calibrated tree to reconstruct the biogeographic history of Callicebinae under alternative models. Accordingly, the ancestral population of titi monkeys occupied an extensive area spread around the Brazilian and Guyana shields. In contrast, more recent lineages only occupied the western Amazonian lowland during the Pleistocene, which coincides the lacustrine-floodplain-lowland forest transition after the drainage of Pebas lake – according to the timescale proposed by the "Young Amazon" model (Lynch-Alfaro 2017; Byrne et al. 2018). This pattern is similar to what was found for some avian species (Ribas et al. 2012).

Another genus that is strongly associated with the flooded forests is *Cacajao* (Ayres and Prance 2013; Silva-Júnior et al. 2013; Barnett and Jucá 2018). *Cacajao* is the only Pitheciinae – which also includes *Pithecia* and *Chiropotes* – with the distribution centred on the western Amazonian lowlands. While *Pithecia* is widely distributed in Amazon Rainforest and co-occur with *Chiropotes* and *Cacajao*, these two genera are mostly allopatric (Silva Jr et al. 2013, but see Boubli 2002). *Chiropotes* occurs in the north bank of Amazon and Negro rivers (Guyana Shield), and from the east bank of Madeira River to beyond the easternmost bank of Tocantins River (Brazilian Shield) (Silva Jr et al. 2013). *Cacajao* has a patchy distribution, occurring between the Negro–Branco and Ucayali–Solimões–Juruá river systems (Silva Jr et al. 2013).

In addition to the inadequate information on the geographic distribution of Pitheciinae, its taxonomic classification is controversial. The number of valid species in each of these genera is controversial. For example, although six new species of *Pithecia* were proposed in a taxonomic revision based on pelage colouration (Marsh 2014), a recent publication using the same evidence – pelage colouration – contested these new species descriptions (Serrano-Villavicencio et al. 2019). For *Chiropotes*, five species are recognized (Silva Jr et al. 2013), although an analysis using different genes and that includes individuals from different locations would clarify the number of valid species for the genus (see Bonvicino et al. 2003).

Cacajao includes two main groups: the black-headed uakaris and the bald uakaris. For the first, Boubli et al. (2008) proposed three species: *Cacajao melanocephalus*, *C. ayresi*, and *C. hosomi*. The authors used new evidence, which included the analyses of pelage colouration, new localities, and a mitochondrial molecular phylogeny to support this taxonomic arrangement (Boubli et al. 2008). For the bald uakaris, the taxonomic classification follows Hershkovitz (1987a), which proposed four subspecies according to the patterns of the pelage colouration: *Cacajao calvus calvus*, *C. rubicundus*, *C. ucayalii*, and *C. c. novaesi*.

In a first attempt to understand the phylogenetic and geographic relationship of the genus *Cacajao*, Figueiredo-Ready et al. (2013) presented a molecular phylogeography using cytochrome *b.* The authors found that the subspecies *C. c. calvus*, *C. rubicundus*, *C. ucayalii,* from the Solimões-Ucayali-Javari River system, are a monophyletic group, with an intra-lineage distance of no more than 0.7%. Interestingly, however, the subspecies *C. c. calvus* was paraphyletic in their analyses, with the specimens from the upper Juruá River basin grouping in a well-defined clade. The genetic distance between these two clades varied between 2.7–4.2% (Figueiredo-Ready et al. 2013). These values are similar to those recorded between the species of black-headed uakaris from opposite sides of the Negro River (2.5–3.8%; see Figueiredo-Ready et al. 2013).

Accordingly, the populations of white bald uakaris — *C. calvus calvus* — from north Solimões River would be evolutionarily closer to the red bald *C. calvus rubicundus* and *C. calvus ucayalii* than to the population of white uakaris from the Juruá River basin. Figueiredo-Ready et al. 2013, then, pointed out that the molecular phylogenetic tree contradicts the traditional taxonomic arrangement. Therefore, the taxonomic classification based on pelage colouration was not represented in the molecular phylogeny; although the authors emphasised that their analyses included only a few Museum samples from few localities. The authors' conclusions, however, could have been biased by the misidentification of some samples (see Chapter 5). Therefore, the number of *Cacajao* lineages and its phylogenetic relationship remained unclear.

The analyses of Figueiredo-Ready et al. (2013) pointed out that the bald and black uakaris diverged approximately 5.8Ma, in the Pliocene. The authors also estimated the species level diversification in ~4.1Ma for the two lineages of black-headed uakaris, and ~3.9 Ma for the two lineages of bald uakaris. These findings are similar to the found by Boubli and Ditchfield (2000). These authors explicitly tested the divergence time between bald and black uakaris using cytochrome *b* sequences and estimated divergence between them at the beginning of the Pliocene (~5Ma). They also estimated the separation between *Cacajao* and *Chiropotes* at the end of the Miocene (~9Ma) (Boubli and Ditchfield 2000). The investigation of the timing of the cladogenetic events in the Pitheciinae phylogenetic tree is essential to determine what historical and ecological forces were at play throughout *Cacajao* evolutionary history.

A recent review on the divergence time of the main Primates lineages using phylogenomic data estimated that the main genera of Neotropical Primates are dated from the early Miocene (~20Ma) (dos Reis et al. 2018). However, the species-level diversification was estimated from 5 Ma, in the Plio/Pleistocene for several Amazonian Primates, with a diversity explosion occurring only from ~ 2Ma (Boubli et al. 2015; Buckner et al. 2015; Lynch-Alfaro et al. 2015; Lynch-Alfaro 2017; Byrne et al. 2018; Silva et al. 2018b).

Accordingly, the clade that originated the Pitheciinae diverged from its sister group – the titi monkeys *Cheracebus*, *Callicebus* and *Plecturocebus* – approximately between 20.8-24.7Ma (dos Reis et al. 2018). After that, the genus *Pithecia* diverged from *Chiropotes* and *Cacajao* about 15.5Ma (13.1-17.9Ma) with subsequent separation of these two genera estimated in 8.95Ma (6.8-11.1). The divergence time between bald and black uakaris was estimated in ~4.2Mya, i.e. in the Pliocene (dos Reis et al. 2018). These ages are similar to those found by Boubli and Ditchfield (2000) and Figueredo-Ready (2013) for the divergence between *Chiropotes* and *Cacajao*, and the species-level diversification in *Cacajao*.

In this chapter, I used both mitochondrial and nuclear DNA markers to infer the molecular phylogeny of *Cacajao* including samples of all species and subspecies currently recognised (sensu Hershkovitz, 1987a; Boubli et al. 2008). This analysis allowed to identify the main *Cacajao* lineages and to estimate the divergence time between them. In addition, I applied a Bayesian statistical phylogeographic analysis to investigate if the common ancestor of *Chiropotes* and *Cacajao* was initially a lowland lake-affiliated or an upland forest. While *Cacajao* is a genus with the distribution in the western Amazon, *Chiropotes* is mostly present in upland forests with its distribution centred on the Brazilian and Guianan shields. The findings presented here are important to understand the evolutionary history of *Cacajao* and to verify if the use of different molecular datasets (nuclear only, cytochrome *b* only, nuclear+cytochrome *b*) is consistent with the current taxonomic classification.

2.2 METHODS

2.2.1 SPECIMENS AND SAMPLES

I used samples of fresh tissues and faeces from the following Brazilian Museum collections: Museu Paraense Emílio Goeldi (MPEG); Museu de Zoologia da Universidade de São Paulo (MZUSP); Instituto de Desenvolvimento Sustentavel Mamirauá (IDSM); Instituto Nacional de Pesquisas da Amazonia (INPA); and Field Museum of Natural History (FMNH). I also included sequences available from Genbank 2.5 Supplementary Material - Chapter 2). Therefore, I maximised the geographic coverage by adding samples from most of the localities where *Cacajao* occurs, which represent an updated dataset from the previous publication (Boubli et al. 2008; Figueiredo-Ready et al. 2013) (Figure *2.1*).

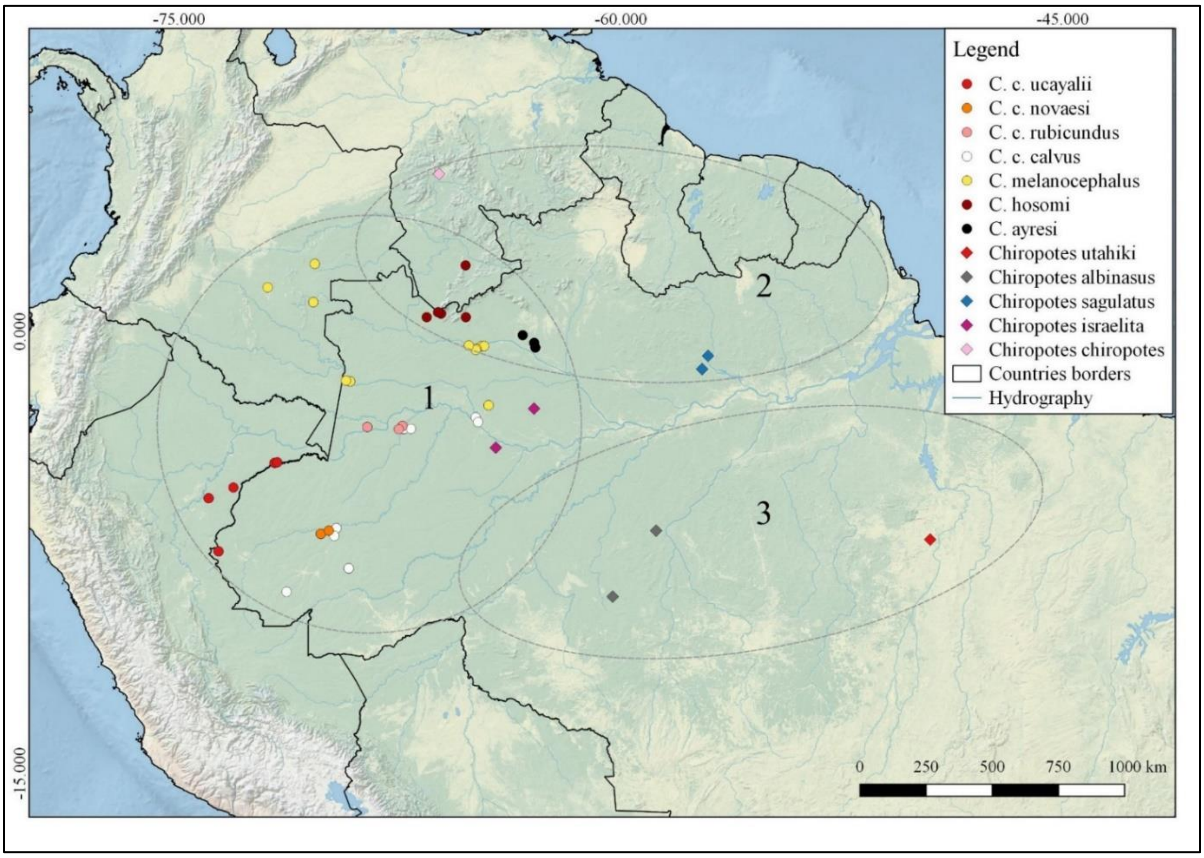


Figure 2.1 The *Cacajao* and *Chiropotes* sample region. 1 – Western Amazon. 2 – Guiana Shield. 3 – Brazilian Shield

2.2.2 DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

A total of 41 individuals were sequenced for one mitochondrial (cytochrome *b*) and four nuclear genes (ABCA1, ADORA1, RAG1, ZFX) (Table *2-1*). I used the phenol-chloroform protocol to isolate the DNA from tissue samples (Sambrook and Russell 2006), and the genomic DNA product was used as the template for the polymerase chain reaction (PCR) to amplify portions of these genes (Table *2-1*) (Byrne et al. 2016). Each PCR had a final volume of 25 µl and contained 100 ng of DNA, 2.5 µl of reaction buffer, 0.5 mM of each primer, 0.03 U/µl Taq DNA polymerase, 1.5 mM MgCl2, 0.1 lg/µl bovine 245 serum albumin and 1.25 mM of each dNTP. The amplification cycles were carried out under the following conditions: the initial denaturation at 95 °C for 5 min; followed by 35 cycles of denaturing at 94 °C for 1 min, primer annealing between 45 °C and 60 °C (temperature varies per primer, see Table *2-1*) for 1 min, and extension at 72 °C for 1 min; a final extension was carried out at 72 °C for 5 min.

I analysed the PCR products on 1.5 % agarose gels, and the sequencing was performed commercially (Macrogen Inc., Amsterdam) in two reactions with forward and reverse primers. I used Geneious Pro 4.8.5 for sequence edition and assembling, and Mafft online service (Katoh and Standley 2013; Katoh et al. 2017) for the alignment under the iterative refinement option (FFT-NS-i Standard), which is known to effectively improve the alignment accuracy for small number of sequences (Katoh et al. 2002, 2017)

2.2.3 GENETIC VARIATION AND PHYLOGENETIC INFERENCE

For the phylogenetic inference, I prepared three distinct datasets and ran three maximum likelihood analyses in parallel. For all datasets, I only added samples from which the origin of the individuals was known. For the first dataset, I included 79 sequences (69 *Cacajao* and 10 *Chiropotes*) of cytochrome *b* only. For the second dataset, I included 35 sequences of concatenated nuclear genes. Finally, for the third dataset, I concatenated nuclear and cytochrome *b* genes in two partitions. The three datasets include all the species and subspecies of *Cacajao* currently recognised (*sensu* Boubli et al., 2008; Hershkovitz, 1987).

Table 2-1 DNA markers and the primers used in this study.

Locus ID	Full Name	Forward primer sequence	Reverse primer sequence	Description	Reference	Primer annealing°C
CYTB	cytochrome *b*	GCACAACCTACAGCACCACTA	CAGCTTTGGGTGTTGAYGGTRGAA	Exonic; Mitchondrial	Byrne et al. 2016	60
ABCA1	ATP-binding cassette, sub-family A (ABC1), member 1	CCTCCATCTTTTCAGCTCTACCTAC	ACAAGAGCCTGGAGATTGGATAAC	Intronic	Byrne et al. 2016	56
ADORA3	adenosine A3 receptor	ACCCCCATGTTTGGCTGGAA	GATAGGGTTCATCATGGAGTT	Exonic	Byrne et al. 2016	60
RAG1	recombination activating gene 1	GCTTTGATGGACATGGAAGAAGACAT	GAGCCATCCCTCTCAATAATTTCAGG	Exonic	Byrne et al. 2016	57
ZFX	zinc finger protein, X-linked	TGGAATGAAATCCCTCAAATA	ATGTCCATCAGGGCCAATAAT	Intronic; X-chromosome	Byrne et al. 2016	52

I used the software DNAsp 6.12.03 (Librado and Rozas 2009) (http://www.ub.edu/dnasp/) to analyses the DNA polymorphism of nuclear and mitochondrial sequences. This software has been used to summarise the genetic diversity in different datasets and organisms (Werneck et al. 2015; Kirikci et al. 2018; Diringer et al. 2019; Mazlan et al. 2019). I compared the genetic diversity in each of the main lineages recovered by calculating the following parameters:

1. Number of polymorphic sites (S)
2. Number of haplotypes (h)
3. Haplotype diversity (Hd)
4. Nucleotide diversity per site (Pi)
5. Watterson’s theta (per site) from S (θw)
6. The average number of nucleotide differences between sequences (k)

I used the program IQTree (Nguyen et al. 2015) as implemented in W-IQ-Tree (http://iqtree.cibiv.univie.ac.at/, Trifinopoulos et al., 2016) for the maximum likelihood phylogenetic inference. I used the algorithm ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQTree to select the best substitution model, and the option ultrafast bootstrap approach (UFBoot) (Minh et al. 2013; Hoang et al. 2018) with 1000 bootstrap pseudoreplicates to assess branch support.

2.2.4 DIVERGENCE TIME ESTIMATION

I employed Beast 1.10 (Suchard et al. 2018) to estimate the time of divergence between *Chiropotes* and *Cacajao* clade and to estimate when the diversification of *Cacajao* started using 91 cytochrome *b* sequences, which includes all Pithecidae genera. Of these 91 sequences, 58 were downloaded from Genebank, and 33 were newly generated in this study. *Chiropotes* (n=8) and *Cacajao* (n=72) were assigned as ingroup, while *Pithecia* (n=5), *Plecturocebus* (n=2), *Cheracebus* (n=2) and *Callicebus* (n=2) as outgroup (2.5 Supplementary Material - Chapter 2). I used the ModelFinder (Kalyaanamoorthy et al. 2017) to set the option HKY as the best substitution model for this dataset. The molecular clock was set as uncorrelated lognormal relaxed clock, in which the substitution rates in each branch are independently estimated under a lognormal distribution (Drummond et al. 2006). The tree prior used was “Speciation: Yule Process” (Gernhard 2008), which is suitable for analysis using inter-species sequences. To obtain the posterior distribution of the estimated divergence times, I set the hard minimum and soft maximum bounds with an exponential prior to calibrating the divergence between Callicebinae/Pitheciinae (95%: 15.7–26.0 Ma) according to the age estimated for the fossil genus *Proteropithecia* (Kay et al. 1998). *Proteropithecia*, the oldest pitheciin fossil, was found in the Collón Cura formation at Cañadón del Tordillo in Neuquén Province, Argentina. It has dental characteristics possibly adapted to feeding on hard-objects, characteristic of Pithecinae. I used two calibration points from the dates recovered in dos Reis et al. (2018) under a normal distribution prior: (i) *Chiropotes*/*Cacajao* (95%: 6.8–11.1); (ii) *Cacajao melanocephalus*/*Cacajao calvus* (95%: 2.8–5.7). I ran the Markov chain for 500,000,000 generations, sampling every 5,000 steps. I used CIPRES Science Gateway v.3.3 server (Miller et al. 2010) to run the analysis, and I visually assessed the convergence, performance, and burn-in using Tracer 1.7.1 (Rambaut et al. 2018).

2.2.5 PHYLOGEOGRAPHIC ANALYSES

I applied a Bayesian framework to perform a continuous spatiotemporal phylogeographic reconstruction using the software Beast 1.10 (Suchard et al. 2018). The spatiotemporal diffusion was proposed originally as a method to investigate the viral epidemiology since rapidly evolving virus groups have a high mutation rate. Therefore, by incorporating the molecular and geographic information in the spatiotemporal diffusion models, it is possible to get insights on the patterns of virus dispersion throughout its evolutionary history and to assign the potential epidemic origin – or the relationship between the epidemiology and the geographic locations (Lemey et al. 2009a, b). More recently, this model has been successfully applied to investigate the phylogeography and the evolutionary history of vertebrates (Camargo et al. 2013; Nascimento et al. 2013; Werneck et al. 2015; Lynch-Alfaro et al. 2015). Because this model employs a Brownian motion – i.e. assumes constancy – the same rates of diffusion are applied to all branches in the phylogeny, which can be unrealistic in dynamics and complex scenarios such as in Amazon Rainforest. Therefore, I used the lognormal relaxed random walk (RRW) model to fit the time and rate heterogeneity across the branches of the phylogeny to infer the geographic location of ancestors and the continuous spatiotemporal diffusion of the lineages (Lemey et al. 2010).

I only included in this analysis the ingroup, i.e., *Cacajao* and *Chiropotes*. Considering that some specimen coordinates were duplicated, I used the option “add random jitter to tips” and set the values to 0.50. I ran the Markov chain using the same settings described above for the Divergence Time Estimation. Finally, I used the Continuous Tree module in the software SPREAD v1.0.7 (Bielejec et al. 2011) to generate a keyhole markup language (KML) file to visualise the spatiotemporal diffusion of the lineages in Google Earth.

2.3 RESULTS

2.3.1 GENETIC VARIATION AND PHYLOGENETIC INFERENCE

In total, I obtained 1137bp for the dataset 1 (cytochrome *b*) for 73 individuals – 37 newly sequenced *Cacajao* and 36 from Genbank (35 *Cacajao* and 1 *Chiropotes*). The data set 2 (concatenated nuclear) had 3203bp (ABCA1=878bp, ADORA3=412bp, RAG1=1069bp, ZFX=844bp), which included 33 *Cacajao* individuals newly sequenced and one *Chiropotes* from GenBank. Using the same individuals, I obtained 4340bp for the dataset 3 (cyt*b* + nuclear genes). For the Divergence Time Estimation and the Phylogeographic analysis, I got a dataset of 1092bp of cytochrome *b* for 91 individuals, including 58 genebank sequences.

Although the nuclear dataset was about thrice the length as the mitochondrial, the overall genetic variability of the first was lower than that found for the second (Table *2-2*). The haplotype diversity for the nuclear-concatenated dataset was 0.961, and for the cytochrome *b* dataset was 0.986. When comparing the haplotype diversity in each nuclear gene, ABCA1 had the lowest value, 0.648, and the ZFX gene the higher, 0.768. Nucleotide diversity in the nuclear-concatenated dataset (0.00235) was about 20.7x lower than that found for the cytochrome *b* (0.04873) (Table *2-2*).

The maximum likelihood phylogenetic tree retrieved from the nuclear-concatenated dataset had strong support for the clades that separate black uakaris (*C. melanocephalus*, *C. hosomi*, and *C. ayresi*) and the bald uakaris (*C. calvus*, *C. rubicundus*, *C. ucayalii*, and *C. novaesi*) (Figure 2.2); there is a shallow resolution within these clades, however. The trees retrieved using the cytochrome *b* dataset (Figure 2.3) and the concatenated cytochrome *b* + nuclear dataset (Figure 2.4) are well structured with strong support for the main clades. Both trees have four main clades, two for black uakaris and two for bald uakaris (Figure 2.3, Figure 2.4). The first clade of black uakaris is composed only by *Cacajao melanocephalus* (sensu (Boubli et al. 2008) while the second has *C. ayresi* and *C. hosomi*, each one in well-defined clades. For bald uakaris, one clade is composed only by the white uakaris (*Cacajao calvus*), and the other includes all three species of red bald uakaris, i.e., *C. rubicundus*, *C. ucayalii*, and *C. novaesi* (Figure 2.3, Figure 2.4). However, these subspecies are interpolated within this clade with poor resolution in any of the three datasets.

Table 2-2 Genetic metrics for *Cacajao* and *Chiropotes*.

Dataset	**Number of sequences**	**Number of polymorphic sites, S**	**Number of Haplotypes, h**	**Haplotype (gene) diversity, Hd**	**Nucleotide diversity, Pi**	**Theta (per site) from S, Theta-W**	**Average number of nucleotide differences, k**
Nuclear (phased)							
Concatenated	68	68	33	0.961	0.00235	0.00456	7.335
ABCA1	68	20	6	0.648	0.00215	0.00523	1.714
ADORA3	68	16	10	0.715	0.00771	0.00952	2.707
RAG1	68	21	11	0.723	0.0022	0.0041	2.353
ZFX	68	18	8	0.768	0.0024	0.00458	1.969
Mitochondrial							
All individuals	80	246	51	0.986	0.04873	0.04569	52.974
Cacajao	72	138	45	0.983	0.03465	0.0261	37.805
Chiropotes	8	97	6	0.929	0.03706	0.03438	40.321
calvus	13	16	9	0.949	0.00385	0.00472	4.205
ucayalii	14	27	10	0.945	0.0071	0.00777	7.758
novaesi	5	6	3	0.8	0.00293	0.00264	3.2
rubicundus	8	2	3	0.75	0.00088	0.00071	0.964
hosomi	7	4	5	0.857	0.00148	0.0015	1.619
ayresi	5	4	3	0.8	0.00201	0.00176	2.2
melanocephalus	18	27	14	0.967	0.00669	0.0072	7.294

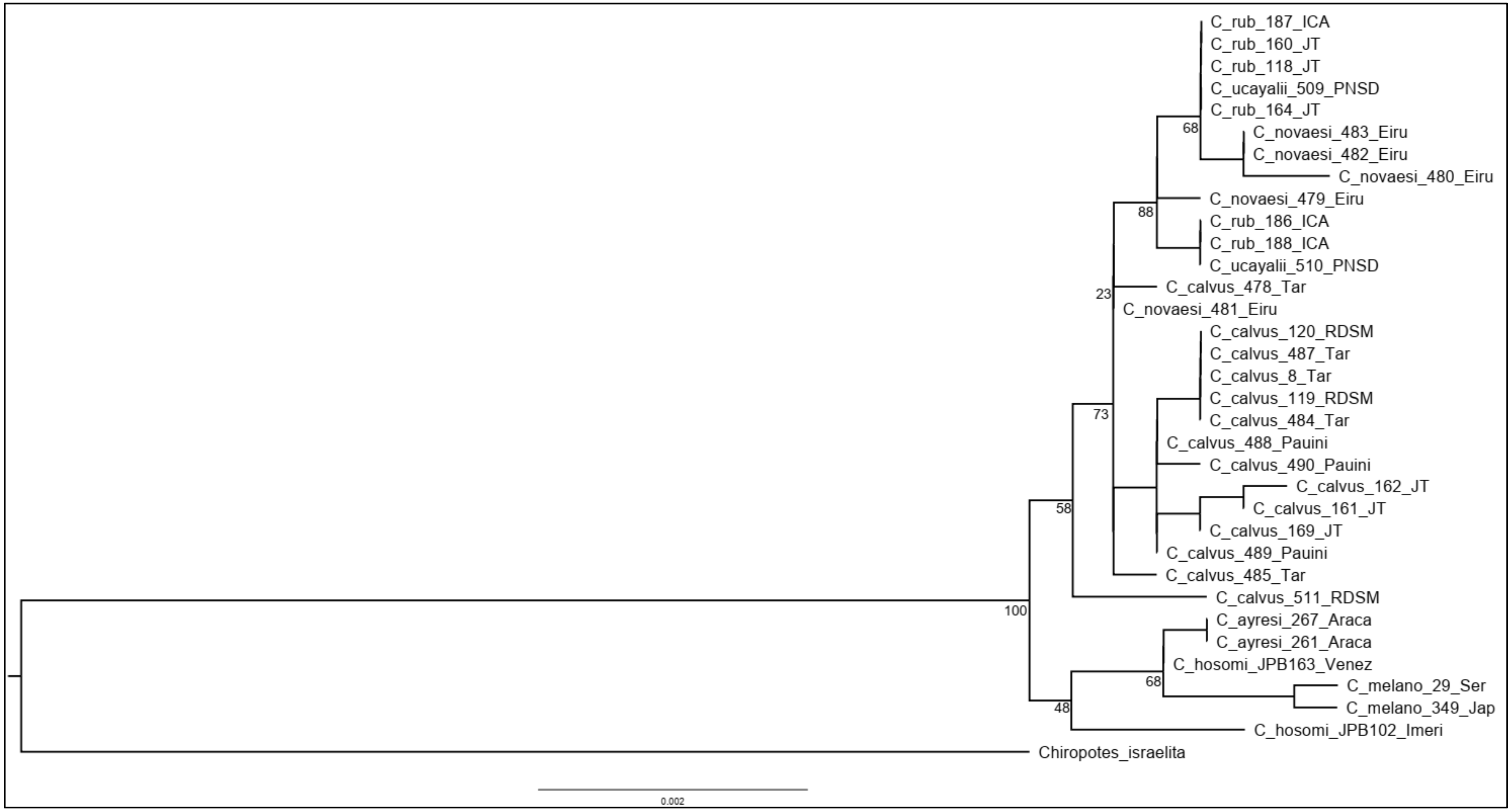


Figure 2.2 Nuclear-concatenated maximum likelihood tree.

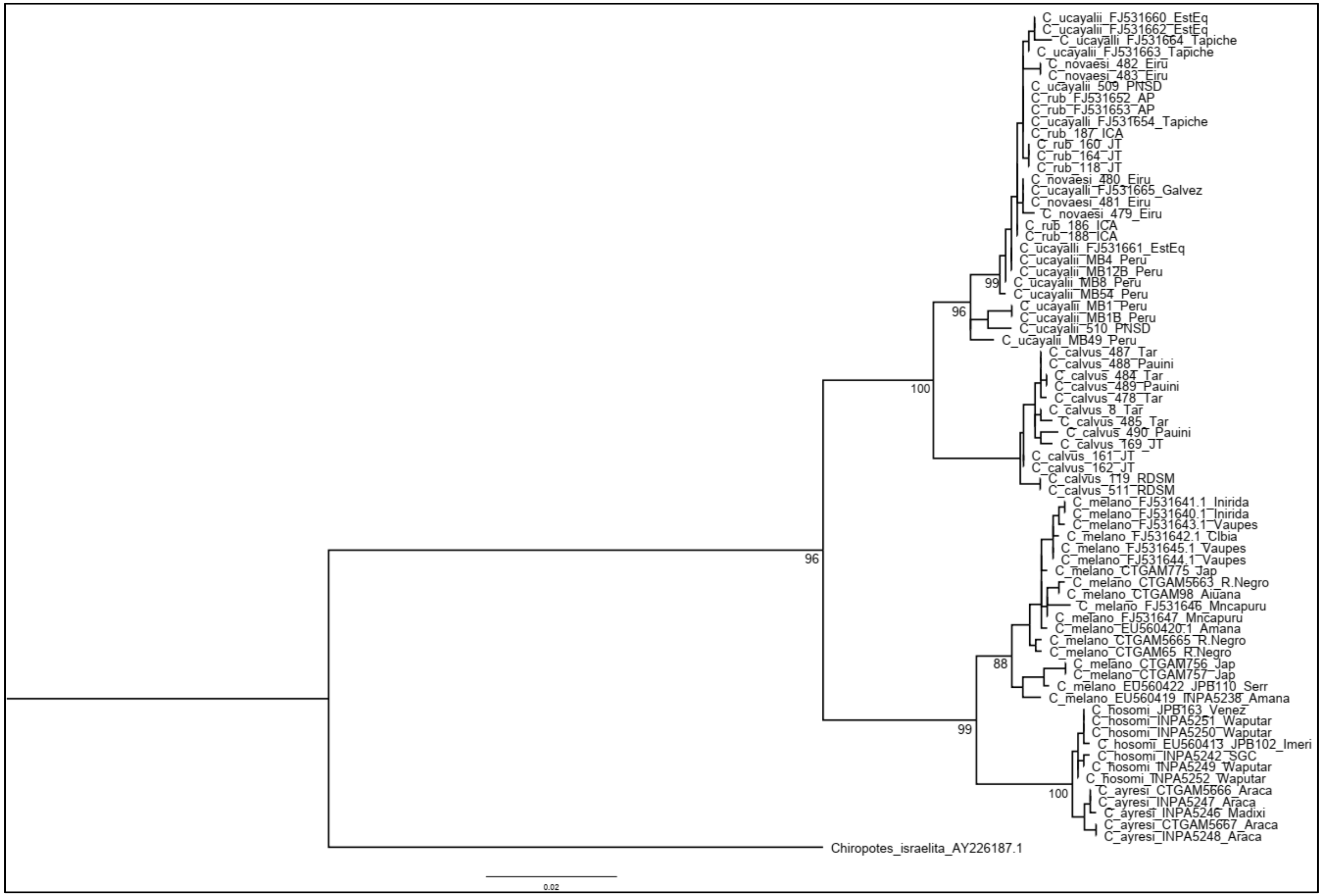


Figure 2.3 Cytochrome b maximum likelihood tree

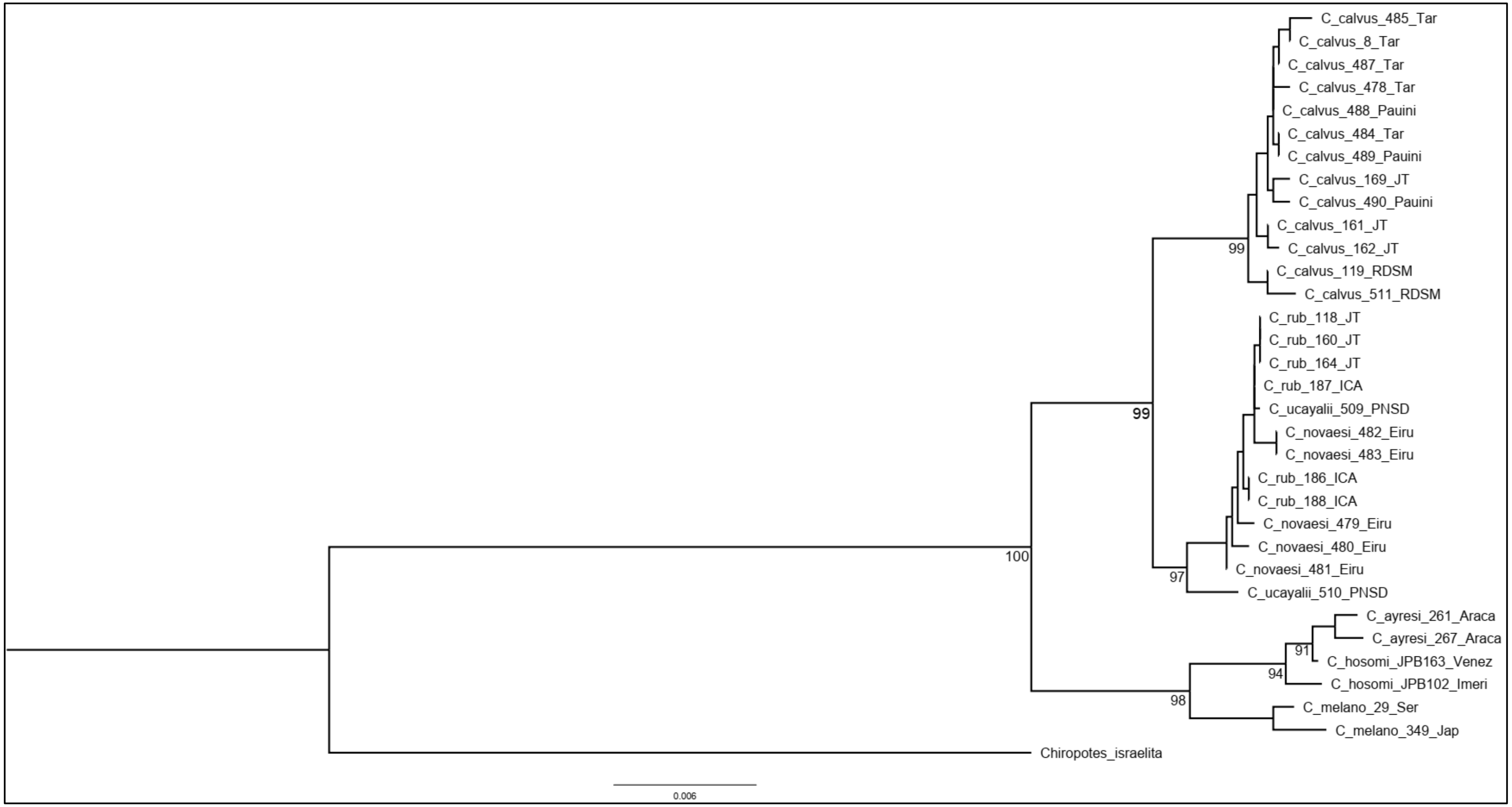


Figure 2.4 Concatenated (Cytochrome b + nuclear) maximum likelihood tree

2.3.2 DIVERGENCE TIME ESTIMATION AND PHYLOGEOGRAPHY

The cytochrome *b* tree retrieved from the Bayesian inference was consistent with the maximum likelihood tree and had the same topology for *Cacajao*, i.e., two clades for the bald uakaris and two for the black uakaris. The Pitheciinae clade diverged from the clade of titi monkeys – *Plecturocebus*, *Cheracebus*, and *Callicebus* – at 16.7 Mya (95% Highest Posterior Density [HPD]: 15.7 – 18.7Mya), originating *Pithecia* and the ancestral of *Chiropotes* and *Cacajao* (Figure 2.5). The divergence time between *Pithecia* and *Chiropotes*/*Cacajao* occurred in the mid-Miocene, at 14.4Mya (95% Highest Posterior Density [HPD]: 12.0 – 16.7Mya), with the split between *Chiropotes* and *Cacajao* estimated at 9.0Mya (95% Highest Posterior Density [HPD]: 7.0 – 11.1Mya).

The species-level diversification in *Cacajao* and *Chiropotes* started between 6 and 5 Mya. The RRW diffusion model points to the flooded forests (*várzea*) of the mid-Solimões River as its geographic origin of this clade (Figure 2.6A). From 4 Mya, *Chiropotes* lineages began their expansion towards the Brazilian and Guyana shields, and the main lineages of *Cacajao* dispersed in two directions: the black uakaris to the north of Solimões River basin and the bald uakaris to the south (Figure 2.6B). At 2.5Mya, the *Chiropotes* lineages reached the Brazilian and Guyana shields and the two long dispersals in *Cacajao* lineages extended even further, and these lineages begin to branch out (Figure 2.6C). At this point, the black uakaris' lineages dispersed toward the North of Brazil, nearby the border with Colombia and Venezuela and the white bald uakaris' lineages dispersed toward the upper Juruá River. From 2.5Mya to 1.0Mya, the red bald uakaris' lineages spread through the Javari and *Ucayalii* River basin (*C. ucayalii*), Gregório-Tarauacá interfluve (*C. novaesi*), and toward low Jutaí River and middle Solimões River (*C. rubicundus* (Figure 2.6D). At the same period, the white bald uakaris (*C. calvus*) reached the upper Juruá River basin and dispersed toward the region where today is the Mamirauá Sustainable Development Reserve (SDR Mamirauá) – a protected area located between Japurá, Solimões and Auati-Paraná Rivers, in the Central Amazon, Brazil (Figure 2.6D). Also, from 2.5Mya to 1.0Mya, the *melanocephalus* lineages spread through Japurá and Negro interfluve, while *C. hosomi* reached the mountains region from North of Brazil and South of Venezuela (Figure 2.6D). The lineage that originated *C.*

ayresi dispersed toward the Curuduri River basin. From 1Mya, *Chiropotes* and *Cacajao* were spread through their current known geographic range (Figure 2.6E).

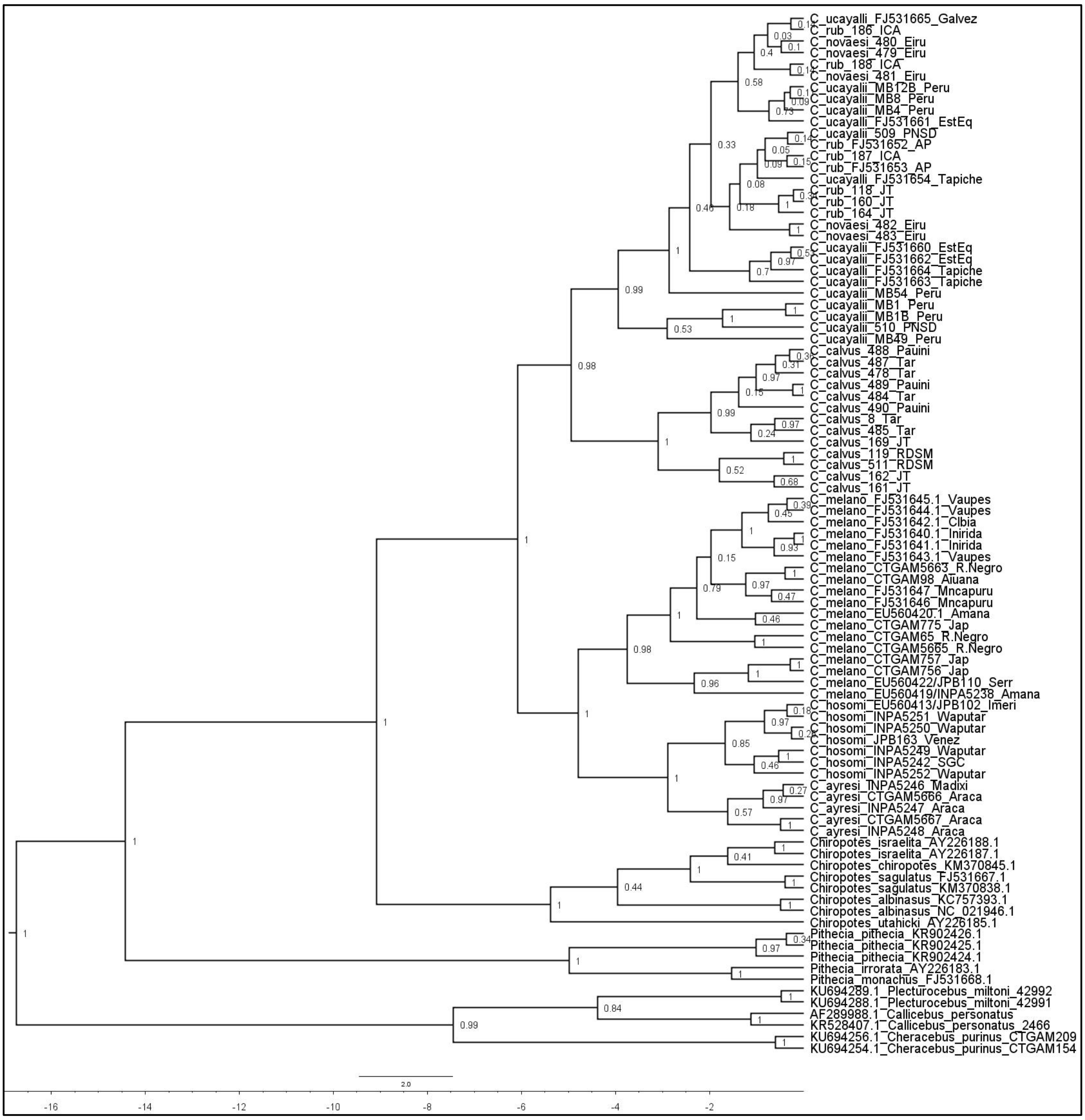


Figure 2.5 The Bayesian time tree of *Cacajao* and *Chiropotes*. The numbers in the nodes represent the posterior probability, and below the cladogram is the timescale

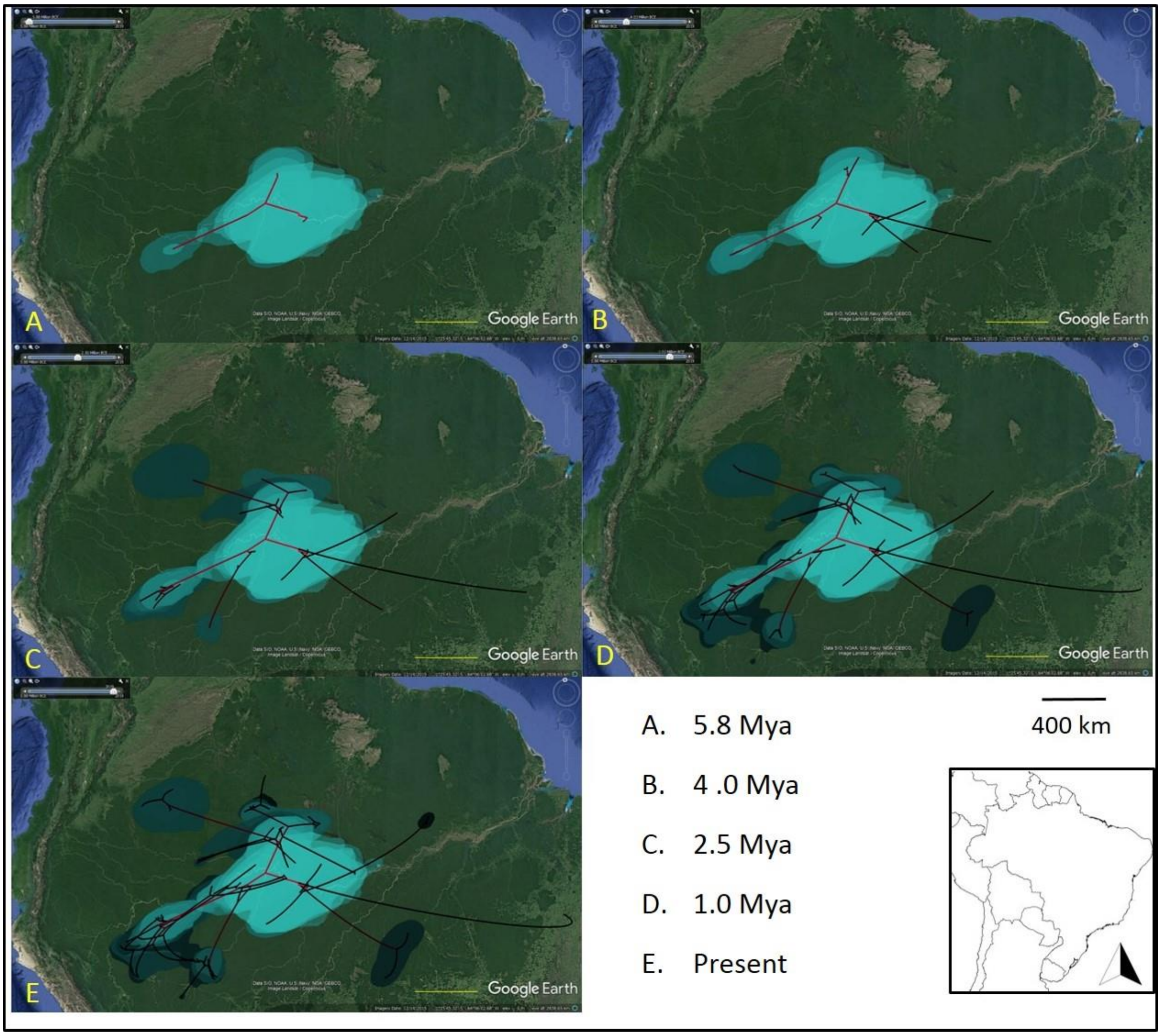


Figure 2.6 Bayesian spatiotemporal diffusion of *Chiropotes* and *Cacajao*. Shading represents 80%-HPD uncertainty in the location of ancestral branches (lighter=old diffusion; darker=young diffusion).

2.4 DISCUSSION

2.4.1 THE PHYLOGENETIC INFERENCE IN CACAJAO USING NUCLEAR AND MITOCHONDRIAL DNA

The inference of the phylogenetic relationship of the *Cacajao* lineages was sensitive to the dataset combination. When using only the nuclear markers in a concatenated analysis, the phylogenetic tree had a poor resolution due to the low genetic variability of this dataset. Consequently, the phylogenetic inference with the nuclear dataset only retrieved two clades, which represent the split between bald and black uakaris, but without resolution within each one. However, the higher genetic diversity found in the mitochondrial DNA allowed the recovering of four distinct clades of *Cacajao* with strong bootstrap support (>98%) for both analysis using cytochrome *b* only and the concatenated dataset (nuclear+cytochrome *b*). Therefore, the phylogenetic trees from these datasets have two lineages of bald uakaris (*C. calvus* (*C. rubicundus, C. ucayalii, C.novaesi*)) and two of black-headed uakaris (*C. melanocephalus* (*C. hosomi*, *C. ayresi*)). The Bayesian analysis recovered a similar topology with a high posterior probability (>98%).

The separation between white (*calvus*) and red (*rubicundus+ucayalii+novaesi*) uakaris is similar to that found between the two main clades of black uakaris. Although the markers used here successfully detected the genetic diversity between red and white uakaris, the structure within these groups is unclear when using few DNA markers. The three species of red uakaris (*rubicundus+ucayalii+novaesi*) are interpolated without any structure in a well-defined clade. Similarly, *C. calvus* form a monophyletic group including individuals from all population where white uakaris are known, i.e. Juruá, Tarauacá, Jutaí and Solimões rivers. For the black uakaris, the primary separation occurs between the individuals from the North (*ayresi* + *hosomi*) and South (*melanocephalus*) of Negro River. However, there is a substructure separating *C. ayresi* and *C. hosomi* into two small clades, which is consistent with the morphological diagnostic characters assigned to them and with the geographic distribution of both taxa (Boubli et al. 2008).

In terms of phylogenetic inference, these findings are similar to that presented by Figueiredo-Ready et al. (2013) in three aspects. First, *Cacajao* is a monophyletic group closely related to *Chiropotes*. Second, the molecular data reinforce the primary morphological division in *Cacajao* with bald and black uakaris being reciprocally monophyletic. Finally, the cytochrome *b* tree only retrieved the two main lineages of black uakaris and bald uakaris, but it was not sensible to recover the shallower relationship in bald uakaris. Figueiredo-Ready et al. (2013) found a similar pattern. However, the interpretation of the relationship within these clades by Figueiredo-Ready et al. (2013) was biased by two points.

The first was the number of ambiguities found in the museum sample MPEG 8991 (Genebank FJ531650) which in turn influenced their tree topology leading the authors to conclude that *C. ayresi* clade was nested within *C. hosomi* clade[1]; therefore, arguing against the validity of *C. ayresi*. Although I tested the phylogenetic inference using this sample in the preliminary analysis, I did not include it in the final datasets due to the number of ambiguities and its influence in the results. The second point is the misidentification of bald uakaris from upper Juruá (samples INPA5241 and UFPA-Ccn1), which the authors referred to as *C. novaesi*, when, they are, actually, white uakaris, therefore, *C. calvus* (see Chapter 4, p 144).

2.4.2 FLOODPLAIN OR UPLAND ORIGIN?

Cacajao diverged from *Chiropotes* at 9Ma, and the diversification at the species level occurred in the Pliocene (~5Ma). These findings are similar to previous studies using cytochrome *b* to infer the divergence time in Pithecinae (Boubli and Ditchfield, 2000; Figueiredo-Ready et al., 2013). Although our findings are also similar to the estimated by dos Reis et al. (2018), their analyses only included few *Cacajao* sequences (*C. calvus* N=1, *C. melanocephalus* N=1; *C. ayresi* N=1 and *C. hosomi* N=1) since their phylogenomic approach focused on the effects of the calibration strategies in the divergence time estimation in the main lineages of the order Primates. Therefore, the inclusion of more samples in a phylogenomic approach using different parameter settings to test the divergence time of the

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[1] Figueiredo-Ready et al. (2013) followed the nomenclature proposed by Hershkovitz (1987) for the black uakaris; therefore, the samples MPEG8991 was mentioned by the authors as *C. melanocephalus*.

main Pitheciinae lineages is essential to understand the evolutionary history of this group.

The low resolution in the clade of red bald uakaris can be related to the recent and successive episodes of dispersion in areas of middle Solimões River and Ucayali-Javari interfluve. The analysis presented here included samples from different localities where red uakaris occur; therefore, there are representatives of the three species (*rubicundus*, *ucayalii*, and *novaesi*) with accrued morphological differences that are consistent with each geographic cluster. Nevertheless, the dynamic changes in the western Amazonia during the Plio-Pleistocene (Rossetti et al. 2015) and the dispersion showed in the phylogeographic analysis may have promoted a recent gene flow between these lineages. Thus, the more recently diverged lineages may be overlooked in the phylogenetic tree when using few DNA markers.

The Bayesian phylogeographic analysis supported that the Pitheciinae clade *Cacajao/Chiropotes* had a common ancestor that was a lowland water-affiliated taxon, with *Cacajao* occupying the floodplain of Negro–Branco and Ucayali–Solimões–Juruá river systems, in the western Amazonia; and *Chiropotes* dispersing to the Brazilian and Guiana shield. These findings are similar to what Lynch-Alfaro et al. (2015) found for *Saimiri*. Indeed, both *Cacajao* and *Saimiri* are ecologically associated to the flooded forests (Ayres 1986, 1989; Barnett et al. 2013; Lynch-Alfaro et al. 2015; Barnett and Jucá 2018; Paim et al. 2018), although they also use other forest types.

2.4.3 A FLOODED FOREST SPECIALIST IN A "WORLD IN CHANGES"

The genus *Cacajao* is considered a flooded forest specialist. However, the ecological specialisation in flooded forests and the geographic distribution of uakaris has been revealed quite complex and variable. While bald uakaris use mostly the floodplain of white water rivers (*várzea*) (Ayres 1986, 1989; Barnett et al. 2013), the black uakaris use the flooded forests of black rivers (*igapó*) (Barnett et al. 2013; Barnett and Jucá 2018). Even though the strong association between flooded forests and the occurrence of these primates, the seasonality in the food availability is a critical variable for their use of the resources in adjacent unflooded forests (Peres 1997; Barnett et al. 2013).

There are some populations, however, that were recorded in upland forests that contradict this ecological association generally found in uakari monkeys (Boubli and Tokuda 2008; Heymann and Aquino 2010; Vermeer et al. 2013). For example, a compilation of reports on the occurrence Peruvian red uakari (*C. ucayalii*) in unflooded forests was used to argue against the perception of this subspecies is a habitat specialist restricted to flooded forests (Heymann and Aquino 2010). The authors also concluded that *C. ucayalii* is resilient in terms of habitat requirement and frequently use the unflooded Peruvian forests (*Terra Firme*).

The most extreme cases of the occurrence of uakari monkeys in unflooded forests are those from high altitude. For example, a new and isolated Peruvian red uakari population was found in a mountain region of northern San Martin district, far from the known western limit for this subspecies (Vermeer 2013). The animals were encountered at an altitude of more than 1,000m a.s.l., separated by more 365 kilometres from the west bank of Ucayali River. Similarly, a population of *C. ucayalii* was recorded in the Serra do Divisor National Park (Supporting Information), a set of geomorphological formation with altitudes of up to 650 a.s.l. (MMA and Brasil 1998). The black uakaris from Pico da Neblina National Park use different forest types that are not only separated from the floodplain areas but at the altitudes of up to 1,500m a.s.l. (Boubli 1999; Boubli and Tokuda 2008).

These findings shed light on how variable can be the habitat requirements of bald-headed uakaris; and how far is our knowledge of the ecology and distribution of *Cacajao*. As a lowland water-affiliate primate that dispersed to different areas of western Amazonia, the dynamic geomorphological changes related with the drainage of the Pebas Lake may have played an essential role in the current pattern of occupancy of uakaris throughout its geographic distribution. The disjunct distribution found in bald uakaris subspecies may have its origin in the process of dispersion followed by the rapid changes in the landscape such as the meandering of the lowland rivers in the western Amazonia (Rossetti et al. 2015), and the retraction of the flooded forests (*várzea*) during the late Pleistocene (Pupim et al. 2019). Long term ecological studies were conducted only in two field sites for black uakaris – Jaú National Park (Barnett et al. 2005; Bezerra et al. 2010, 2011) and Pico da Neblina National Park (Boubli 1999; Boubli and Tokuda 2008), and two for bald uakaris – Mamirauá SDR (Ayres 1986) and Lago Preto Conservation Concession (Bowler and Bodmer 2009, 2011).

Considering the complexity and the dynamic of the changes in the western Amazonia that underlies the evolutionary history of *Cacajao*, these studies possibly represent only a small fraction (although essential) of the ecology and behaviour of the uakari monkeys.

2.5 Supplementary Material - Chapter 2

Table Suppl 2-1 - Samples and localities used in the analyses.

Tree code	Taxon	Sample_ID/ Code	Locality	Long	Lat	Reference
C_*ayresi*_CTGAM5666_Araca	*C. ayresi*	CTGAM5666	Acará River, left bank, Brazil	-62.950	-0.380	Bertuol 2015
C_*ayresi*_CTGAM5667_Araca	*C. ayresi*	CTGAM5667	Acará River, left bank, Brazil	-62.950	-0.380	Bertuol 2015
C_*ayresi*_INPA5246_Madixi	*C. ayresi*	INPA5246	Igarapé Madixi, Brazil	-63.340	-0.120	Boubli et al. 2008
C_*ayresi*_INPA5247_Araca	*C. ayresi*	INPA5247	Acará River, left bank, Brazil	-62.910	-0.540	Boubli et al. 2008
C_*ayresi*_INPA5248_Araca	*C. ayresi*	INPA5248	Acará River, left bank, Brazil	-62.910	-0.540	Boubli et al. 2008
C_*calvus*_119_RDSM	*C. calvus*	119/Masto283	Mamirauá Reserve, Brazil	-64.935	-2.912	This study
C_*calvus*_161_JT	*C. calvus*	161/JT22	Jutaí River, right bank,Brazil	-67.395	-3.313	This study
C_*calvus*_162_JT	*C. calvus*	162/JT03	Jutaí River, right bank,Brazil	-67.374	-3.300	This study
C_*calvus*_169_JT	*C. calvus*	169/JT85	Riozinho, left bank,Brazil	-67.137	-3.298	This study
C_*calvus*_478_Tar	*C. calvus*	478/FES64	Tarauacá River, right bank, Brazil	-69.925	-6.753	This study
C_*calvus*_484_Tar	*C. calvus*	484/FES70	Tarauacá River, right bank, Brazil	-69.667	-6.671	This study
C_*calvus*_485_Tar	*C. calvus*	485/FES71	Tarauacá River, right bank, Brazil	-69.667	-6.671	This study
C_*calvus*_487_Tar	*C. calvus*	487/FES95	Tucumã Lake, Tarauacá River, right bank, Brazil	-69.738	-6.935	This study
C_*calvus*_488_Pauini	*C. calvus*	488/RS62	Pauini River, left bank, Brazil	-69.248	-8.034	This study

C_*calvus*_489_Pauini	*C. calvus*	489/RS63	Pauini River, left bank, Brazil	-69.248	-8.034	This study
C_*calvus*_490_Pauini	*C. calvus*	490/RS64	Pauini River, left bank, Brazil	-69.248	-8.034	This study
C_*calvus*_511_RDSM	*C. calvus*	511	Mamirauá Reserve, Brazil	-64.854	-3.071	This study
C_*calvus*_8_Tar	*C. calvus*	8/CCM112	Tarauacá River, right bank, Brazil	-71.360	-8.830	This study
C_*hosomi*_EU560413/JPB102_Imeri	*C. hosomi*	EU560413/JPB102	Serra do Imeri, Xamata, Brazil	-65.270	0.490	Boubli et al. 2008
C_*hosomi*_INPA5242_SGC	*C. hosomi*	INPA5242	São Gabriel da Cacheira, Brazil	-66.110	0.610	Boubli et al. 2008
C_*hosomi*_INPA5249_Waputar	*C. hosomi*	INPA5249	Serra do Padre e Waputar, Brazil	-66.210	0.660	Boubli et al. 2008
C_*hosomi*_INPA5250_Waputar	*C. hosomi*	INPA5250	Serra do Padre e Waputar, Brazil	-66.210	0.660	Boubli et al. 2008
C_*hosomi*_INPA5251_Waputar	*C. hosomi*	INPA5251	Serra do Padre e Waputar, Brazil	-66.210	0.660	Boubli et al. 2008
C_*hosomi*_INPA5252_Waputar	*C. hosomi*	INPA5252	Serra do Padre e Waputar, Brazil	-66.600	0.490	Boubli et al. 2008
C_*hosomi*_JPB163_Venez	*C. hosomi*	JPB163	Venezuela	-65.280	2.250	Bertuol 2015
C_melano_CTGAM5663_R.Negro	*C. melanocephalus*	CTGAM5663	Negro River, right bank, Brazil	-64.740	-0.490	Boubli et al. 2008
C_melano_CTGAM5665_R.Negro	*C. melanocephalus*	CTGAM5665	Negro River, right bank, Brazil	-64.650	-0.490	Boubli et al. 2008
C_melano_CTGAM65_R.Negro	*C. melanocephalus*	CTGAM65	Igarapé Parati, Negro River, right bank, Brazil	-64.910	-0.580	Bertuol 2015
C_melano_CTGAM756_Jap	*C. melanocephalus*	CTGAM756	Japurá River, left bank, Brazil	-69.200	-1.690	Bertuol 2015

C_melano_CTGAM757_Jap	*C. melanocephalus*	CTGAM757	Japurá River, left bank, Brazil	-69.200	-1.690	Bertuol 2015
C_melano_CTGAM775_Jap	*C. melanocephalus*	CTGAM775	Japurá River, left bank, Brazil	-69.340	-1.660	Bertuol 2015
C_melano_CTGAM98_Aiuana	*C. melanocephalus*	CTGAM98	Igarapé Aiuanã, Negro River, right bank	-64.930	-0.620	Bertuol 2015
C_melano_EU560419/INPA5238_Amana	*C. melanocephalus*	EU560419/INPA5238	Amanã Lake, Solimões River, Brazil	-64.500	-2.500	Boubli et al. 2008
C_melano_EU560420.1_Amana	*C. melanocephalus*	EU560420.1	Amanã Lake, Solimões River, Brazil	-64.500	-2.500	Boubli et al. 2008
C_melano_EU560422/JPB110_Serr	*C. melanocephalus*	EU560422/JPB110	Amanã Lake, Solimões River, Brazil	-65.170	-0.470	Boubli et al. 2008
C_melano_FJ531640.1_Inirida	*C. melanocephalus*	FJ531640.1	Inirida River, Colômbia	-70.400	2.300	Figueiredo et al. 2013
C_melano_FJ531641.1_Inirida	*C. melanocephalus*	FJ531641.1	Inirida River, Colômbia	-70.400	2.300	Figueiredo et al. 2013
C_melano_FJ531642.1_Clbia	*C. melanocephalus*	FJ531642.1	Barracon, Alto Cano Itilla, Colômbia	-72.690	1.610	Figueiredo et al. 2013
C_melano_FJ531643.1_Vaupes	*C. melanocephalus*	FJ531643.1	Cano Miraflores, Vaupés River, Colômbia	-72.000	1.500	Figueiredo et al. 2013
C_melano_FJ531644.1_Vaupes	*C. melanocephalus*	FJ531644.1	Lago el Dorado, Vaupés River, Colômbia	-70.450	1.000	Figueiredo et al. 2013
C_melano_FJ531645.1_Vaupes	*C. melanocephalus*	FJ531645.1	Lago el Dorado, Vaupés River, Colômbia	-70.450	1.000	Figueiredo et al. 2013

C_melano_FJ531646_Mncapuru	*C. melanocephalus*	FJ531646	Manacapuru River, Brazil	-40.760	73.984	Figueiredo et al. 2013
C_melano_FJ531647_Mncapuru	*C. melanocephalus*	FJ531647	Manacapuru River, Brazil	-40.760	73.984	Figueiredo et al. 2013
C_*novaesi*_479_Eiru	*C. novaesi*	479/FES65	Igarapé Preto, Juruá River, right bank, Brazil	-64.800	-3.117	This study
C_*novaesi*_480_Eiru	*C. novaesi*	480/FES66	Igarapé Preto, Juruá River, right bank, Brazil	-70.196	-6.864	This study
C_*novaesi*_481_Eiru	*C. novaesi*	481/FES67	Igarapé Preto, Juruá River, right bank, Brazil	-70.196	-6.864	This study
C_*novaesi*_482_Eiru	*C. novaesi*	482/FES68	Igarapé Preto, Juruá River, right bank, Brazil	-70.196	-6.864	This study
C_*novaesi*_483_Eiru	*C. novaesi*	483/FES69	Igarapé Preto, Juruá River, right bank, Brazil	-69.925	-6.753	This study
C_rub_118_JT	*C. rubicundus*	118/JT63	ESEC_Jutaí-Solimões, Brazil	-67.423	-3.201	This study
C_rub_160_JT	*C. rubicundus*	160/JT62	ESEC_Jutaí-Solimões, Brazil	-67.423	-3.201	This study
C_rub_164_JT	*C. rubicundus*	164/JT78	ESEC_Jutaí-Solimões, Brazil	-67.548	-3.312	This study
C_rub_186_ICA	*C. rubicundus*	186/FES46	Jacurapá_River, left bank, Brazil	-68.618	-3.237	This study
C_rub_187_ICA	*C. rubicundus*	187/FES47	Jacurapá_River, left bank, Brazil	-68.618	-3.237	This study
C_rub_188_ICA	*C. rubicundus*	188/FES48	Jacurapá_River, left bank, Brazil	-68.618	-3.237	This study
C_rub_FJ531652_AP	*C. rubicundus*	FJ531652	Buiuçu, Auatí-Paraná channel, Brazil	-2.353	-66.447	Figueiredo et al. 2013
C_rub_FJ531653_AP	*C. rubicundus*	FJ531653	Buiuçu, Auatí-Paraná channel, Brazil	-2.353	-66.447	Figueiredo et al. 2013
C_*ucayalii*_509_PNSD	*C. ucayalii*	509/FES100	Moa River, Serra do Divisor National Park, Brazil	-73.668	-7.461	This study
C_*ucayalii*_510_PNSD	*C. ucayalii*	510/FES101	Moa River, Serra do Divisor National Park, Brazil	-73.668	-7.461	This study
C_*ucayalii*_FJ531660_EstEq	*C. ucayalii*	FJ531660	Estirão do Equador, Javari River, Brazil	-71.676	-4.436	Figueiredo et al. 2013

C_*ucayalii*_FJ531662_EstEq	*C. ucayalii*	FJ531662	Estirão do Equador, Javari River, Brazil	-71.676	-4.436	Figueiredo et al. 2013
C_*ucayalii*_FJ531663_Tapiche	*C. ucayalii*	FJ531663	Tapiche River, Peru	-74.004	-5.655	Figueiredo et al. 2013
C_*ucayalii*_MB1_Peru	*C. ucayalii*	MB1	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB12B_Peru	*C. ucayalii*	MB12B	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB1B_Peru	*C. ucayalii*	MB1B	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB4_Peru	*C. ucayalii*	MB4	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB49_Peru	*C. ucayalii*	MB49	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB54_Peru	*C. ucayalii*	MB54	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_*ucayalii*_MB8_Peru	*C. ucayalii*	MB8	Lago Preto Conservation Concession, Loreto, Peru	-71.765	-4.458	x
C_ucayalli_FJ531654_Tapiche	*C. ucayalii*	FJ531654	Tapiche River, Peru	-74.004	-5.655	Figueiredo et al. 2013
C_ucayalli_FJ531661_EstEq	*C. ucayalii*	FJ531661	Estirão do Equador, Javari River, Brazil	-71.676	-4.436	Figueiredo et al. 2013
C_ucayalli_FJ531664_Tapiche	*C. ucayalii*	FJ531664	Tapiche River, Peru	-74.004	-5.655	Figueiredo et al. 2013
C_ucayalli_FJ531665_Galvez	*C. ucayalii*	FJ531665	Rio Galvez, Nuevo San Juan, Peru	-73.164	-5.292	Figueiredo et al. 2013
*Chiropotes*_albinasus_KC757393.1	*Chiropotes albinasus*	KC757393.1	x	-58.809	-6.756	x
*Chiropotes*_albinasus_NC_021946.1	*Chiropotes albinasus*	NC_021946.1	x	-60.284	-8.995	x

*Chiropotes_Chiropotes*_KM370845.1	*Chiropotes Chiropotes*	KM370845.1	x	-66.1800	5.3500	x
*Chiropotes*_israelita_AY226187.1	*Chiropotes israelita*	AY226187.1	x	-62.9552	-2.6126	x
*Chiropotes*_israelita_AY226188.1	*Chiropotes israelita*	AY226188.1	x	-64.2537	-3.9398	x
*Chiropotes*_sagulatus_FJ531667.1	*Chiropotes sagulatus*	FJ531667.1	x	-57.0459	-0.8222	x
*Chiropotes*_sagulatus_KM370838.1	*Chiropotes sagulatus*	KM370838.1	x	-57.2471	-1.2721	x
*Chiropotes*_utahicki_AY226185.1	*Chiropotes utahicki*	AY226185.1	x	-49.504	-7.058	x
Pithecia_irrorata_AY226183.1	*Pithecia irrorata*	AY226183.1	x	x	x	x
Pithecia_monachus_FJ531668.1	*Pithecia monachus*	FJ531668.1	x	x	x	x
Pithecia_pithecia_KR902424.1	*Pithecia pithecia*	KR902424.1	x	x	x	x
Pithecia_pithecia_KR902425.1	*Pithecia pithecia*	KR902425.1	x	x	x	x
Pithecia_pithecia_KR902426.1	*Pithecia pithecia*	KR902426.1	x	x	x	x
KU694289.1_*Plecturocebus*_miltoni_42992	*Plecturocebus miltoni*	KU694289.1	x	x	x	x
KU694288.1_*Plecturocebus*_miltoni_42991	*Plecturocebus miltoni*	KU694288.1	x	x	x	x

KU694256.1_*Cheracebus*_purinus_CTGAM209	*Cheracebus purinus*	KU694256.1	x				x	x	x
KU694254.1_*Cheracebus*_purinus_CTGAM154	*Cheracebus purinus*	KU694254.1	x				x	x	x
AF289988.1_*Callicebus*_personatus	*Callicebus personatus*	AF289988.1	x				x	x	x
KR528407.1_*Callicebus*_personatus_2466	*Callicebus personatus*	KR528407.1	x				x	x	x

Chapter 3. Using RAD-sequencing and parameter optimisation to unveil the population structure and phylogenetic relationship of bald uakaris – implications for their taxonomy

3.1 INTRODUCTION

The genus *Cacajao* remains one of the least studied Neotropical Primate. Currently, four species are recognised. *Cacajao calvus* includes four subspecies – *C. c. calvus*, *C. c. rubicundus*, *C. c. ucayalii*, *C. c. novaesi*, following the taxonomic classification based on pelage colouration proposed by Hershkovitz (1987a). They occur in a patchy distribution in the flooded forests of Ucayali–Solimões–Juruá river system. (Silva-Júnior et al. 2013). Black uakaris are classified into three species – *Cacajao melanocephalus*, *Cacajao hosomi*, and *Cacajao ayresi*, according to Boubli et al. (2008). The black uakaris occur in Negro–Branco river system.

The few studies on the molecular phylogeny of uakaris were based on only one mitochondrial DNA marker (Boubli et al. 2008; Figueiredo-Ready et al. 2013). While Figueiredo-Ready et al. (2013) identified four main clades of *Cacajao* using cytochrome *b*, their phylogenetic analysis did not provide a clear picture of the relationship of *C. calvus* subspecies. Although the four subspecies are geographically structured in terms of pelage colouration, the white uakaris (*C. c. calvus*) were paraphyletic, and the position of red uakaris (*C. c. rubicundus* and *C. c. ucayalii*) was unclear. Therefore, the use of a few markers did not allow for the assessment of the phylogenetic relationship of the bald uakaris (*Cacajao calvus* ssp., Geoffroy 1847) (see Chapter 2). Aiming to identify the main lineages of bald uakaris and its phylogenetic relationship using a new dataset, in this chapter, I am adopting a genomic approach to test the current taxonomic hypothesis for *Cacajao*.

Since the first studies on the molecular phylogeny of Primates (Giri 1987; Koop et al. 1989; Schneider et al. 1993, 1996; Goodman et al. 1994; Hayasaka et al. 1996), the enormous technological advances in DNA sequencing and bioinformatics allowed researchers to move forward in an unprecedented way on questions related to the evolution, biogeography, behavioural biology, and diversity of this order (Di Fiore 2003; Fabre et al. 2009; Jameson et al. 2011; Liedigk et al. 2012; Perez et al. 2012; Scally et al. 2012; Steiper and Seiffert 2012; Pozzi et al. 2014; Lynch-Alfaro 2017). In particular, the advent of Next Generation Sequencing (NGS) and the development of different sequencing platforms enabled the sequencing of a massive number of loci at an ever-decreasing cost and an ever-increasing speed. The parallelisation on the sequencing reaction allowed for the production of thousands or even millions of reads per run, making it possible to perform genome-wide association studies (GWAS) using SNP-arrays (SNP = Single Nucleotide Polymorphism) (Zhang et al. 2011; Buermans and den Dunnen 2014; Thermes 2014; Besser et al. 2018).

One method of NGS rapidly gaining popularity is the Restriction-site Associated DNA sequencing (RADseq). RAD sequences are short fragments of DNA associated with specific restriction enzymes sites. This marker is considered very efficient to identify thousands of SNPs and to create a reduced representation genome (Baird et al. 2008). Several lab techniques and program pipelines for RAD-Seq have been developed to date (Andrews et al. 2016) providing a variety of possibilities for data generation and analysis (Bradbury et al. 2007; Catchen et al. 2011, 2013; Eaton 2014; Lee et al. 2014). One such technique is the Double Digest Restriction Associated DNA (ddRAD) Sequencing (Peterson et al. 2012). This method uses two restriction enzymes, with adaptors specific to each one, allowing a precise selection of the genomic fragment size (Peterson et al. 2012). This characteristic gives more flexibility in reducing the number of fragments to be sequenced and in providing a genome-wide representation (Andrew et al. 2016).

Two of the most popular program pipeline for RADseq analysis are STACKS (Catchen et al. 2011, 2013) and IPYRAD (Eaton, 2014, https://github.com/dereneaton/ipyrad). STACKS is a software pipeline developed for building loci from short-read sequences retrieved from restriction-enzyme data, such as ddRAD. The software has different components that allow performing all steps required for the analysis of RADseq. It has been successfully applied in the analysis of sequences from different taxonomic groups for the investigation of population structure, gene flow, genetic diversity, among other topics in population-level studies (Dierickx et al. 2015; Blanco-Bercial and Bucklin 2016; Rodríguez-Ezpeleta et al. 2016; Wang et al. 2017; Storer et al. 2017; White et al. 2018). The second program frequently used in RAD sequence studies is PYRAD (Eaton 2014) – or its updated version iPYRAD (https://github.com/dereneaton/ipyrad). This program pipeline uses the global alignment clustering algorithm implemented in USEARCH (Edgar 2010), allowing for indel variation within and between samples, and the incomplete overlap among reads – which is particularly useful for ddRAD analysis (Eaton 2014). By including indel variation in downstream analysis, the ipyrad pipeline successfully identifies homology both within and between species and has been used recently to assemble data for phylogenetic studies in different taxonomic levels (Hipp et al.; Fang et al. 2018; Lee et al. 2018; Valencia et al. 2018; Guo et al. 2019).

Although the RADseq analyses are now widespread in studies of several different taxonomic groups, its use in Primate studies has been limited to few recent studies (Dushoff et al. 2017; Malukiewicz et al. 2017; Boubli et al. 2018, 2019; Baiz et al. 2019; Chiou et al. 2019a, b; Costa-Araújo et al. 2019). These studies addressed mostly two main topics. The first is the investigation of gene flow, reproductive isolation, and signature of selection between primates in hybrid zones (Baiz et al. 2019; Chiou et al. 2019a, b). The second is the phylogenetic inference to support species delimitation, an approach that has been used mostly for Neotropical Primates – *Cebuella* (Boubli et al. 2018); *Plecturocebus* (Boubli et al. 2019); and *Mico* (Costa-Araújo et al. 2019).

In a recent comprehensive study on the phylogenetic relationship of Neotropical Primates using ddRAD, Valencia et al. (2018) combined different restriction enzymes and read size selection parameters to develop a protocol to consistently recover loci that would be applicable across all the New World Primate radiation. The authors also tested different assembly pipelines – denovo, denovo+reference, and reference – and clustering thresholds on locus recovery and SNP identification. The denovo was the pipeline that retained the higher number of loci for the subsequent analyses. To check if these different parameters were consistent in supporting the phylogenetic relationship in different taxonomic levels, the authors compared two approaches, the Maximum Likelihood approach using the program IQTree and a quartet-based coalescent using the program Tetrad. Both Maximum likelihood and quartet-based coalescent analyses converged to the same topology, except for the genus *Aotus*, which for the inconsistency on its position and the low support obtained the authors pointed out the need for investigation on incomplete lineage sorting and introgression.

The main objective of this chapter is to verify how the parameter settings influence the loci and SNPs recovery and how it affects the subsequent analyses in the identification of the population structure and phylogenetic inference in *Cacajao*. I am using two datasets. The first includes 28 samples of bald uakaris, and I am using a parametric and a non-parametric approach to identify the population structure of bald uakaris. I am running this analysis in the software pipeline STACKS. For the second dataset, I include all known *Cacajao* taxa (sensu Hershkovitz 1987a; Boubli et al. 2008) from most known localities in Brazil to produce a well-supported phylogenetic tree using the software pipeline IPYRAD. Therefore, I am not aiming to compare these pipelines, but use them to 1) assess the extent of genomic admixture among the populations of bald uakaris; 2) test how the inference of population structuring in bald uakaris is sensible to the parametrisation of the analysis; 3) verify the level of divergence within the populations of white bald and red bald uakaris and among them (white x red); and 4) test how different parameter settings influence the phylogenetic inference in the genus *Cacajao*. I also examined the patterns of pelage colouration of Museum voucher specimens to present a preliminary taxonomic reappraisal for the bald uakaris considering the following points:

1. Disjunct geographic distribution occurs in *Cacajao* (Silva Jr et al. 1999; Vermeer et al. 2013; Cardoso et al. 2014; McHugh et al. 2019)(see Chapter 4) and can be an essential factor in the formation of clusters in the molecular phylogenetic analysis.
2. If the clusters identified in the molecular analysis include only individuals with morphological characteristics that can be used as diagnostic characters and that

are geographically consistent, then these clusters can be placed at the species level under the Phylogenetic Species Concept (monophyly and diagnosability).

3. Although monophyly and diagnosability are consistent with the PSC, it is not always possible to identify unique morphological patterns in populations with significant genetic distinctiveness. For example, cryptic diversity has been shown for several taxonomic groups where the traditional taxonomy based on morphology failed to identify independent evolutionary units (Mayer and Helversen 2001; Fritz et al. 2005; Baird et al. 2008; Neilson and Stepien 2009; Jörger and Schrödl 2013; Munds et al. 2013; Arbogast et al. 2017; Borsa et al. 2018). Therefore, although both criteria (monophyly and diagnosability) are operational and offer a practical approach for the "species problem", there is always a certain level of arbitrariness on where draw the line. Here, if a cluster does not bring a singular pattern of pelage colouration (i.e. diagnosability), I did not attribute new names to them, although I do emphasise the genetic distinctiveness.

3.2 METHODS

3.2.1 SAMPLE SET

To construct a DNA partial representation genomic library, I used tissue samples from the following Brazilian's scientific collections: Museu Paraense Emílio Goeldi (MPEG), Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), and Instituto Nacional de Pesquisas da Amazonia (INPA). The Laboratory procedures were performed by the team of the Laboratory of Evolution, and Animal Genetics (LEGAL) at the Universidade Federal do Amazonas (UFAM), Manaus, Brazil. The population analysis of bald uakaris included the four subspecies currently recognised (Hershkovitz, 1987) – *C. c. calvus* (N=15), *C. c. rubicundus* (N=6), *C. c. ucayalii* (N=2) and *C. c. novaesi* (N=5) **Error! Reference source not found.**Table Suppl. 3-1**Error! Reference source not

found.). For the phylogenetic inference, I also included the sequences of black uakaris – *Cacajao ayresi* (N=5), *Cacajao hosomi* (N=4), and *Cacajao melanocephalus* (N=10). I included *Chiropotes* spp. (N=16) as the outgroup. Although I did not include any sample from Peruvian forests, the sample set used here is geographically well-distributed, and it covers most of the localities where uakaris occur in the Brazilian Amazon (Figure 3.1, **Error! Reference source not found.**). This sample set allowed to assess the consistency of the phylogenetic inference from different parameter settings for all genus *Cacajao* (3.5 Supplementary Material – Chapter 3).

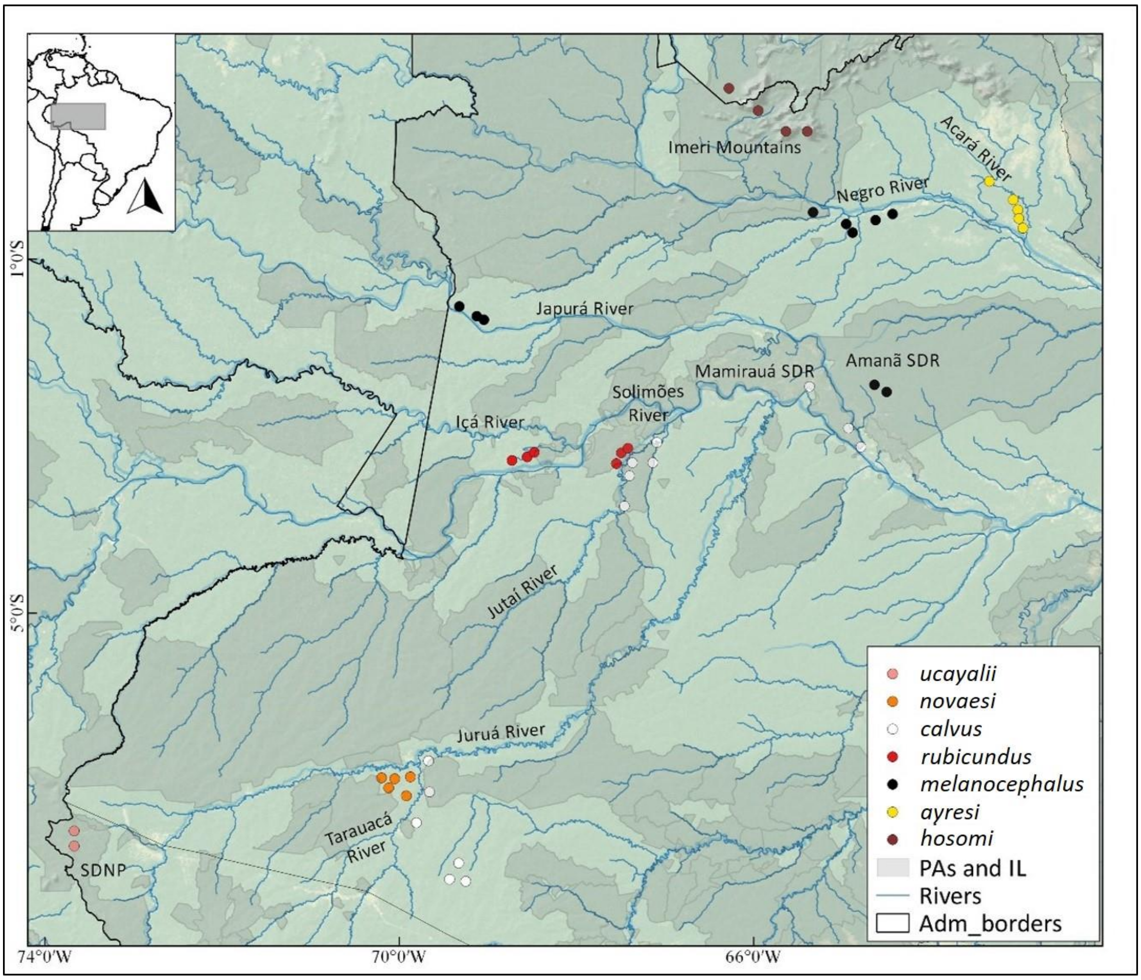

Figure 3.1 Samples localities of *Cacajao* sp. The numbers are indicated in Table Suppl. 3-1**Error! Reference source not found.**.

3.2.2 DNA EXTRACTION AND LIBRARY PREPARATION

The DNA extraction and the library preparation was conducted by the LEGAL lab team (https://www.evoamazon.net/) in Manaus, Brazil. Total genomic DNA was extracted using the standard phenol-chloroform extraction protocol (Sambrook et al. 1989). The concentration of the extracted DNA was quantified using a Nanodrop 2000 spectrophotometer (Thermo Scientific). The RADseq method used was the double digest restriction-site-associated DNA sequencing protocol (ddRADseq) (Peterson et al. 2012). The protocol was adapted to allow simultaneous digestion and adapter ligation, and data generation on the IonTorrent PGM (https://github.com/legalLab/protocols-scripts). In brief, 200 ng of genomic DNA of each sample was digested with SdaI and Csp6I restriction enzymes (ThermoFisher), and the IonTorrent P and A adapters were ligated to the digested fragments, all in one step. The fragments were enriched via PCR; the A adapter contains a unique molecular barcode for identification of individuals and is a divergent “Y” adapter to ensure that only fragments with one P1 and one A adapter are enriched. DNA fragments in the range of 320 to 400 bp were selected using the Pippin Prep (Sage Science), owing to the ability of the IonTorrent PGM to sequence fragments up to 400 bp. The ddRADseq library was sequenced on an Ion Torrent PGM (ThermoFisher) using the 400-bp PGI 318 Ion PGM sequencing kit following manufacturers’ recommendations.

3.2.3 POPULATION ANALYSIS - DATA PREPARATION

To assess how bald uakaris are structured and how sensitive are the population analysis to different parameter settings, I used the denovo pipeline of the program STACKS v.2.4 (Catchen et al. 2011, 2013; Rochette et al. 2019) to analyse the ddRAD data. The first STACKS component I used was the “process_ratags”, which is called to clean and filter the raw reads, check and handle the barcode and restriction enzyme, and to trim the reads to a particular size. I used FastQC v0.11.8 (Andrews 2018) for the quality control of the raw sequences. I trimmed the raw sequences to 100bp using the component “process_radtags” (Figure 3.2). This step is especially important for reads of different lengths such as those produced by Ion Torrent processor and allowed to include in the analysis the highest quality reads.

After that, the core component “ustacks” build the loci within each sample through the parameter “*m*” (Minimum number of raw reads required to form a stack – a putative allele) and “*M*” (Number of mismatches allowed between stacks to merge them into a putative locus). The next step is the use of the component “cstacks” to build a catalogue of loci that represents the homologous loci across all population samples, and the parameter “*n*” will determine the number of mismatches allowed between stacks during the construction of the catalogue. By setting these parameters to different values, it is possible to test the best ones to use the maximum number of reads, but reducing the possibility of building artefactual loci; therefore, considering the effect of the genetic variation or sequencing errors to identify the putative orthologous loci, but being strict enough to distinguish the paralogous loci (Paris et al. 2017; Rochette and Catchen 2017). STACKS provide a pipeline to run each of the components individually, the denovo_map.pl program. For the parameter optimisation, I run the denovo_map.pl setting the same value of *M* and *n*, ranging from 1 to 8 (Figure 3.2). Also, I kept the *m* value set to 3, which is a recommended value for different datasets (Rochette and Catchen 2017).

Finally, I used the component “Population” to filter and to include in the analysis only the number of loci and variant sites (SNPs) present in a specific frequency in the dataset. Specifically, I tested two parameters. The first, “*-r*”, is the minimum percentage of individuals in a population required to process a locus for that population. Considering that the total number of individuals (N=28), and that I want to test how the populations of bald uakaris are structured, I did not assign a putative origin for the individuals. Therefore, I set the -r parameter for three values: 0.50, 0.65, and 0.80 – which means that I recovered only those loci present in at least 50% (i.e. N=14), 65% (i.e. N=18), and 80% (i.e. N=22) of the individuals sampled, respectively (Figure 3.2).

The second parameter tested was the "--*min_maf*", which specify a minimum minor allele frequency required to process a nucleotide site at a locus. The minor allele frequency can strongly influence the inference of the population structure depending on the threshold used to incorporate the genetic variants (Linck and Battey 2019). Accordingly, the relative frequency of an allele will reflect the underlying evolutionary processes (e.g. bottlenecks, population subdivision, gene flow, mutation rate), in a population. Therefore, I tested the --*min_maf* parameter for three values: 0.01, 0.03, and 0.05 (Figure 3.2). I use the filtering option "--*write_single_snp*" to restrict the population analysis to only one SNP per locus, avoiding linkage between SNPs.

3.2.4 POPULATION ANALYSIS

I used two methods to detect the population structure – a nonparametric and a parametric (Figure 3.2). For the first, I run the multivariate Principal Component Analysis (PCA), which is used to identify, summarise, and represent the genetic variation among populations (Martin et al. 2017; Upadhyay et al. 2017; Steely et al. 2017; Baiz et al. 2019; Gauch et al. 2019; Montero et al. 2019). I used the package Adegenet version 2.1.1 (Jombart 2008) to perform the Principal Component Analysis for each filtering combination described above (Table 3-1). Although the PCA is widely used to assess the genetic variation and population stratification, it is not a model-based approach and, therefore, is useful as an exploratory analysis.

I used Structure v. 2.3.4 to infers the population structure (K) and assign individuals to populations based on Bayesian Clustering Approach. The underlying assumptions of Structure are the Hardy-Weinberg equilibrium within populations and the linkage equilibrium between loci within populations (Pritchard et al. 2000), although a linkage disequilibrium within admixture population was later incorporated in the model (Falush et al. 2003). Structure uses a Bayesian iterative algorithm to analyse the differences in the distribution of genetic variants amongst a set of populations. The individuals who share a similar pattern of variation are placed in the same group (K). I used the "admixture" ancestry mode. This model considers that individuals can bring genetic information from ancestors from different populations. It is expected that closely related populations have similar allele frequencies; hence, the *correlated allele frequency* model, which is recommended to detect distinct structure in those population with recent shared ancestry. The parameters were set to a length of 100,000 MCMC (Monte Carlo Markovian Chain) steps for each of K values (1 to 5), a "burnin" period of 100,000. The analysis was repeated ten times to get consistency in the estimates of the ancestry membership proportions of each population. I processed the raw output in Structure Harvester 0.6.94 to estimate the number of clusters (K) based on the method described by Evanno et al. (2005). However, I used the package Pophelper 2.2.9 to analyse and visualise the population structure in the same workflow. Therefore, I called the program CLUMPP 1.1.2 using the function *clumppExport* to summarise the ten independent runs and to generate the aligned and merged files. I performed all analyses in R version 3.6.1

3.2.6 PHYLOGENETIC RECONSTRUCTION

After trimming the raw sequences to 100bp using the component "process_radtags", I used the IPYRAD v 0.7.30 software pipeline (Eaton 2014, https://github.com/dereneaton/ipyrad) to identify the orthologous sequences for the phylogenetic reconstruction. Following the protocol proposed by Valencia et al. (2018), I compared the "denovo" and "reference" assembly pipelines, using the genome sequence of *Pithecia pithecia* as reference (Figure 3.2). (*Pithecia*(*Chiropotes*+*Cacajao*)) comprise the Pitheciinae; therefore, *Pithecia* is the closest related taxa with whole-genome sequence available.

I also tested how different values of "clustering threshold" and "minimum samples per locus" parameters affected the recovery of loci and SNPs and, ultimately, the phylogenetic inference (Figure 3.2). The clustering threshold parameter specifies the level of similarity for two sequences to be considered as homologous (Eaton, 2014). If this value is set too low, non-homologous sequences will cluster together; but if the value is set too high, any polymorphism will hamper homologous sequences to cluster together (Eaton 2014; Valencia et al. 2018). The “minimum samples per locus” parameter specifies the minimum number of samples required to retain a locus in the final dataset. If this value is set too high, the number of loci will decrease, as loci from divergent sequences probably will not be shared. However, if set too low any locus present in a few samples will be retained, and the final matrix will contain a higher number of missing data. Therefore, aiming to maximise the recovery of loci and test how the parametrisation influences the phylogenetic inference, I combine different “cluster threshold” (0.80, 0.85, 0.90, 0.95) and “minimum samples per locus” values (5, 10, 15, 31, 46) (Figure 3.2).

I used the program IQTree (Nguyen et al. 2015) as implemented in CIPRES Science Gateway V. 3.3 (Miller et al. 2010) for the maximum likelihood phylogenetic inference. I used the algorithm ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQTree to select the best substitution model, and the option ultrafast bootstrap approach (UFBoot) (Minh et al. 2013; Hoang et al. 2018) with 1000 bootstrap pseudoreplicates to assess branch support.

3.2.7 MORPHOLOGICAL ANALYSIS OF BALD UAKARIS

I examined 100 vouchers specimens stored in the following scientific collections: Mamirauá Institute for Sustainable Development (IDSM), Instituto Nacional de Pesquisas da Amazônia (INPA), Museu de Zoologia da Universidade de São Paulo (MUZUSP), Museu Paraense Emílio Goeldi (MPEG), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), and Field Museum of Natural History (FMNH) (3.5.3 Material examined (Total 100 vouchers), **Error! Reference source not found.**). I followed the diagnostic characters presented by Hershkovitz (1987a) to identify the pattern of pelage colouration in different populations. Finally, I assessed if the clusters retrieved from in the molecular analysis included only individuals with a unique pattern of pelage colouration; therefore, supporting the monophyly of each taxon presented in the taxonomic revision of Hershkovitz (1987a). For the synonymy of the taxa presented here, I am providing a list of the first use of the names aiming to clarify misidentifications in the literature (3.5 Supplementary Material – Chapter 3). This list, therefore, is not exhaustive but aims to clarify eventual confusions, especially after Hershkovitz (1987a) – the author provided a historical perspective of the names used, especially before the 1980s.

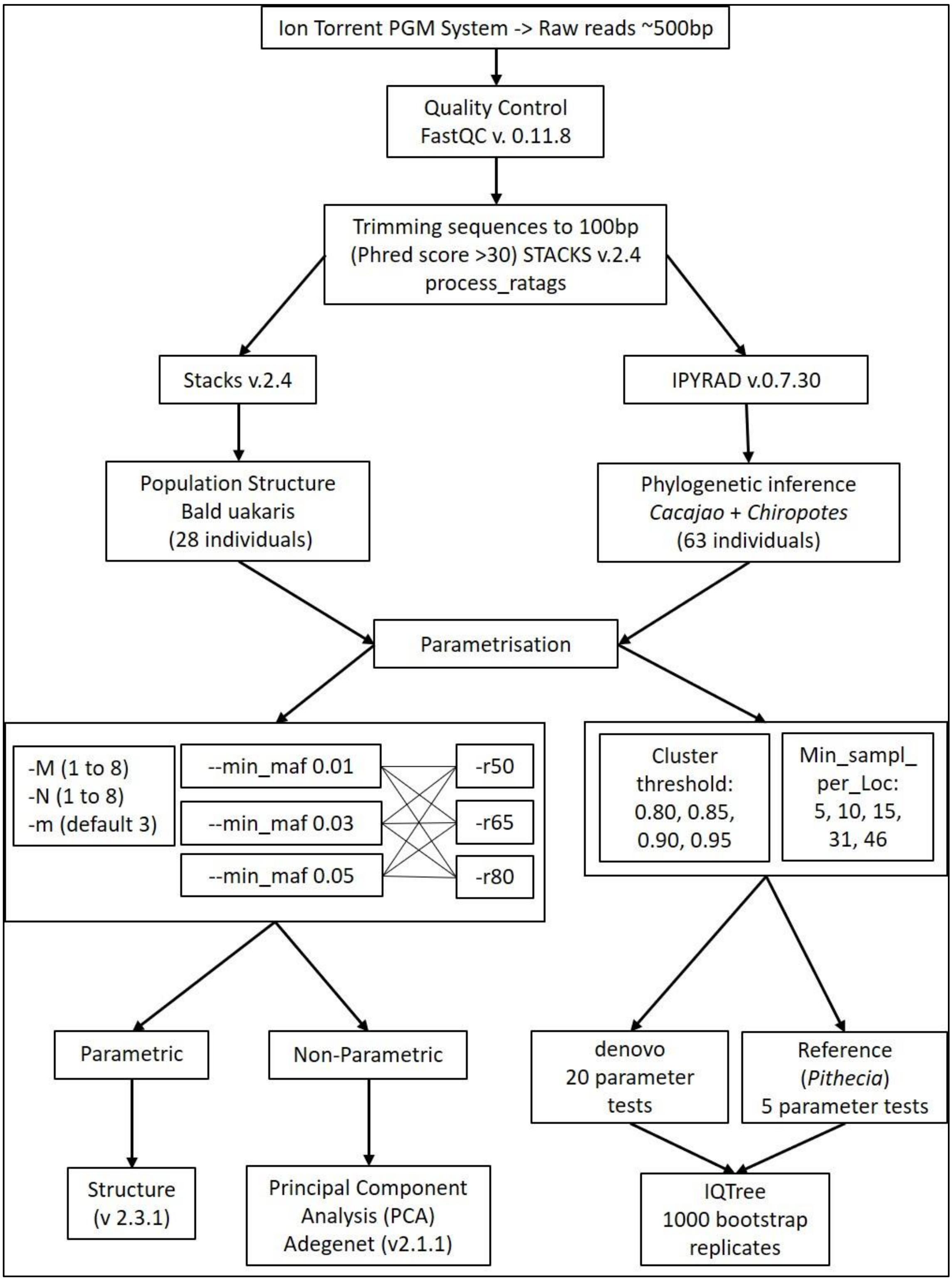

Figure 3.2 The pipeline used in this chapter for the ddRAD data analysis. Explanations of the parameters are in Methods session.

3.3 RESULTS

3.3.1 STACKS RADSEQ PROCESSING AND SNPS RECOVERING

The number of reads retained after using the process_radtags component considering the 28 bald uakari samples used in the population analysis was 4,741,361. The average of reads kept per sample was 169,334.3, ranging from 70,911 to 373,049. The mean depth coverage was 18.3x, ranging from 11.33x to 23.34x. The number of RAD loci obtained decreased with higher mismatches parameter values (*m* and *n* parameter). Therefore, the more restrictive the parameter setting, the lower was the number of loci retained (Figure 3.3).

However, the number of variant sites (i.e. SNPs) increased sharply from the first parameters values tested, reaching a plateau in *M=3* and *n=3* (Figure 3.4). Thus, I did all the subsequent analysis (filtering, Structure, and PCA) using these parameter values (*M=3* and *n=3*), which recovered 39,969 loci. The number of SNPs retained after the filtering steps varied markedly depending on the percentage of individuals required to process a locus (-*r* parameter) and on the minimum minor allele frequency specified (*min_maf* parameter) (Table *3-1* The number of SNPs (variant sites) recovered according to the mismatch value allowed between stacks to merge them into a putative locus (M parameter) and to include them in the catalogue loci (n parameter).Table 3-1). In the more relaxed parameter setting (-*r* 50%, *min_maf* 0.01) I got 1,982 SNPs, while in the more stringent option (-*r* 80%, *min_maf* 0.05) only 269 SNPs were retained (Table *3-1* The number of SNPs (variant sites) recovered according to the mismatch value allowed between stacks to merge them into a putative locus (M parameter) and to include them in the catalogue loci (n parameter).Table 3-1).

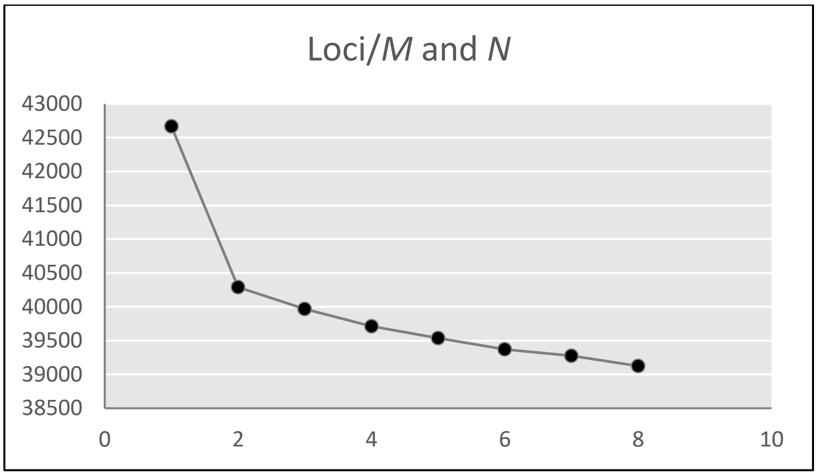

Figure 3.3 The number of loci recovered according to the mismatch value allowed between stacks to merge them into a putative locus (M parameter) and to include them in the catalogue loci (n parameter).

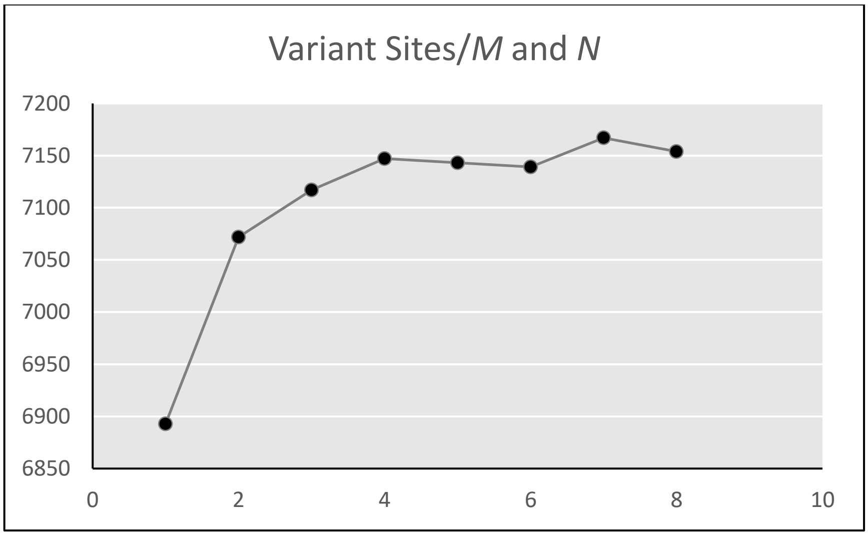

Figure 3.4 The number of SNPs (variant sites) recovered according to the mismatch value allowed between stacks to merge them into a putative locus (M parameter) and to include them in the catalogue loci (n parameter).

Table 3-1 The number of SNPs (variant sites) recovered according to the mismatch value allowed between stacks to merge them into a putative locus (M parameter) and to include them in the catalogue loci (n parameter).

Min samples/locus (-r) (%)	min_maf	Total Loci	Removed Loci	Kept loci	Total sites (from those loci kept)	Filtered	variant sites
50	0.01	39969	35006	4963	499769	53	1982
50	0.03	39969	35006	4963	499769	719	1640
50	0.05	39969	35006	4963	499769	1090	1402
65	0.01	39969	37336	2633	265274	66	1172
65	0.03	39969	37336	2633	265274	597	907
65	0.05	39969	37336	2633	265274	788	787
80	0.01	39969	39062	907	91496	32	446
80	0.03	39969	39062	907	91496	266	339
80	0.05	39969	39062	907	91496	376	269

3.3.2 Parametrisation and the population structure

Both nonparametric and parametric analyses were consistent in revealing two main genetically distinct groups of bald uakaris. The first includes the white bald uakaris, subspecies *calvus* from Solimões/Jutaí/Juruá rivers; and the second consists of the three subspecies of red bald uakaris, *ucayalii* from upper Juruá; *novaesi* from the left bank of Tarauacá River, and *rubicundus* from Solimões/Jutaí rivers (Figure 3.5, Figure 3.6, Figure 3.7; Supplementary Material

3.5.1 Parametrisation – STACKS). However, these two approaches differ in how they represented the difference within each of these two groups (white and red uakaris). Also, for both methods, the intermediate parameters settings make more sense in representing the population characteristics of bald uakaris when we compare them to the extremely lower and higher values tested here (Supplementary Material

3.5.1 Parametrisation – STACKS). Thus, I am considering the most accurate those analyses based on -*r* parameter of 0.65, which means that only those loci present in at least 65% (i.e. N=18) of the individuals were kept in the analyses; and the --*min_maf* parameter of 0.03, which specify a minimum minor allele frequency of 3% required to process a nucleotide site at a locus (Figure 3.5, Figure 3.6, Figure 3.7; Supplementary Material

3.5.1 Parametrisation – STACKS).

3.3.3 STRUCTURE ANALYSIS

The Bayesian clustering approach to infer the population structure (K) and assign individuals to populations were consistent for all parameter settings. Mean likelihood (-11897.98, Stdev=23.15), and the Evanno method (ΔK= 86.9896) indicated K=3, closely followed by K=2 (3.5.1 Parametrisation – STACKS) as the best explanation for the number of clusters in this dataset. When K=2 is assumed, one cluster corresponds to the white uakaris and the other to the red ones. When K=3 is considered, red uakaris continues to be represented in one cluster, while the white uakaris are represented by two – one for individuals from the upper Juruá and the other for those individuals from low Jutaí River. Interestingly, the white uakaris from the north (left) bank of the Solimões River present an evident admixture between these two populations (Figure 3.5, Figure 3.6).

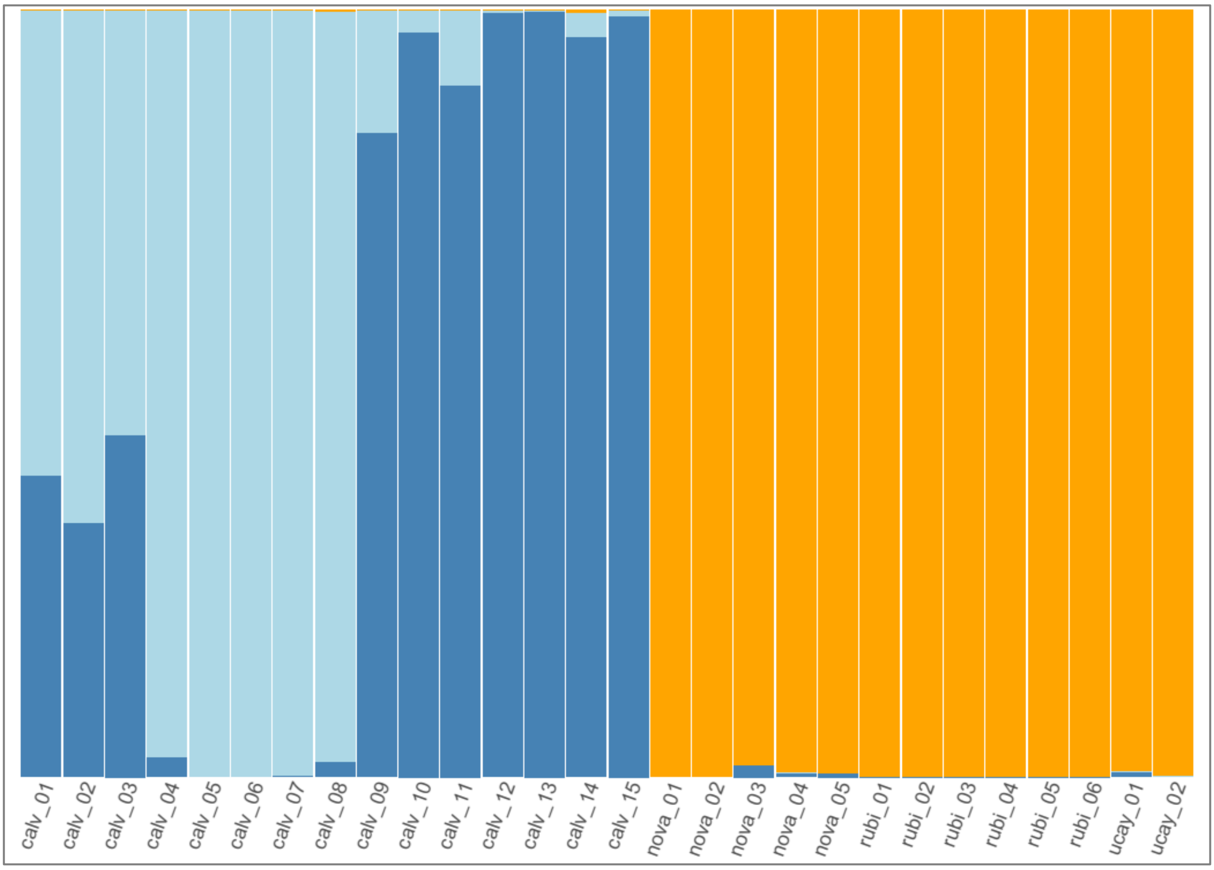

Figure 3.5 Genetic structure of bald uakaris inferred from the “structure” dataset considering –r 0.65 and min_maf 0.03 parameters. Blue bars = white uakaris; Yellow bars = red uakaris. Sample ID provided in Supplementary Material.

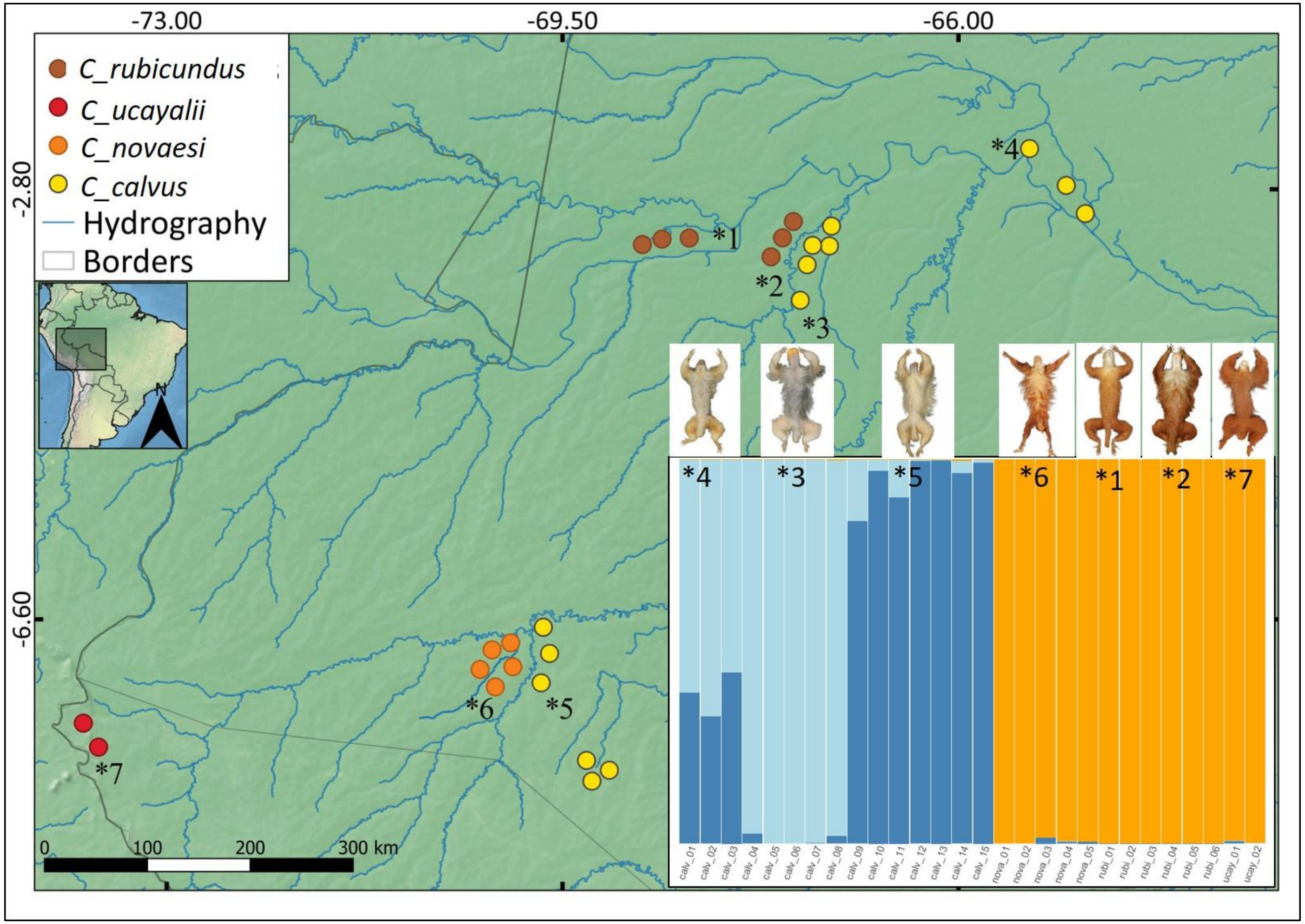

Figure 3.6 Genetic structure of bald uakaris and the population localities. *1 – Jacurapá Channel; *2 – left bank of Jutaí River; *3 – right bank of Jutaí River; *4 – Mamirauá SDR; *5 – right bank of Tarauacá River; *6 – left bank of Tarauacá River; *7 – Serra do Divisor National Park.

3.3.4 PCA ANALYSIS

The PCA analysis emphasises the same two main genetically differentiable groups: red and white uakaris. However, except by the more relaxed parameter setting (-r 0.50, min_maf 0.01), the nonparametric approach also distinguishes a substructure within each of these groups (Figure 3.7, **Error! Reference source not found.**). For the red bald uakaris, the central split occurs between "*novaesi*" and "*rubicundus+ucayalii*". This distinction is more evident in the intermediate parameters settings and became overshadowed in the extremely lower and higher values tested here. For the white bald uakaris, the same distinction is apparent between the populations from the upper Juruá River and lower Jutaí River. Here again, the population of white uakaris from the north bank of Solimões (i.e. the flooded forests of Mamirauá Sustainable Development Reserve – SDR Mamirauá) is an intermediate between that from upper Juruá River and that from lower Jutaí River (Figure 3.7).

3.3.5 PHYLOGENETIC INFERENCE

The 62 samples used for the IPYRAD phylogenetic inference had an average of 203,789 of raw reads. The final number of consensus reads, clusters (stacks) retained, and loci assembled varied depending on the filtering parameters and on the assembly pipeline (Table 3-2). The more stringent the cluster threshold parameter in the denovo pipeline, the higher the number of consensus reads (Figure 3.8), and clusters retained for the analysis (Figure 3.8, Figure 3.9, Table 3-2). As expected, the average number of loci assembled and variant sites (SNPs) markedly decreased when we set the minimum samples per locus parameter to higher values, especially >50% (Figure 3.10, Figure 3.11, Table 3-2).

A total of 25 consensus trees were reconstructed using the concatenated ddRAD data alignment, twenty from the denovo assembly parametrisation and five from the reference one. Four main *Cacajao* clades were consistently retrieved with

100% bootstrap support for all parameters tested: two for bald uakaris, two for black uakaris (Figure 3.12). However, the topology within these four clades was sensitive to the parametrisation. The setting of the “minimum samples per locus” to higher values (e.g. 31 or 46) and the “cluster threshold” to a more permissive percentage (e.g. 80% or 85%) influenced the number of loci assembled and the number of SNPs retained for the analysis. Consequently, it caused a loss of resolution and lower overall support within these four main clades. The tree with higher global support and resolution was retrieved using denovo pipeline, setting the “minimum samples per locus” to 10 and the “cluster threshold” to 90% (Figure 3.12).

Therefore, there are distinct clusters within the four main clades, which are consistent with their geographical location and, in some cases, with an identifiable phenotypic pattern. For the white uakaris (*calvus*), the primary division occurs between individuals from upper Juruá River and those from low Jutaí and middle Solimões River. These later also separated into two clades, which represent the population from North (Mamirauá SDR) and South (Rio Jutaí Extractive Reserve) of Solimões River (Figure 3.12). The red uakaris are organised into three main clades, which are consistent with the subspecies classification. The main split with 100% of bootstrap support occurs between *novaesi* and the clade that includes *rubicundus* and *ucayalii* (Figure 3.12). Similarly to white uakaris, the two clades of *rubicundus* represent the population from North (Jacurapá channel) and South (Jutaí-Solimões Ecological Station) of Solimões River. *Cacajao ucayalii* is a sister group of *rubicundus*, although I only included two individuals from the Divisor National Park in the analysis. Therefore, more individuals from the Peruvian population would clarify this relationship. Two main clusters in *melanocephalus* separate the individuals from middle Japurá River (codes CTAGM 756, 757, 775) to those from Amanã Reserve for Sustainable Development (Amanã SDR) and Negro River (Figure 3.12). These two population (Amanã SDR and Negro River) also separated in small clades, although with low bootstrap support (55%) (Figure 3.12). Finally, the clade involving the black uakaris from the north (left) bank of Negro River presents a clear separation between *ayresi* and *hosomi* (sensu Boubli et al. 2008) with 100% of support (Figure 3.12)..

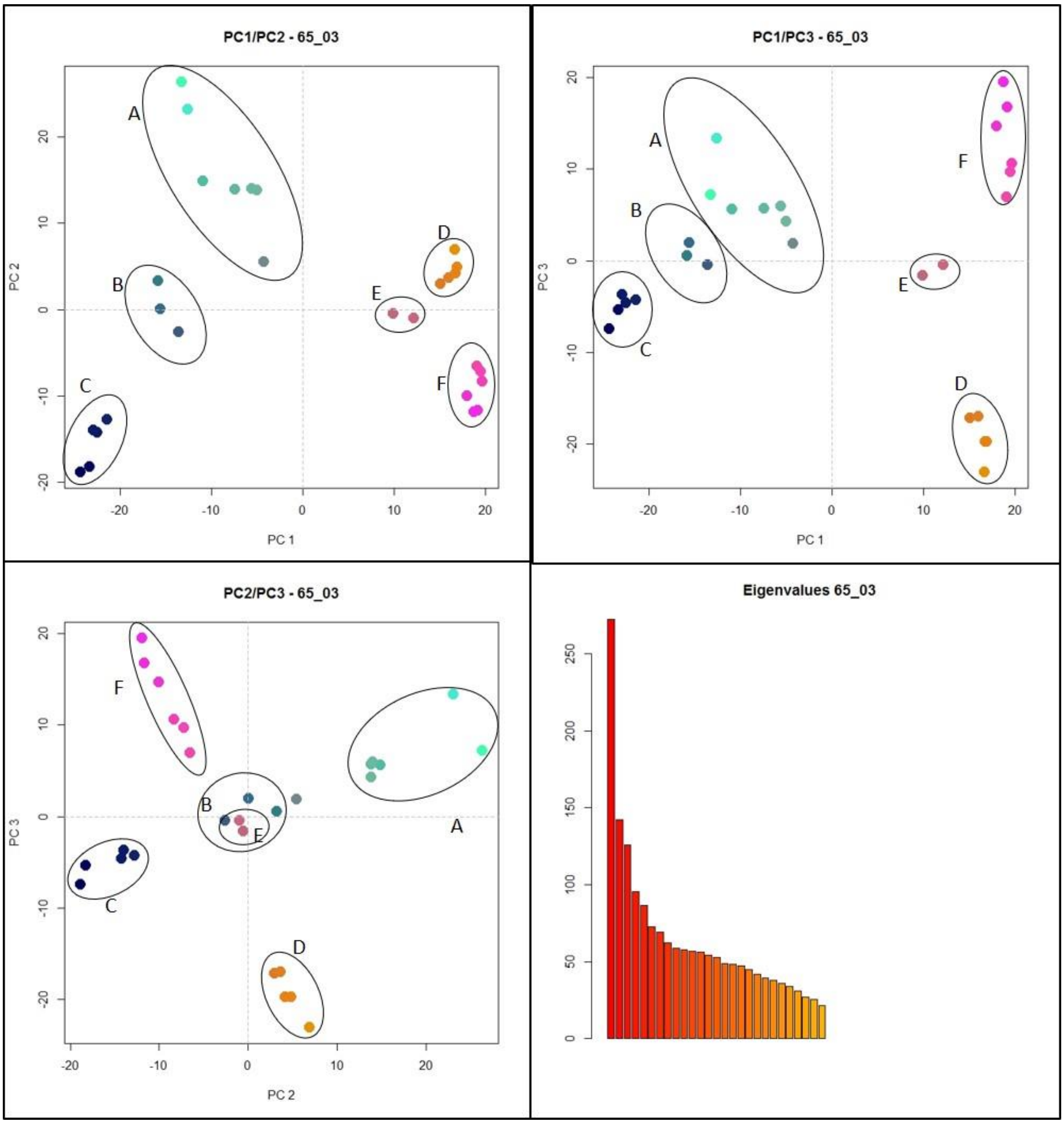

Figure 3.7 Principal Component Analysis. The colour groups correspond to the following populations: A) *calvus* from upper Juruá River; B) *calvus* from the north bank of Solimões River (Mamirauá SDR); C) *calvus* from Jutaí River; D) *rubicundus*; E) *ucayalii*; F) *novaesi*. Parameter settings: -r 0.65, min_maf 0.03.

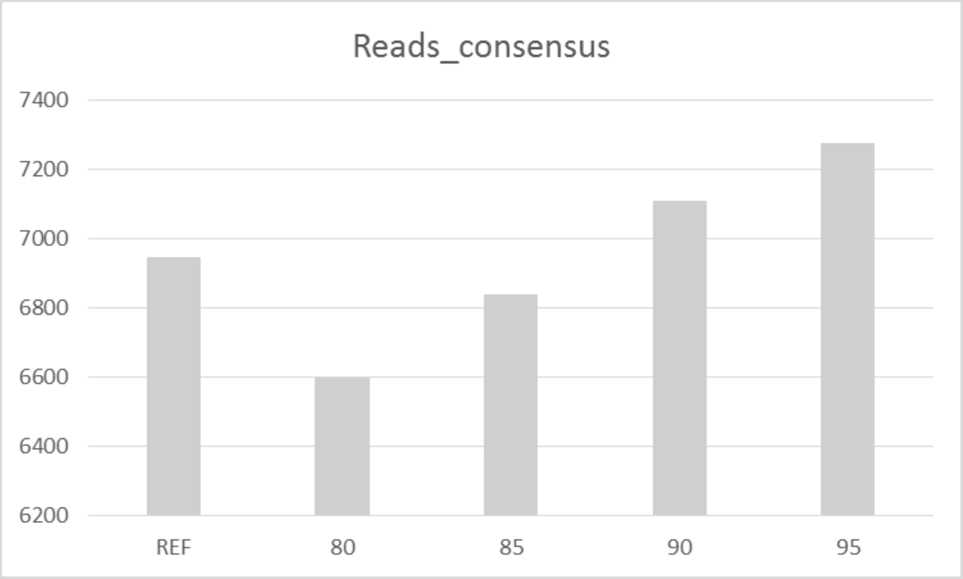

Figure 3.8 Average number of consensus reads per sample for the Reference and denovo assembly. The consensus reads are shown under different “cluster threshold” values in denovo assembly.

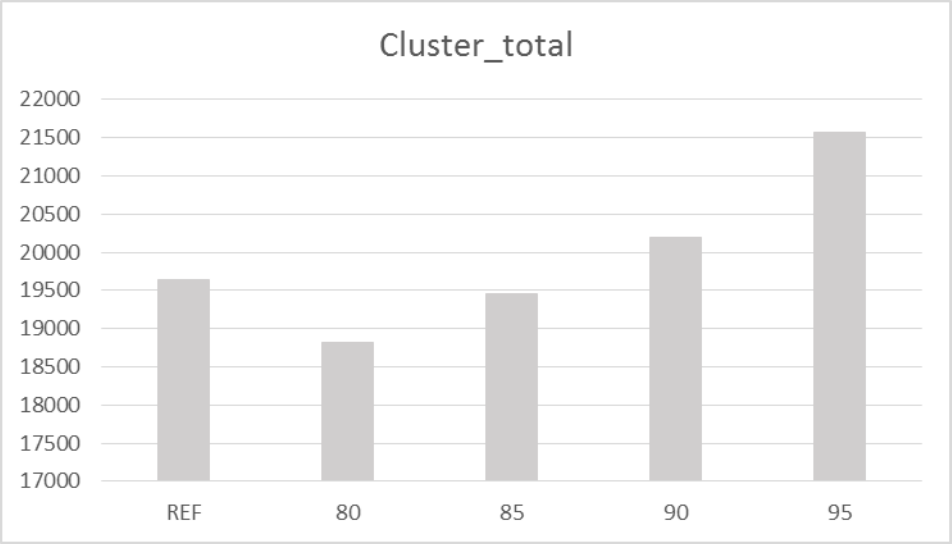

Figure 3.9 Average number of clusters (stacks) per sample for the Reference and denovo assembly. The consensus reads are shown under different “cluster threshold” values in denovo assembly.

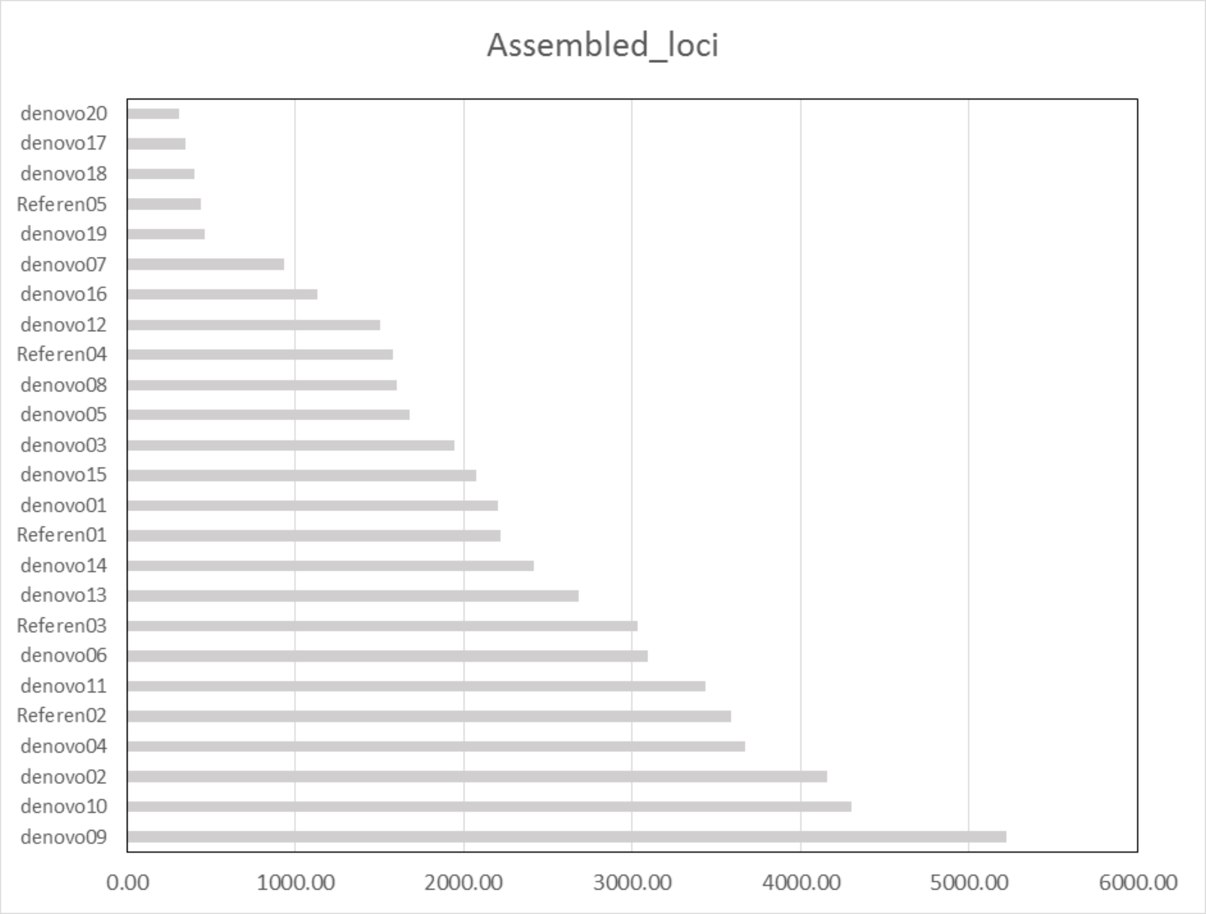

Figure 3.10 Number of loci assembled according to different parameter setting for Reference and denovo assembly. Parameter settings specified in table 3-2.

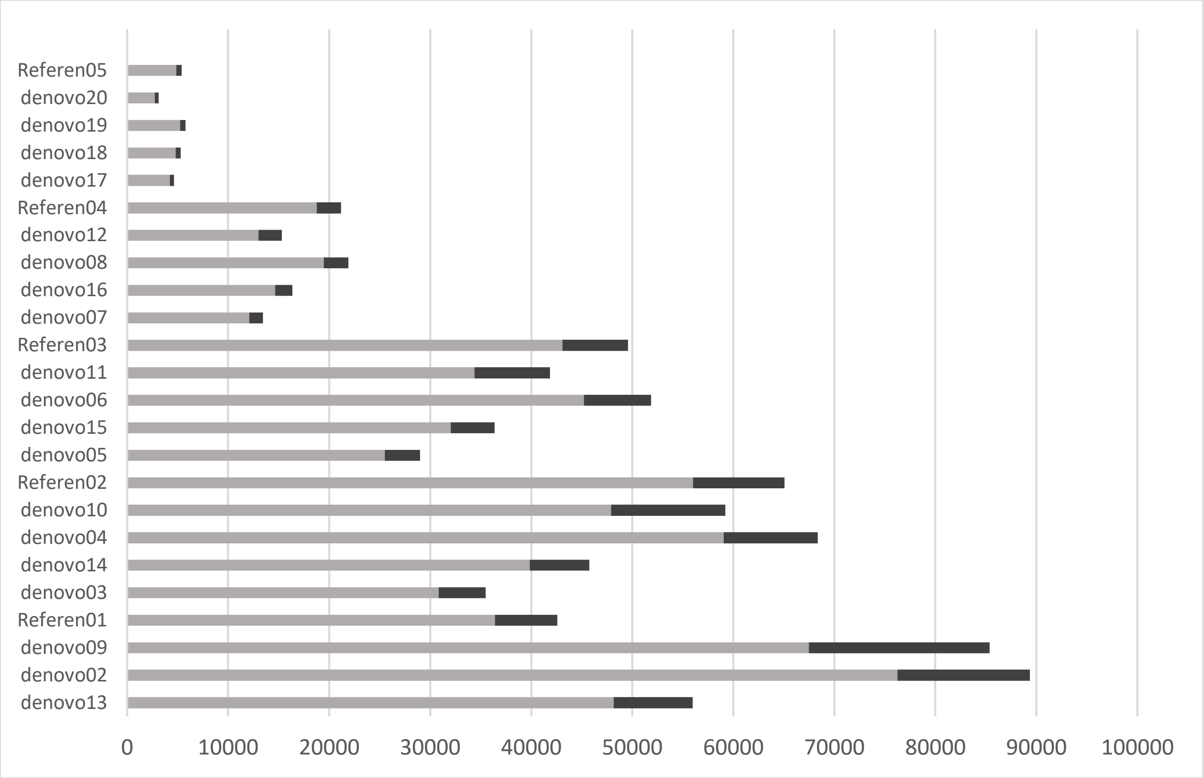

Figure 3.11 Number of variant sites (light grey) assembled according to different parameter setting for Reference and denovo assembly. Parameter settings specified in table 3-2. Dark grey is the number of single SNP per locus for each assembly parameter.

Table 3-2 Parametrisation and the loci and SNPs (variant sites) recovering in IPYRAD for different assembly pipelines. In bold is the parameter settings used to recover a phylogenomic tree with better overall support (see Figure 3.12).

Assembly	*Code*	Min samples per locus	Cluster Threshold (%)	Concatenated matrix (bp)	Variant sites (bp)	Unique SNPs	Assembled loci
denovo	denovo02	5	80	789681	37916	6707	2206
denovo	denovo03	10	80	501879	30817	4652	1943
denovo	denovo04	15	80	364040	25514	3469	1675
denovo	denovo05	31	80	140272	12084	1367	932
denovo	denovo06	46	80	42290	4210	413	351
denovo	denovo07	5	85	881053	48161	7804	2678
denovo	denovo08	10	85	631603	39862	5893	2416
denovo	denovo09	15	85	453245	32047	4332	2072
denovo	denovo10	31	85	172738	14656	1685	1134
denovo	denovo11	46	85	48895	4808	478	404
denovo	denovo12	5	90	1458024	76262	13111	4160
denovo	denovo13	**10**	**90**	**993569**	**59051**	**9307**	**3667**
denovo	denovo14	15	90	693193	45218	6632	3093
denovo	denovo15	31	90	250321	19452	2439	1602
denovo	denovo16	46	90	57098	5224	559	465
denovo	denovo17	5	95	2105239	67461	17904	5219
denovo	denovo18	10	95	1252965	47894	11308	4301
denovo	denovo19	15	95	803551	34391	7474	3437
denovo	denovo20	31	95	241115	12982	2326	1507
denovo	denovo21	46	95	38780	2739	381	313
Reference	REF01	5	x	708905	36392	6179	2214
Reference	REF02	10	x	967197	55996	9057	3584
Reference	REF03	15	x	677334	43078	6487	3030
Reference	REF04	31	x	247704	18748	2418	1581
Reference	REF05	46	x	54469	4853	533	442

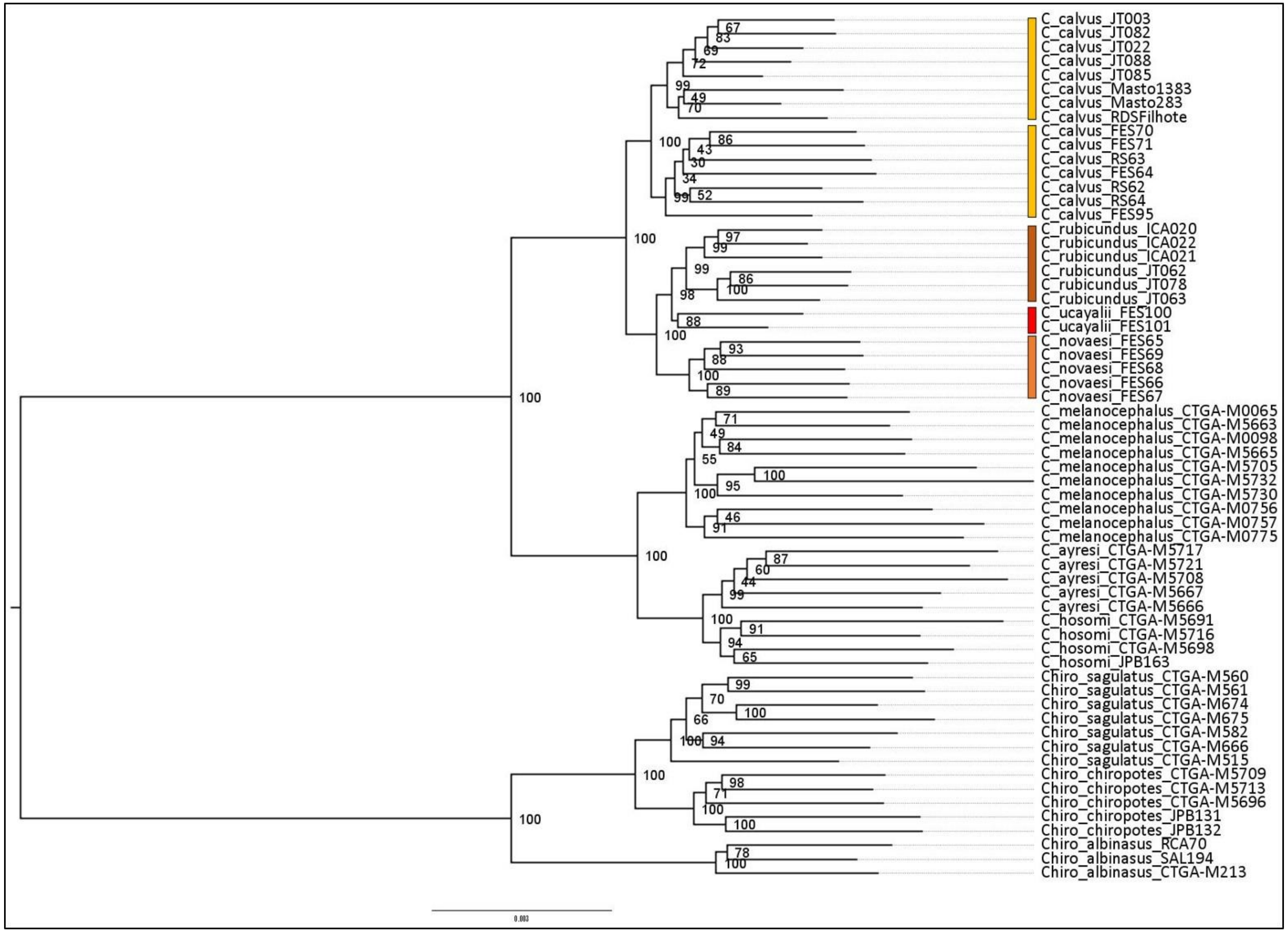

Figure 3.12 IQTree Maximum likelihood tree inferred using “minimum samples per locus” = 10, and “cluster threshold” = 0.90. The details on the parameter sets are provided in Table 3-2.

3.3.6 Shades of uakaris - the number of bald uakaris species

When Tomas (1928) reported the red uakaris from the Ucayali River basin as a new taxon, only two species were recognised: the white uakaris, *Cacajao calvus* (Geoffroy, 1847) and *Cacajao rubicundus* (Geoffroy and Deville, 1848). The author emphasized the overall reddish pelage colouration of the Peruvian populations – without the contrasting whitish or pale yellowish pelage colouration in the nape, which is found in *C. rubicundus*. The author, however, proposed the new form as a subspecies, *Cacajao rubicundus ucayalii*, apparently suggesting a putative intergradation zone between the Peruvian and Brazilian red uakaris:

The discovery of a member of the remarkable genus Cacajao on the Ucayali is of much interest, as the genus had been supposed to have a very restricted distribution in the Teffe-Tonantins region of the Middle Amazon while the Ucayali is a very long way further up the river. The character of the country is, however, of a sufficiently uniform nature to make it not improbable that examples of the red Uacari will be found in the intervening districts, and I therefore do not distinguish this animal as a separate species.

The Museum has recently received from Herr Ehrhardt two excellent specimens of C. rubicundus from the Auty-Parana, close to Fonte Boa, precisely agreeing with the various figures and descriptions of that animal, while the present three skins are uniformly distinguished by the characters above indicated. (Thomas, 1928, p. 253)

I did not examine the "two excellent specimens of *C. rubicundus* from the Auty-Parana" that Thomas mentioned. However, I did analyse an adult male and an adult female collected in the 1980s in the same locality, Auati-Paraná channel (Figure 3.21). These skins differ from those from Jutaí and Içá rivers by the pale yellowish or whitish dorsum from the nape to the mid-back in the females and tail in adult males. Hershkovitz (1987a) recognized this different pattern and the fact that this population is completely isolated from those populations from Jutaí and Içá rivers:

A total of 8 specimens from Auati-Paraná *range in coloration from nearly uniformly reddish orange except for pale buffy nuchal whorl and small of back, to pale orange or buffy on entire dorsum as in extremely saturate samples of C. c. calvus. Most of the wholly reddish uacaries seen by me in zoos or laboratories or figured in recent publications are actually the*

Peruvian Cacajao calvus ucayalii Thomas. Until recently, all reddish uacaries including ucayalii were identified as C. rubicundus and regarded as specifically distinct from C. calvus (Hershkovitz, 1987a, p. 37).

Another seeming anomaly is that the Auati-Paraná rubicundus are widely separated from their nearest relatives in the area between the lower Rio Ica and Solimões. Until the problem can be resolved, perhaps by closer scrutiny of available data or possibly with more material, the Auati-Paraná *series is regarded as intermediate between calvus and rubicundus but with the Auati-Paraná region tentatively excluded from the range of either subspecies* (Hershkovitz, 1987a, p. 36).

The disjunct distribution in *Cacajao* was unclear when Hershkovitz (1987a) reviewed its taxonomic classification of the genus. The author suggested the existence of a secondary contact zone and intergradation between *calvus* and *rubicundus* and reinforced his proposal for all bald uakaris classified at the subspecies level (Hershkovitz 1972, 1987a). Unfortunately, I did not get any sample from Auati-Paraná channel. Thus, I could not test if there is any gene flow between the populations of white (*calvus*) and red (*rubicundus*) from that region, and how those populations are related to the others included in the analysis present here.

According to the molecular analysis and the examination of the pattern of pelage colouration, the four subspecies considered by Hershkovitz (1987a) are monophyletic and include only individuals with a consistent pattern of pelage colouration, which are considered as diagnostic characters. Therefore, under the Phylogenetic Species Concept (monophyly+diagnosability), they can be classified at the species level. The phylogenomic analysis was also sensitive to retrieve the population level structure in two taxa: *C. rubicundus* and *C. calvus* (Figure 3.13). These populations also have a pattern of pelage colouration that varies geographically (Figure 3.13). Although the white uakaris from Tarauacá River form a distinct and monophyletic group (similar relationship to *C. novaesi* x *C. ucayalii* + *C. rubicundus*; or *C. hosomi* x *C. ayresi*), I consider premature to name them as a new taxon without examining additional specimens to identify the putative diagnostic characters that could support this decision. For example, an analysis including the white uakaris from middle Juruá River (Peres 1988, 1990, 1997) is essential to investigate the genetic structure of the populations from Juruá, Tarauacá, and Jutaí rivers.

The black uakaris follow a similar pattern in the phylogenomic analysis; however, I did not analyse its population structure. The species proposed by Boubli et al. (2008) – *C. hosomi* and *C. ayresi* – are well structured in two monophyletic clades with 100% of bootstrap support. Similarly, the *C. melanocephalus* from upper Japurá River is an offshoot of the clade that includes those population from lower Japurá and Negro rivers. This structure is consistent throughout *Cacajao* tree, with monophyletic groups including only individuals with a similar pattern of pelage colouration that were used as diagnostic characters. Below, I present my considerations for the taxonomic classification of bald uakaris.

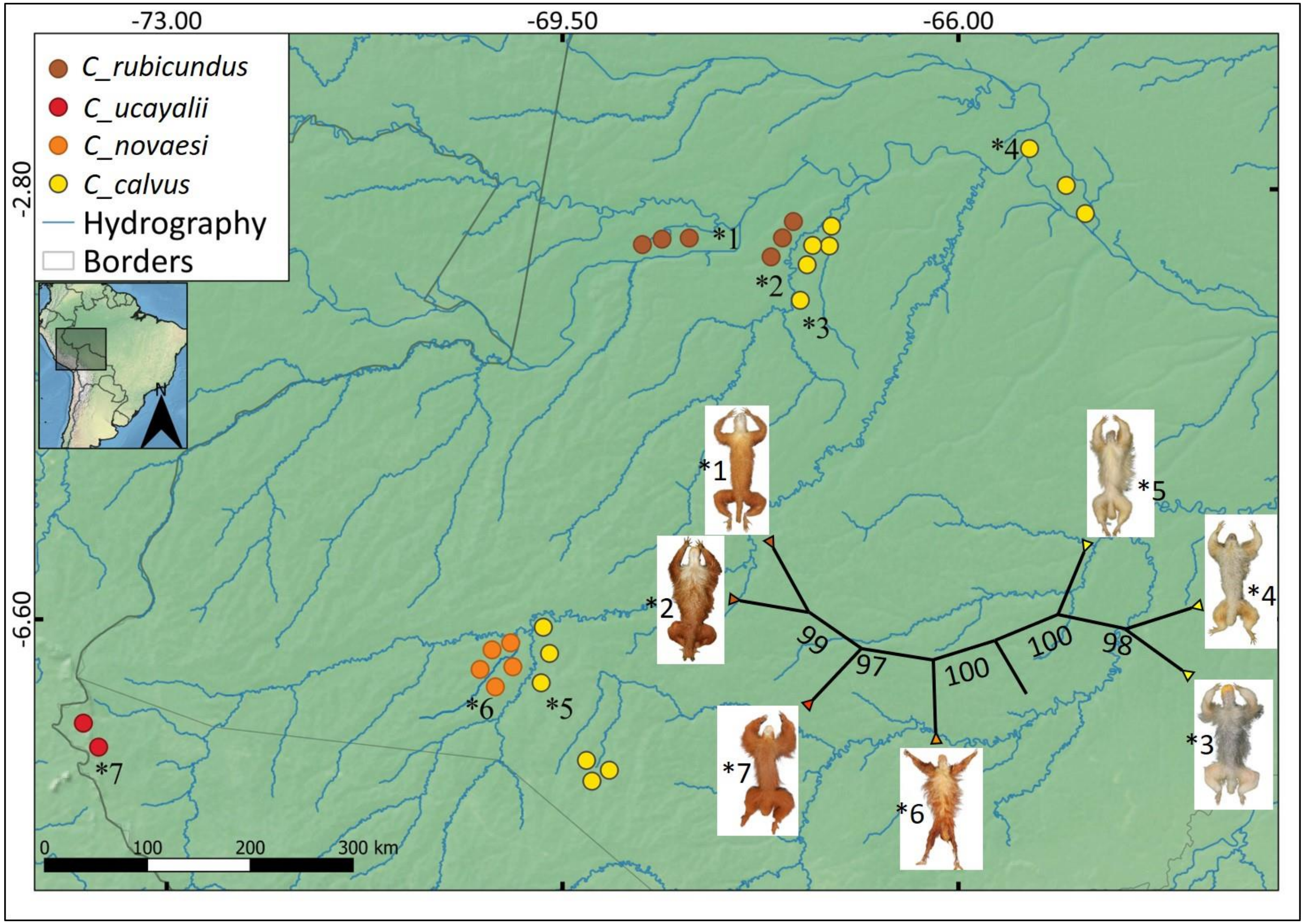

Figure 3.13 The unrooted tree of bald uakaris retrieved from the ddRAD dataset. Numbers in the nodes represent bootstrap support (%). The vouchers are representatives of each population included in the analysis: *1 – Jacurapá Channel; *2 – left bank of Jutaí River; *3 – right bank of Jutaí River; *4 – Mamirauá SDR; *5 – right bank of Tarauacá River; *6 – left bank of Tarauacá River; *7 – Serra do Divisor National Park.

2.3.6.1 *Cacajao calvus* (I. Geoffroy, 1847) – White bald uakari

Holotype

The individual considered the holotype is an adult male stored in the mammal collection of the Museum National d'Histoire Naturelle, Paris – Catalogue number MO-1997-1591 (http://coldb.mnhn.fr/catalognumber/mnhn/zm/mo-1997-1591).

On the type locality of Cacajao calvus (I. Geoffroy, 1847)

The precise location is unknown. The holotype was a donation by M. D'Alcantara Lisboa in 1807, and the origin of this specimen was considered as "Pará" (Geoffroy 1851, p 57). Castelnau and Deville sent four other specimens which Geoffroy (1852) mentioned:

"It is Para, as I said above, that the type of this species has come. The individuals whom the Museum received a few months later from MM. from Castelnau and Deville, come from Peru, Haut-Amazon, near Fonteboa. In spite of the difference of the localities, the same characters are found almost exactly in all." (Geoffroy 1852 p. 564).

Hershkovitz (1987) mentioned:

"Para" where the species does not occur; the Castelnau Expedition specimens recorded by I. Geoffroy (1852, p. 560) are from the vicinity of Fonte Boa but must have originated on the left bank of the Solimões opposite Fonte Boa. This has generally been regarded as the type locality and is here so restricted. (Hershkovitz 1987a p. 44)

The region mentioned above falls within the Mamirauá SDR, nearby the Paraná do Maiana channel, where indeed white uakaris occur (Ayres 1986; Cardoso et al. 2014). Two considerations are important here. First, there is no evidence on the occurrence of uakari monkeys nearby the mouth of the Juruá River, which is in the same bank of Fonte Boa city – in the south bank of Solimões River. Surveys had been conducted in that region, but uakaris were never reported there (e.g. Cardoso et al. 2014). The specimen considered the holotype probably was collected in the left (north) bank of Solimões, as Hershkovitz (1987a) suggested, and should be nearby the Paraná do Maiana channel. Second, I did not get any sample from this region to include in the molecular analysis, although I did examine the skins of white uakaris from Auati-Paraná and Paraná do Maiana channels (MUZUSP and MNRJ series), which is in the north bank of Solimões, opposite to Fonte Boa. These skins have a pattern of pelage colouration that is slightly different from the other population of white uakaris (see description below).

General Characters

The three populations examined here present a slight variation in the overall pattern of pelage colouration. The series from the north bank of Solimões River include the specimens from the mouth of Japurá River and Auati-Paraná channel, within the Mamirauá Sustainable Development Reserve (Mamirauá SDR). The males present a yellowish and greyish white pattern in the nape, dorsum and sides of the trunk due to the presence of yellowish hairs with terminal portion blackish or with the presence of some sparse greyish hairs (Figure 3.14). This characteristic of the dorsum contrast with the buffy or pale orange pattern of the ventral region, especially in the chest and in the inner parts of the limbs (Figure 3.14). The adult females from Auati-Paraná channel, however, present a variation on this pattern with some individuals with the same contrastingly characteristics and others with a more uniform buffy yellowish or whitish (Figure 3.15). In both males and females, the beard has a darker reddish-brown pattern.

The white uakaris from Jutaí River have a greyish pattern in the nape, dorsum and sides of the trunk contrasting to the whitish (or yellowish-white in some individuals). The remarkable greyish aspect is due to the higher frequency of hairs entirely greyish or blackish interspersed with whitish hairs (but not yellowish as in Mamirauá SDR series) with the terminal portion blackish or greyish (Figure 3.16). The specimens from the Jutaí River series have the ventral region and the inner parts of the limbs with whitish or yellowish-white hairs (Figure 3.16).

Finally, I could identify two different patterns in the specimens from the Juruá and Tarauacá rivers. First, the individuals from Pauini and Tarauacá rivers present a predominantly whitish colouration throughout the dorsum, sides of the trunk, ventral region and limbs with the hairs entirely whitish or whitish with the terminal portion greyish (Figure 3.17). Some individuals have the hairs in the dorsum entirely greyish interspersed with the whitish ones giving a greyish-white aspect, but still in a much lighter tone than the series from Jutaí River series (Figure 3.16, Figure 3.17). The three individuals from Jurupari River also have the whitish pattern throughout the dorsum, sides of the trunk, but with an evident contrast with the yellowish or buffy orange colouration of the inner parts of the limbs (Figure 3.18). Both populations have individuals with the beard in orange to a reddish-brown pattern.

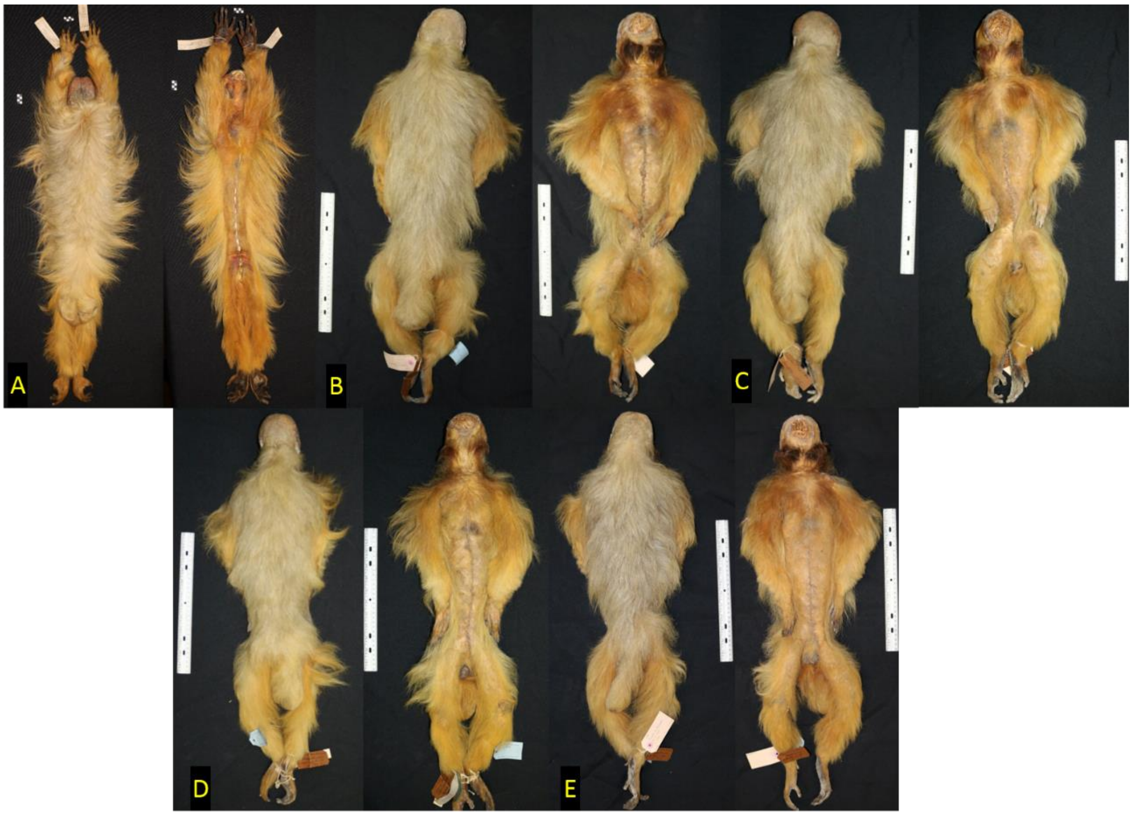

Figure 3.14 Adult males from Mamirauá SDR series. A) MUZUSP 17535, B) MNRJ 1706, C) MNRJ 1705, D) MNRJ 2445, E) MNRJ 1703. See Table I for details.

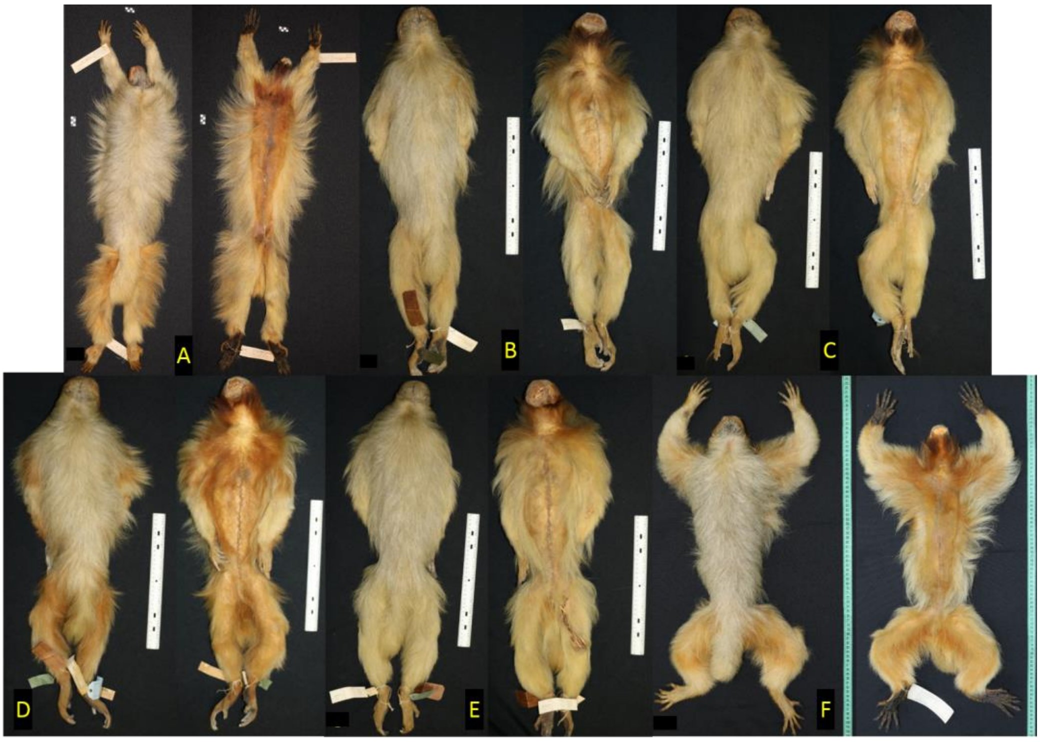

Figure 3.15 Adult females from Mamirauá SDR series. A) MUZUSP 17537, B) MNRJ 2441, C) MNRJ 2442, D) MNRJ 2447, E) MNRJ 2452, F) MNRJ 0283. See Table I for details.

Figure 3.16 The series from Jutaí River. A) Adult male JT090, B) Adult male JT022, C) Subadult male JT088, D) Subadult female JT082. See Table I for details.

Figure 3.17 The series from Tarauacá and Pauini rivers. A) Adult male RS063, B) Adult male FES095, C) Adult female RS064, D) Adult female FES064, E) Adult female FES070, F) Subadult female FES071. See Table I for details.

Figure 3.18 The series from Jurupari River. A) Adult male MPEG 21861, B) Adult female MPEG 21862, C) Adult male MPEG 21863. See Table I for details.

2.3.6.2 *Cacajao rubicundus* (I. Geoffroy and Deville, 1848) – red bald uakari

On the Type series of Cacajao rubicundus

When Geoffroy and Deville (1848) reported the new species of uakari, *Brachyurus rubicundus*, they did not attribute a holotype. Geoffroy (1952) presented a more detailed description of both *B. calvus* and *B. rubicundus* and mentioned that the specimens were sent to the National Museum of Natural History, Paris (NMNH-Paris), by Castelnau and Deville in 1847:

C'est en mars 1847 que ce don précieux nous a été fait, et, en avril, que j'ai fait connaître le Brachyurus calvus. J'étais loin alors de me douter que, dans la même année, le Muséum allait recevoir, par MM. de Castelnau et Deville, une belle suite d'individus de cette espèce, et, avec eux, plusieurs représentants d'une espèce voisine, plus curieuse, ou, pour mieux dire, plus étrange encore, celle qui va être décrite ci-après sous le nom de Brachyurus rubicundus (Geoffroy 1852, p. 561).

It was in March 1847 that this precious gift was sent to us, and in April, that I reported the Brachyurus calvus. I was far from suspecting that in the same year the Museum would receive, by MM. de Castelnau and Deville, a succession of individuals of this species, and with them several representatives of a sister species, which will be described hereinafter under the name of Brachyurus rubicundus (Geoffroy 1852, p. 561).

Hershkovitz (1987a), reported the two males and three females sent to NMNH-Paris by Castelnau and Deville as the syntypes. The lectotype is an adult male mounted (Catalogue number MNHN-ZM-MO-1861-574 - https://science.mnhn.fr/institution/mnhn/collection/zm/item/mo-1861-574).

Type locality

Geoffroy and Deville (1948, p.498) indicated São Paulo de Olivença (AM) as the origin of the specimens used to describe C. rubicundus: "*Du Brésil, village de Saint-Paul*". Some years later, Geoffroy (1852, p.567) provided some more details on the occurrence of *C. rubicundus*, according to what Castelnau reported:

Ainsi, l'espèce à poils roux habite assez communément les bois qui s'étendent en face d'Olivença, et ne paraît pas dépasser le Putumayo.

Thus, the species with red hair inhabits the forests which extend in the opposite of Olivença, and does not seem to exceed the Putumayo.

I surveyed that region throughout the Içá River (Putumayo) in 2014 and I only got records of *C. rubicundus* in the várzea forests of Solimões and Jacurapá channel (a right-bank tributary of Içá River). The reports of local people consistently confirmed that uakari monkeys only occur in that region (várzea forests of Solimões and Jacurapá channel). In 2016, a Scientific Expedition organised by the IDSM at the Juami-Japurá Ecological Station – left bank of upper Içá River – did not get any evidence of bald uakaris, confirming that *C. rubicundus* does not occur in the mid or upper Içá River.

General Characters

I identified three patterns of pelage colouration in *C. rubicundus,* which are consistent with the geographic distribution of each population. The individuals from the type locality (north bank of Solimões, flooded forests of Jacurapá channel) present the nape with whitish hairs contrasting to the reddish-orange general colouration of the mid-back, rump, sides of the trunk and limbs. In some individuals, the whitish hairs from the nape are gradually being replaced by light orange hairs in the mantle (Figure 3.19). The specimens from the Jutaí River (a south bank tributary of Solimões River) have whitish hairs from the nape to the mantle gradually being replaced by the pale orange in the saddle contrastingly reddish-chestnut pattern of the mid-back, rump, and sides of the trunk and limbs (Figure 3.20). The overall pattern of these individuals is reddish-chestnut – different from the reddish-orange of the series from Jacurapá channel. The specimens of Auati-Paraná are considered *C. rubicundus*, although they present a unique pattern of pelage colouration (Figure 3.21). They have a similar reddish-chestnut colouring tone to the series from Jutaí River in the sides of the trunk and limbs, but with an evident whitish or pale buffy colouration throughout the dorsum, from the nape to the tail (or saddle in some individuals) (Figure 3.21). The arms and legs in the adult males are reddish-orange interspersed with some hairs entirely yellowish or with the basal portion reddish-orange becoming more whitish-yellow in the terminal portion (Figure 3.21).

Figure 3.19 *Cacajao rubicundus* from nearby the type locality: opposite to São Paulo de Olivença, várzea forests from Jacurapá channel and the north bank of Solimões River. A) Adult male FES046; B) Adult female FES047.

Figure 3.20 *Cacajao rubicundus* from Jutaí River, south bank of Solimões River. A) Adult male JT062; B) Adult female JT063.

Figure 3.21 *Cacajao rubicundus* from Auati-Paraná channel, north bank of Solimões River. A) Adult male MPEG17552; B) Adult female MPEG17553

2.6.3.3 *Cacajao ucayalii* (Thomas, 1928) – Ucayali bald uakari.

The Peruvian red uakaris are clearly different from the populations of red uakaris from Brazil. For the RADseq analysis, I only got two samples from Serra do Divisor National Park (Brazil). These individuals are grouped in a sister clade of *C. rubicundus*.

In the report on the mammals of the Ucayali River, from the Godman-Thomas Expedition to Peru, Thomas (1928) identified the different patterns of pelage colouration between the Peruvian populations of red uakaris and the population from Brazilian Amazon Rainforest, which motivate him to describe this new taxon. According to the author, the Peruvian uakaris present a "*General colouration as in true rubicundus, but the nape instead of being whitish or pale yellowish is bright chestnut-red like the rest of the body*" (Thomas, 1928, p 252).

Holotype

An adult male collected in 29th October 1927 and stored in the British Museum of Natural History (number 28.5.2.41)

Type locality

Cerro Azul, Contamana, Peru (Thomas, 1928), altitude about 609.6m (2000ft) asl.

General Characters

An overall reddish-chestnut or reddish-orange without the contrastingly whitish or yellowish colouration in the dorsum, as found in *C. rubicundus* and *C. novaesi*. Hershkovitz (1987) mentioned "north-to-south bleaching gradient" in the Peruvian bald uakaris. Although I identified some differences in the overall tone of reddish coat colour between the populations, I did not examine all scientific collections where red uakaris are stored to identify this north-south cline variation. For example, Kalinowski's series from FMNH were collected in Javari Mirim River (Loreto District in Peru) and present an overall reddish-chestnut pelage colouration with some dark-reddish or blackish hairs in the limbs and dorsal surface of the tail (Figure 3.22). The series from MPEG (collected in the Solimões River, opposite bank of the mouth of Napo River), however, present a lighter tone with an overall reddish-orange and with some hairs from the side of the trunk gradually becoming yellowish from the basal to the terminal portion (Figure 3.23). The adult males also present a lighter tone of reddish-orange in the dorsum, which is more evident in the juveniles individuals (Figure 3.23).

Figure 3.22 *Cacajao ucayalii* from Javari Mirim River. Adult males: A) FMNH 88821; B) FMNH 88822; C) FMNH 88824. Adult females: D) FMNH 88816; E) FMNH 88817; F) FMNH 88819.

Figure 3.23 – *Cacajao ucayalii* from Amazon River, opposite the mouth of Napo River. A) Immature male MPEG 468; B) Adult male MPEG049; C) Adult male MPEG511. Note the difference in the overall pattern of reddish-chestnut and reddish-orange between the adults from Amazon and Javari Mirim rivers (Fig.15).

2.3.6.4 *Cacajao novaesi* (Hershkovitz, 1987) – Novaes’ bald uakari

Holotype

Adult male, skin and skull, Royal Natural History Museum, Stockholm, catalogue number 612508 (see also Hershkovitz 1987a for the type series).

Type locality

Santo Antônio, Rio Eiru, Amazonas, Brazil

General Characters

Overall colouration reddish-orange or reddish-chestnut in some individuals with the contrasting colouration of the dorsum, from the nape to the rump or to the tail. The whitish and yellowish pattern of the dorsum is gradually being replaced by light orange hairs in the saddle, limbs and side of the trunk. The arms and legs are reddish-orange interspersed with some hairs entirely yellowish or with the basal portion reddish-orange becoming more whitish-yellow in the terminal portion (Figure 3.24).

Figure 3.24 *Cacajao novaesi* from Eiru River. Adult males: A) MUZUSP 5496; B) MUZUSP 4339; C) MUZUSP 4333; D) FES068. Adult females: E) MUZUSP 4331; F) MUZUSP 19359; G) MUZUSP 4149; H) FES066.

3.4 DISCUSSION

The genome-wide representation is a powerful approach to investigate the relationship in different taxonomic levels, and especially useful for recently divergent groups such as the *Cacajao* species. While the use of a few DNA markers did not provide an accurate view of the bald uakaris' relationship (Figueiredo-Ready et al. 2013; chapter 2), the ddRAD sequences allowed a robust phylogenetic and population analysis using different pipelines and parameter settings, unveiling a population structure that is consistent to the geographic distribution and phenotypic characteristics of this group of primates.

The PCA and Structure analysis differed in how they represent the bald uakaris' populations, although the central division between white and red uakaris was evident in both. When looking for the consistency in the number of main *Cacajao* lineages, the phylogenetic inference recovered four main clades in both reference and denovo pipelines and all parameter settings. However, the parametrisation was an essential step to clarify the relationship within these clades and support an analysis that is consistent with other aspects such as phenotypic characters and geographic distribution of uakaris.

3.4.1 BALD UAKARIS POPULATION STRUCTURE

The Stacks population analysis was consistent in representing the primary separation between red and white bald uakaris phenotypes. Also, the genetic variation between the white bald uakaris from upper Juruá River and lower Jutaí River is visible in both PCA and Structure (k=3), with the individuals from Mamirauá presenting an admixture between these two well-defined clusters. The difference in how these two methods represent the genetic variation in red bald uakaris can be related to how sensitive these approaches are to the number of samples required to assign them into a putative population (clusters) (Alhusain and Hafez 2018).

For example, Structure uses several *priors* parameters for the population inference in a Bayesian framework – (see Porras-Hurtado et al. 2013 and Wang 2017 for a complete description of these *priors*). As a parametric approach, Structure infers the individual ancestry proportions and the population allele frequencies to assign individuals into populations (Porras-Hurtado et al. 2013; Alhusain and Hafez 2018). The program tests the posterior probability of K assumed populations according to the allele frequencies of the individuals set (Porras-Hurtado et al. 2013). Therefore, the program is sensitive to the sample size (Alhusain and Hafez 2018) and can respond differently to datasets that include an unbalanced number of samples per population and to different parameters settings (Wang 2017). However, nonparametric approaches do not make any assumption on the genetic data and are not dependent on the allele frequencies; consequently, they are much less sensitive to the number of individuals representing each population or subpopulation (Alhusain and Hafez 2018).

These differences are particularly important for red bald uakaris because the sampling is unbalanced both in terms of the number of individuals and geographic locations. For example, *C. ucayalii* occurs over a large area between Javari and Ucayali river, in Peru, with isolated populations far west (>350km) from this interfluve (Vermeer et al. 2013); however, I only got two individuals from one locality in the south of its distribution – Serra do Divisor National Park, Brazil. Therefore, an analysis including individuals from Peruvian populations and other localities in Brazil (e.g. Auati-Paraná channel) will clarify the population structure of red uakaris.

3.4.2 TOWARDS A RESOLVED MOLECULAR PHYLOGENETIC TREE OF UAKARIS

In both pipelines (denovo and reference), the parameter settings had a strong influence on the SNPs and loci recovering and, consequently, on the resolution of the phylogenetic tree. While more permissive parameter settings overshadow the tree resolution especially in the more shallows relationships, the over-parametrisation can strongly affect the analysis by removing polymorphic and informative loci (Huang and Lacey Knowles 2016; Crotti et al. 2019). Therefore, the global bootstrap support was higher for those trees with intermediate parameter settings, i.e. the minimum samples per locus of 10, and a cluster threshold of 90.

Five main lineages of bald uakaris were retrieved from the phylogenomic analysis. The main split occurs between white (*calvus*) and red (*rubicundus*/*ucayalii*/*novaesi*) uakaris, similarly to what is found for *C. melanocephalus* and the two species from north of Negro River, *C. ayresi* and *C. hosomi* (sensu Boubli et al. 2008). The white uakaris ("*calvus*" clade) from upper Juruá River form an offshoot with 100% of support separating them from white uakaris of the lower Jutaí River and North bank of Solimões River (Mamirauá SDR), which is more than 500km to the north. These two populations (Jutaí River and Mamirauá SDR) are separated by a significant geographic barrier, the Solimões River, and they group into two distinct clades with 99% of bootstrap support.

Similarly, the geographic distance in "*melanocephalus*" specimens is essential to understand the genetic variation in those populations. The three specimens from the left bank of upper Japurá River form an offshoot with 100% of support and are more than 500 km distant to West from those samples of Amanã SDR and Negro River. These two population (Amanã SDR and Negro River), however, are much closer from each other, and the low bootstrap support between them (55%) can be a result of low genetic divergence. The red uakaris (*rubicundus*/*ucayalii*/*novaesi*) and the black uakaris (*ayresi*/*hosomi*) present a similar pattern: the genetic difference within these groups is consistent with the phenotypic variation. Therefore, the diagnostic characters of pelage colouration and the phylogenetic relationship retrieved from the molecular analysis support the species level status of these groups (Hershkovitz 1987a; Boubli et al. 2008).

3.4.3 Conclusions and further recommendations for Primates studies

Here, I used RADseq to investigate the population structure of bald uakaris and to infer the phylogeny of the genus *Cacajao*. The parameter settings can influence in both population and phylogenetic analyses, and the parameter optimisation is highly recommended since it can affect the results in different ways. In the population analysis, the use of different approaches (parametric and nonparametric) and the parameter optimisation was essential to unveil the main population structure in bald uakaris, overcoming the sample size limitation.

In the phylogenetic inference, all parameter settings and pipelines (denovo and *reference*) successfully recovered phylogenetic trees with a high bootstrap support. However, the different parameter settings strongly affect the resolution in the shallowest phylogenetic relationship. Therefore, the parameter optimisation was essential to unveil the species level structure in *Cacajao*, which is consistent in terms of geography and phenotypic characteristics.

The population analysis and the phylogenetic inference presented here can be applied in other groups, especially to unveil the relationship of those species which the description was based on morphology only. It is the case of several Amazonian primates described in the 80s and early 90s when the molecular was unavailable for studies in diversity and evolution. While RADseq was successfully used in some recent publications to support the description of new Amazonian species (Costa-Araújo et al. 2019; Boubli et al. 2019), these studies did not explicitly test the parameter optimisation to support their findings – although other lines of evidence were presented to support their conclusions. Nevertheless, the parameter optimisation and the use of different approaches for phylogenetic inference and population analyses can elucidate some recent taxonomic controversies in Amazonian primates (e.g. the number of valid species of *Pithecia*, see Marsh, 2014; Serrano-Villavicencio et al., 2019). Such an approach is particularly important to understand the diversity of these genera and to provide a baseline for any other study.

Species is the basic unit of evolution, and it is also the basic unit for directing the limited resources for conservation. For the first time since Hershkovitz (1987a), it is possible to identify the main *Cacajao* lineages using a robust molecular analysis and to reassess its taxonomic classification under an integrative approach. As a follow up of this study, I suggest the following steps for the study of the molecular phylogeny and taxonomy of *Cacajao*:

1. *Cacajao calvus*. A molecular analysis including the population from Auati-Paraná channel (right bank) and from the middle Juruá River, nearby Carauari city. These populations are particularly relevant to assess how separated they are from individuals from the upper Juruá and Tarauacá rivers. The dichotomy found in the molecular analysis for the white uakaris is similar to that found in red uakaris (*C. rubicundus* and *C. novaesi*) and black-headed uakaris (*C. ayresi* and *C. hosomi*). Therefore, the classification of white uakaris as *Cacajao calvus* is tentative until new evidence supports another arrangement.

2. *Cacajao rubicundus*. The individuals from Auati-Paraná channel (left bank) are essential to assess the taxonomic status of red uakaris. In addition, surveys in the flooded forests to the west from São Paulo de Olivença and Içá River are important to assess if there is a contact zone with the Peruvian populations.
3. *Cacajao ucayalii.* Although this is the taxon with the most extensive distribution, it was the least represented in the molecular analysis and samples from the Peruvian population are essential to investigate the phylogenetic relationship in *Cacajao* and to assess the taxonomic status of the main lineages. I only got two samples of *C. ucayalii,* and it is unclear the level of gene flow between these populations. It is especially important to include samples from the isolated populations from the mountain forests of western Peru (Vermeer et al. 2013; McHugh et al. 2019).
4. *Cacajao novaesi.* The taxon is well-defined in the molecular phylogeny, grouping individuals with a consistent morphological characteristic and geographically well delimitated. Surveys in the upper Tarauacá River are urgent to clarify the south limit of its distribution and to investigate if *C. novaesi* (left bank of Tarauacá River) and *C. calvus* (right bank of Tarauacá River) have a contact zone, which is essential to identify gene flow among their populations.

Finally, although I focused my analysis on the bald uakaris, I could identify a pattern of diversification that is consistent in all the genus *Cacajao*. It is beyond the scope of this study to discuss in detail the taxonomy of black-headed uakaris, but few words are important to moving towards a consistent classification for the genus *Cacajao*. The ddRAD analysis supports a similar topology found in the cytochrome *b* tree present by Boubli et al. (2008) for the black-headed uakaris – i.e. three clades including *Cacajao melanocephalus* in the south bank of the Negro River and *Cacajao hosomi* + *Cacajao ayresi* in the north bank. The Negro River is the main barrier that implied in a more significant genetic difference, which in turn resulted in the main differences in pelage colouration. The two forms found in the north bank of Negro River (i.e. *hosomi* and *ayresi*) are separated into two well-defined clades, that are consistent with what I found for *C. novaesi* and *C. rubicundus*.

In summary, for both bald and black uakaris, the most significant phenotypical differences are reflected in the highest genetic divergence. The phylogenetic relationship found here for the bald uakaris' lineages is consistent to the black uakaris and *Chiropotes*. The decision on what should be recognised as species (or subspecies, depending on the species concept adopted) is arbitrary in some situations, and each author will present the pros and cons of this decision. Therefore, the use of different evidence is essential to support a classification scheme, and a specific reference to the philosophical foundation behind the scheme proposed should facilitate the communication on what are the species the author is considering. Here, I am considering that if the molecular analysis of ddRADseq support the reciprocal monophyly between two groups, and they accrue differences in the pelage colouration that are geographically consistent, then they can be placed at the species level under the PSC.

3.5 Supplementary Material – Chapter 3

Table Suppl. 3-1 Samples used in ddRAD analysis.

Taxon	Code	Structure Code	Map code	Locality	Long	Lat
C. ucayalii	FES100	ucay_01	1	Divisor National Park, Brazil	-73.67	-7.46
C. ucayalii	FES101	ucay_02	2	Divisor National Park, Brazil	-73.67	-7.46
C. novaesi	FES65	nova_01	3	Eiru River	-70.2	-6.86
C. novaesi	FES66	nova_02	4	Eiru River	-70.2	-6.86
C. novaesi	FES67	nova_03	5	Eiru River	-70.2	-6.86
C. novaesi	FES68	nova_04	6	Eiru River	-69.92	-6.75
C. novaesi	FES69	nova_05	7	Eiru River	-69.92	-6.75
C. calvus	FES64	calv_09	8	Tarauacá River, right bank	-69.67	-6.67
C. calvus	FES70	calv_10	9	Tarauacá River, right bank	-69.67	-6.67
C. calvus	FES71	calv_11	10	Tarauacá River, right bank	-69.67	-6.67
C. calvus	FES95	calv_12	11	Tarauacá River, right bank	-69.74	-6.94
C. calvus	RS62	calv_13	12	Pauini River	-69.24	-8.03
C. calvus	RS63	calv_14	13	Pauini River	-69.24	-8.03
C. calvus	RS64	calv_15	14	Pauini River	-69.24	-8.03
C. calvus	JT082	calv_06	15	Jutaí_RESEX_Rio_Jutaí	-67.15	-3.06
C. calvus	JT085	calv_07	16	Jutaí_RESEX_Rio_Jutaí	-67.14	-3.3
C. calvus	JT088	calv_08	17	Jutaí_RESEX_Rio_Jutaí	-67.46	-3.79
C. calvus	JT003	calv_04	18	Jutaí_RESEX_Rio_Jutaí	-67.37	-3.3
C. calvus	JT022	calv_05	19	Jutaí_RESEX_Rio_Jutaí	-67.39	-3.31
C. calvus	Masto 1383	calv_01	20	SDR Mamirauá	-65.37	-2.44
C. calvus	Masto 283	calv_02	21	SDR Mamirauá	-64.93	-2.91

C. calvus	RDSM	calv_03	22	SDR Mamirauá	-64.79	-3.12
C. rubicundus	JT062	rubi_04	23	Jutai_ESEC_Jutai_Solimões	-67.42	-3.2
C. rubicundus	JT063	rubi_05	24	Jutai_ESEC_Jutai_Solimões	-67.42	-3.2
C. rubicundus	JT078	rubi_06	25	Jutai_ESEC_Jutai_Solimões	-67.55	-3.31
C. rubicundus	ICA020	rubi_01	26	Parana do Jacurapá	-68.62	-3.24
C. rubicundus	ICA021	rubi_02	27	Parana do Jacurapá	-68.62	-3.24
C. rubicundus	ICA022	rubi_03	28	Parana do Jacurapá	-68.62	-3.24
C. melanocephalus	CTGA-M0756		29	Japurá River, left bank	-69.2	-1.69
C. melanocephalus	CTGA-M0757		30	Japurá River, left bank	-69.2	-1.69
C. melanocephalus	CTGA-M0775		31	Japurá River, left bank	-69.34	-1.66
C. melanocephalus	CTGA-M5705		32	Solimoes River, left bank, Amana SDR	-65.17	-0.47
C. melanocephalus	CTGA-M5730		33	Solimoes River, left bank, Amana SDR	-64.5	-2.5
C. melanocephalus	CTGA-M5732		34	Solimoes River, left bank, Amana SDR	-64.5	-2.5
C. melanocephalus	CTGA-M0065		35	Negro River, right bank	-64.91	-0.58
C. melanocephalus	CTGA-M0098		36	Negro River, right bank	-64.93	-0.62
C. melanocephalus	CTGA-M5663		37	Negro River, right bank	-64.74	-0.49
C. melanocephalus	CTGA-M5665		38	Negro River, right bank	-64.65	-0.49
C. hosomi	CTGA-M5691		39	São Gabriel da Cachoeira	-66.11	0.61
C. hosomi	CTGA-M5698		40	Serra do Imeri, Xamata	-65.27	0.49
C. hosomi	CTGA-M5716		41	Serra do Imeri, Xamata	-65.27	0.49
C. hosomi	JPB163		42	Venezuela	-66.28	0.93
C. ayresi	CTGA-M5666		43	Acará River, left bank	-62.95	-0.38
C. ayresi	CTGA-M5667		44	Acará River, left bank	-62.95	-0.38
C. ayresi	CTGA-M5708		45	Igarapé Madixi	-63.34	-0.12
C. ayresi	CTGA-M5717		46	Acará River, left bank	-62.91	-0.54
C. ayresi	CTGA-M5721		47	Acará River, left bank	-62.91	-0.54

3.5.1 PARAMETRISATION – STACKS

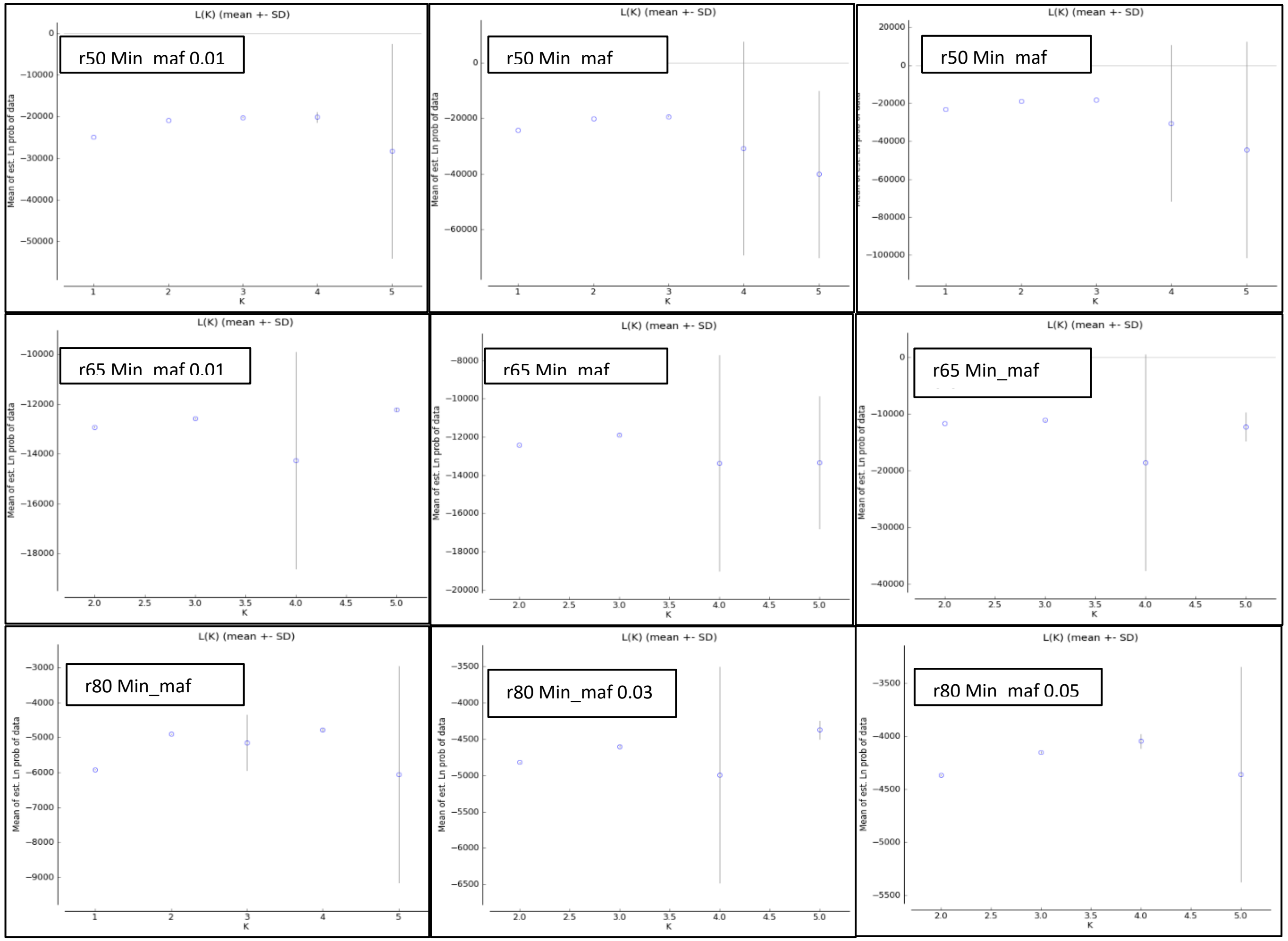

Figure Suppl. 3-1 Mean likelihood [LnP(D) ± SD] for different parameter settings calculated for the Structure analysis using 10 independent runs for each K value from 1 to 5.

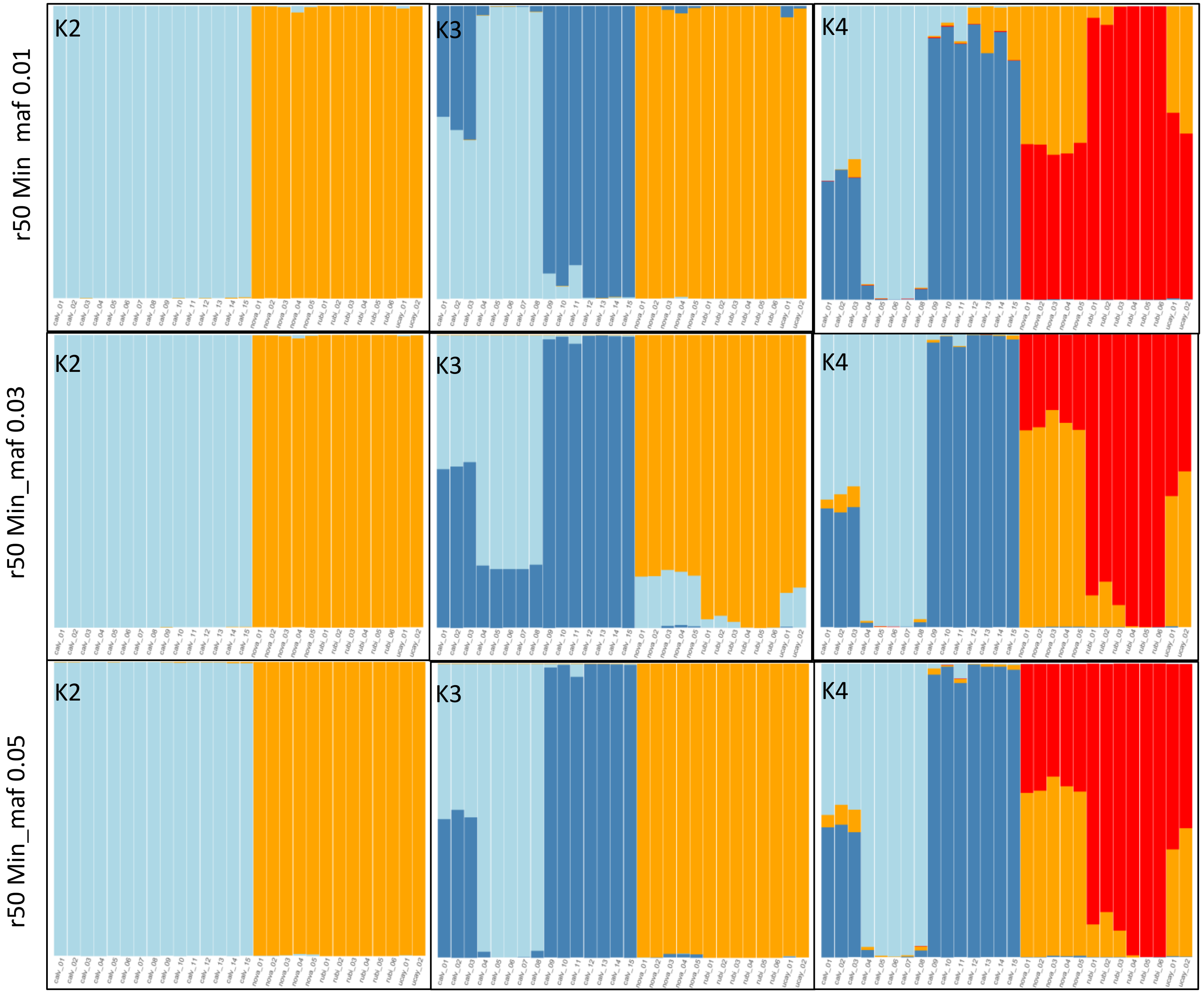

Figure Suppl. 3-2 Genetic structure of bald uakaris inferred from the “structure” dataset considering –r 0.50 parameter. Light and dark blue bars are the white uakaris; yellow and red bars are the red uakaris.

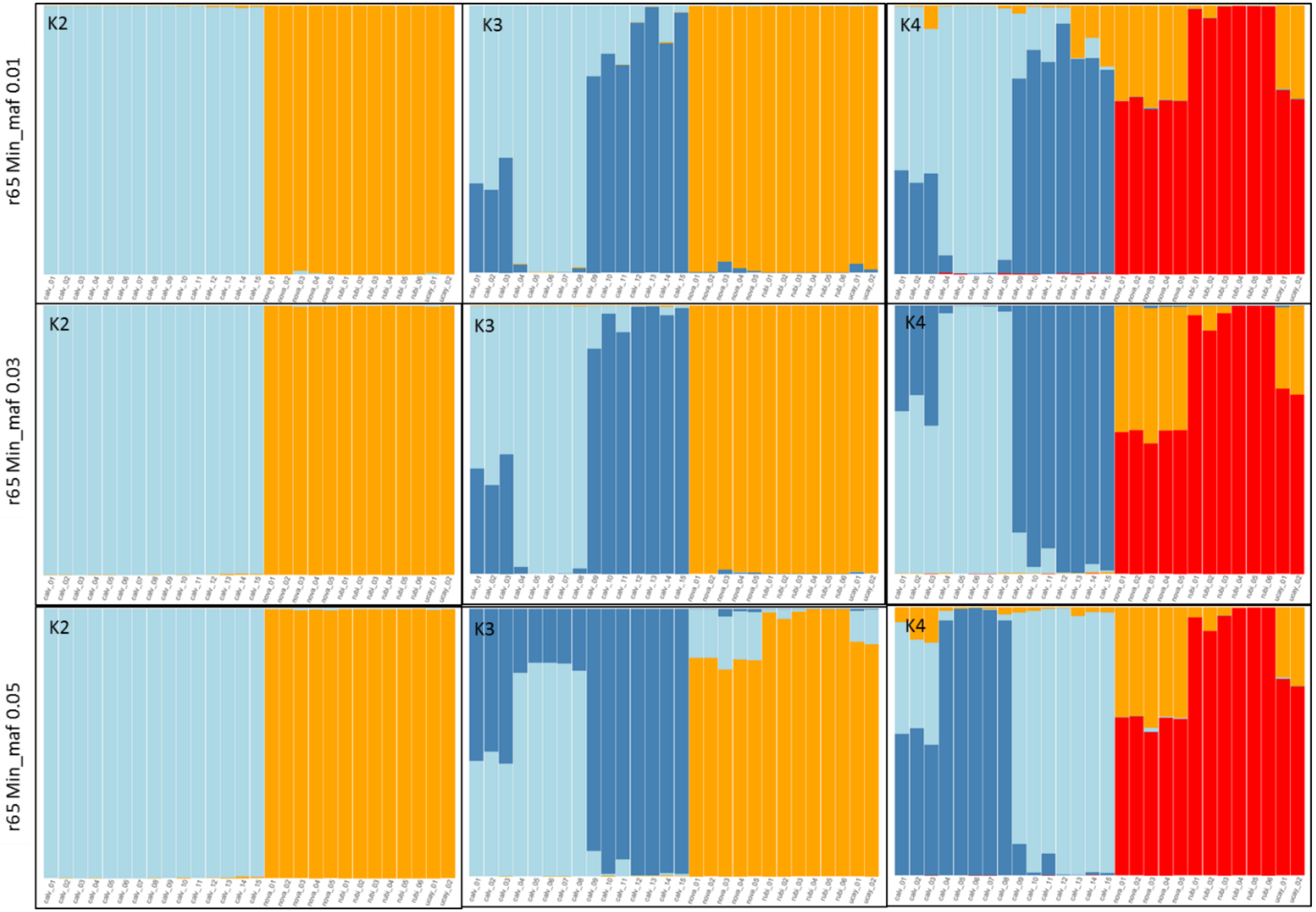

Figure Suppl. 3-3 Genetic structure of bald uakaris inferred from the “structure” dataset considering –r 0.65 parameter. Light and dark blue bars are the white uakaris; yellow and red bars are the red uakaris.

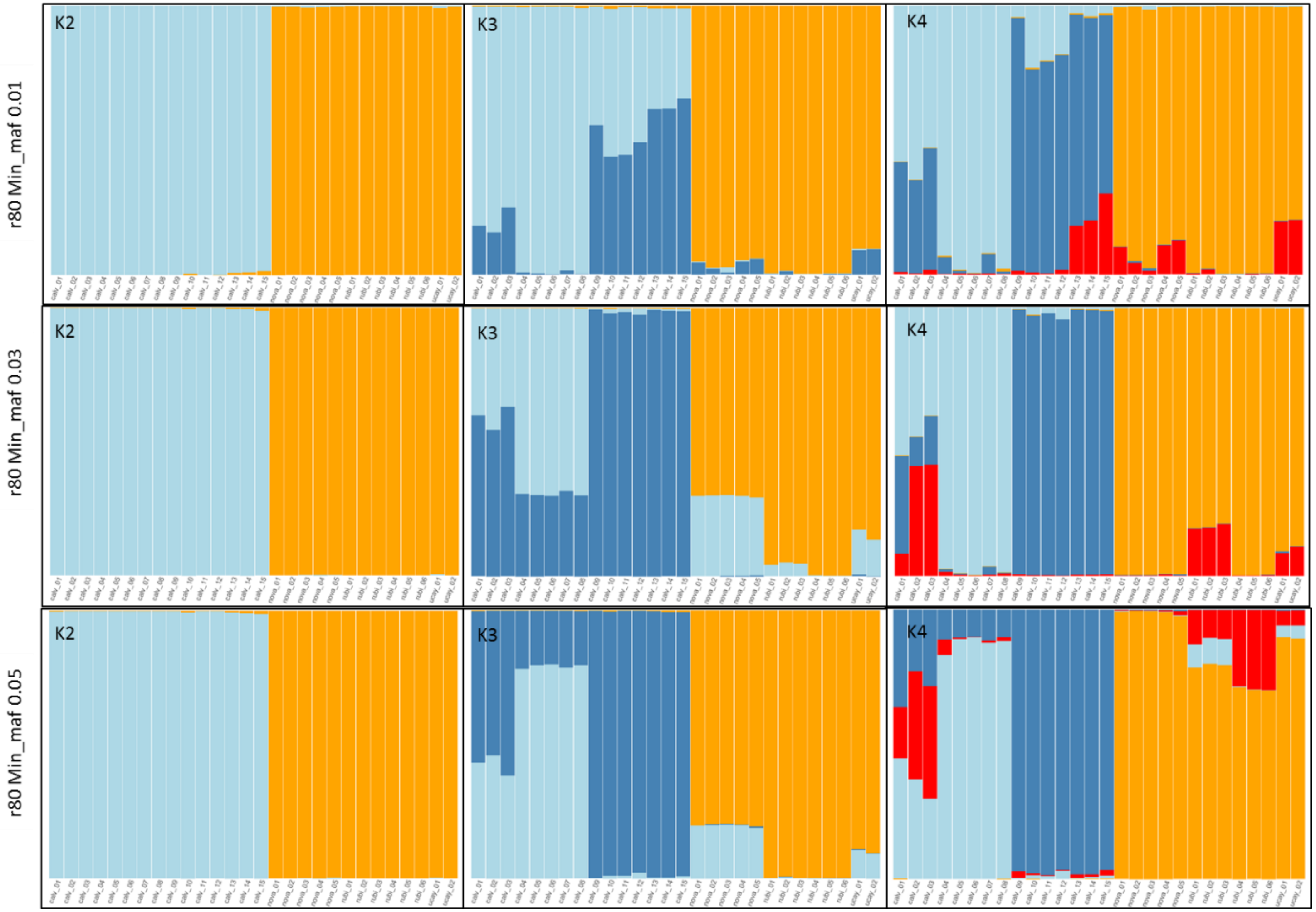

Figure Suppl. 3-4 Genetic structure of bald uakaris inferred from the “structure” dataset considering –r 0.80 parameter. Light and dark blue bars are the white uakaris; yellow and red bars are the red uakaris.

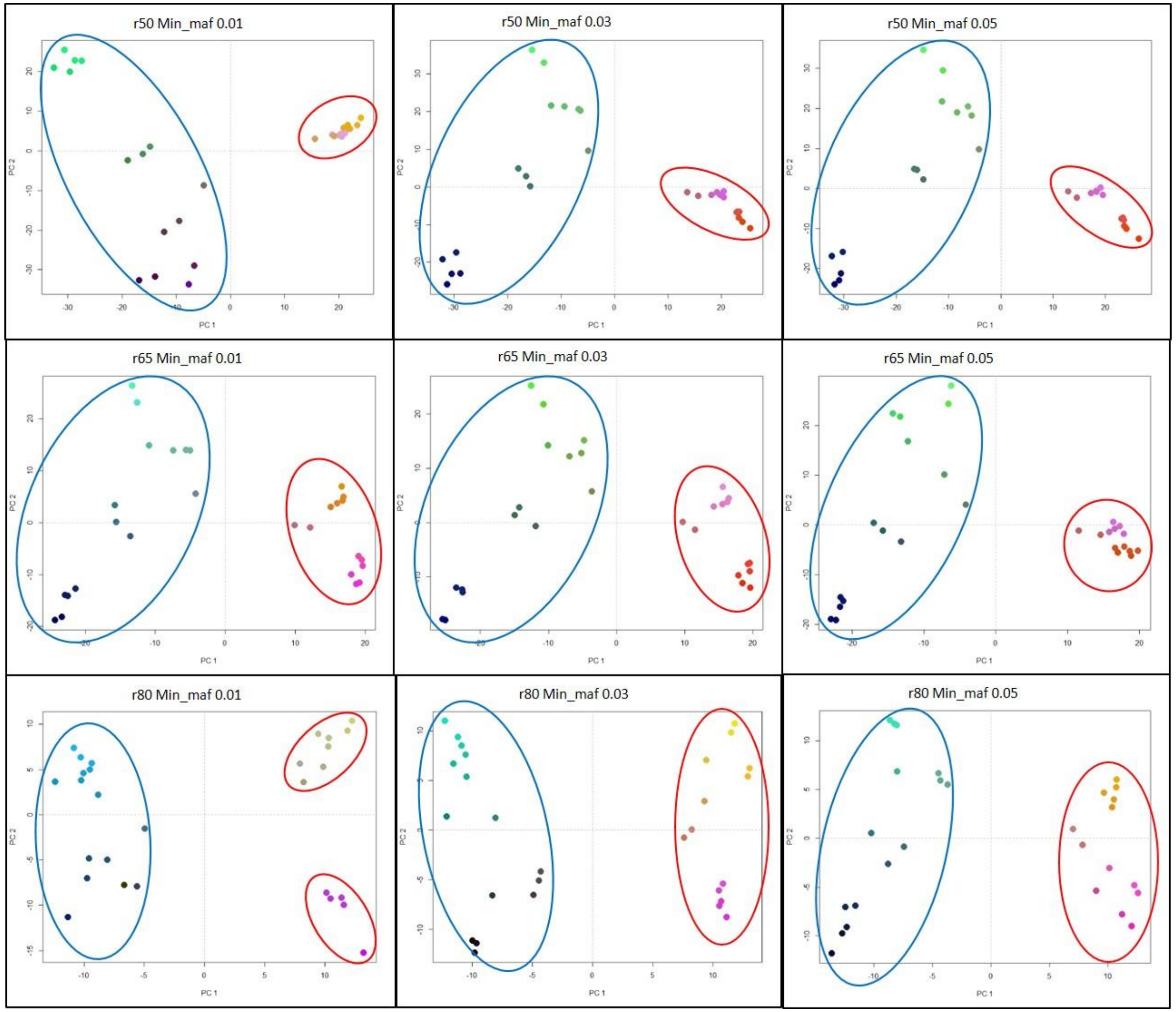

Figure Suppl. 3-5 The first two principal components of the Principal Component Analysis of the allele frequencies found for each parameter settings tested.

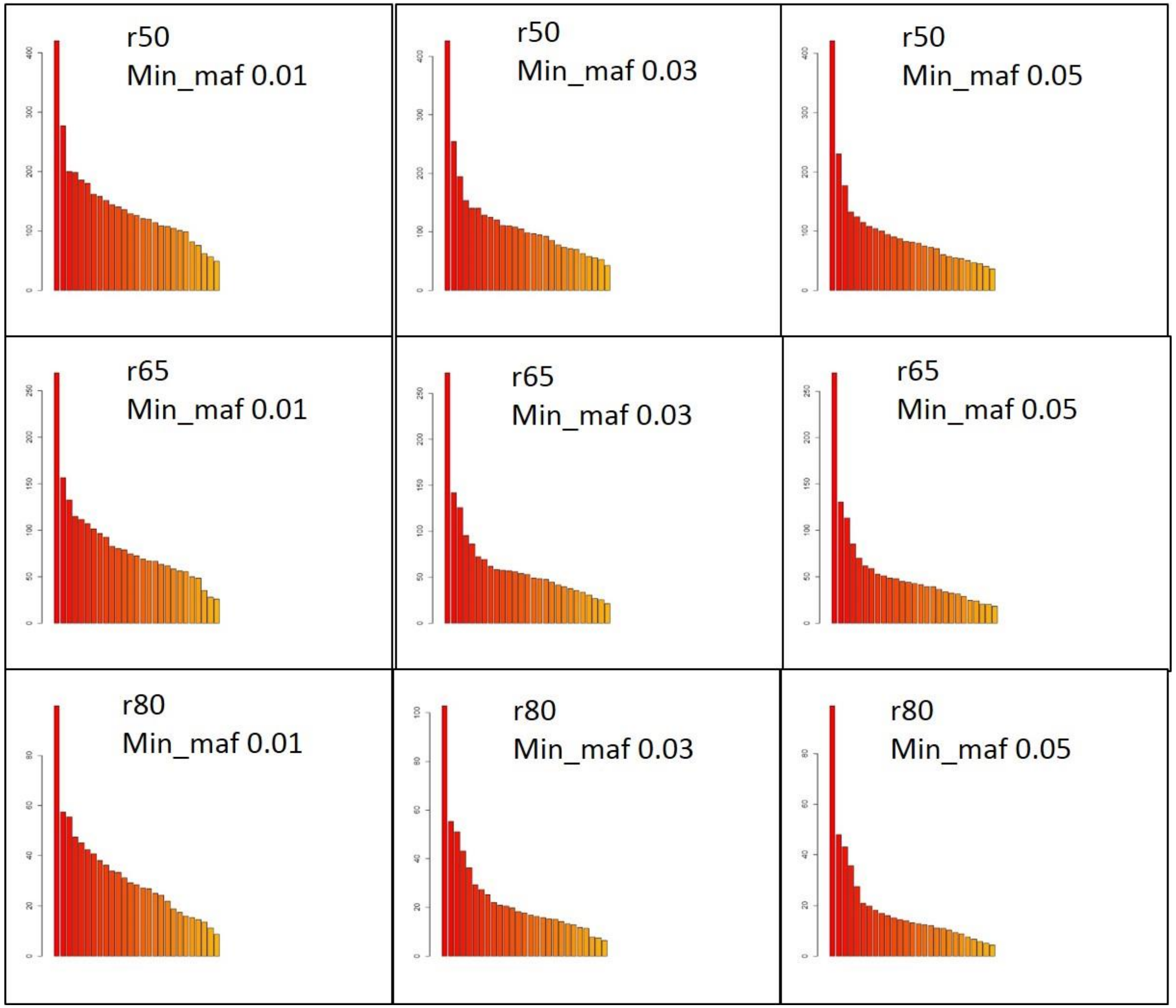

Figure Suppl. 3-6 The eigenvalues plot of the Principal Component Analysis of the allele frequencies for each parameter settings tested.

3.5.2 SYNONYMY

3.5.2.1 *Cacajao calvus* (I. Geoffroy, 1847) – White bald uakari

Brachyurus calvus I. Geoffroy, 1847:576 – Species description

B. calvus**,** I. Geoffroy, 1851:57 – type series, holotype: male, paratypes: one male and three females; characters; Reichenbach, 1862:76 – Taxonomic classification of *Simiae brachyurae*, *Cacajao – Brachyurus*.

Scarlet-faced monkey, Bates, 1863:308 - BRAZIL: Amazonas

> *Their bodies (about eighteen inches in height, exclusive of limbs) were clothed from neck to tail with very long, straight, and shining whitish hair; their heads were nearly bald, owing to the very short crop of thin grey hairs, and their faces glowed with the most vivid scarlet hue. As a finish to their striking physiognomy, they had bushy whiskers of a sandy colour, meeting under the chin, and reddish-yellow eyes. These red-faced apes belonged to a species called by the Indians Uakarí, which is peculiar to the Ega district.*
>
> *They had been obtained with great difficulty in the forests which cover the lowlands near the principal mouth of the Japura, about thirty miles from Ega* (Bates, 1863:308).

Pithecia calva, Schlegel, 1876:228 - BRAZIL: Amazonas

> *Teinte générale d'un jaune roussâtre pâle, mais très foncé sur la gorge et la poitrine, et tirant par contre, sur le dos, un peu au blanchâtre. Poils ras de la tête à pointes noires. Ce singe habite, suivant Castelnau et Deville, les forêts de la rive septentrionale du Solimoëns, vis-à-vis de Fonteboa jusqu'à la rive gauche ou septentrionale du Putomayo, également nommé Iça* (Schlegel, 1876, p.228)
>
> *General tinge of a pale, but very dark yellowish russet on the throat and chest, and on the other side, slightly whitish on the back. Head hair with black tips. This monkey inhabits, according to Castelnau and Deville, the forests of the northern bank of the Solimões, opposite Fonteboa to the left or northern bank of the Putomayo, also called Içá.* (Schlegel, 1876, p.228)

Pithecia alba, Schlegel, 1876:229 - BRAZIL: Amazonas. Name based on the scarlet-faced monkey of Bates, 1864 (ed. 2).

> *Scarlet faced Monkey, Bates, Amazons – Le voyageur Bates rapporte que l'on trouve dans les bois environnant la bouche principale du Japura, un singe à queue courte, dont le corps haut de 18 pouces, est couvert, de la nuque à la queue, de poils très longs, droits et d'un blan châtre luisant. Les figures données par Bates représentent, en effet, ce singe couvert de poils beaucoup plus longs que ne l'offrent ses congénères.* (Schlegel, 1876, p.228)

> *The traveller Bates reports that in the forests surrounding the of Japurá, a short-tailed monkey, whose 18-inch tall body, is covered, from the nape to the tail, with very long, straight hairs of a shiny white. The figures given by Bates represent, indeed, this monkey covered with much longer hairs than do his congeners*. (Schlegel, 1876, p.228)

C. calvus, Elliot, 1913:301 – BRAZIL: Amazonas. Geographic distribution of the species.

> *Briefly it may be said that C. calvus is confined to the west side of the Japura River near its mouth; to the banks of the Uatiparana near Tonantins.* (Elliot, 1913:301)

Cacajao calvus, Elliot, 1913: lxxxviii – Neotropical Region, Range of the Species (*194.* Cacajao calvus*. Angle formed by the union of the Rios Japuri* [sic, Japurá] *and Amazon, Brazil*).

B. calvus, Elliot, 1913: 300 – (*1845. E. Geoffroy Saint-Hilaire, in Archives du Museum d'Histoire Naturelle, Paris. Two species are here first described under the genus Brachyurus: B. rubicundus, and B. calvus.*) – Taxonomic revision

Cacajao calvus calvus, Hershkovitz, 1972:5-8 – classification and distribution.

C. calvus calvus, Mittermeier and Coimbra-Filho, 1977:143 - BRAZIL: Amazonas (*restricted to the huge várzea "island" formed by the Solimões, the Japurá, and the Auatí-Paraná*).

C. c. calvus, Rylands and Mittermeier, 1983:83 - BRAZIL: Amazonas; Silva Jr & Martins, 1999:119 – BRAZIL: Acre and Amazonas border, Rio Jurupari.

> *The white uakari C. c. calvus, which is classified as vulnerable but which should be considered endangered, is sometimes shot for food, and has a tiny range. An urgent need exists for the creation of the Auatí-Paraná National Park, proposed by*

Mittermeier (1973) in the Panauá refuge of the conservation plan. This would cover its entire known range. (Rylands and Mittermeier, 1983, p.83)

The uakaris of the Rio Juruparí are almost entirely white on the upperparts, without a contrasting mantle on the back, and yellowish on the underparts (including throat and beard), as in C. c. calvus. (Silva Jr & Martins, 1999:119)

Cacajao calvus novaesi, Peres, 1988:84 – Brazil: Amazonas, Lago Fortuna, Juruá River.

A recently described subspecies of white uakari (Cacajao calvus novaesi Hershkovitz, 1987a), known only from the south bank of the upper Rio Juruá, occurs at the site and downriver, at least until Carauari, thus extending its range to the west bank of the Rio Juruá by almost 500km); Peres, 1990:54 (*In Lago da Fortuna and Riozinho, white uacaris Cacajao calvus novaesi (mean weight = 3.2 kg: Ayres, 1986) were never shot because of their 'human-like' physical appearance*. (Peres, 1988, p. 84)

Cacajao *sp.*, Sampaio et al., 2018:10-11 – Brazil: Amazonas, Moaco River.

Preliminary molecular assessment, including three specimens from the Rio Moaco population, have indicated an uncertain taxonomic arrangement for all white bald-headed uacaris subspecies (Ennes, F., Boubli, J., R. Sampaio, F. Röhe, F. E. Silva, T. Hrbek, I. P. Farias, unpublished results) and we are provisionally assuming this population as Cacajao sp. (Sampaio et al., 2018:10-11)

3.5.2.2 *Cacajao rubicundus* (I. Geoffroy and Deville, 1848) – red bald uakari.

Brachyurus rubicundus I. Geoffroy and Deville, 1848:498; I. Geoffroy, 1852:564 – BRAZIL: AMAZONAS, São Paulo de Olivença – Characters description, pelage and facial colouration, occurrence.

B. rubicundus, I. Geoffroy, 1851:57 - type series: two males, three females.

Pithecia rubicunda, Wagner, 1855:104 - characters. Schlegel, 1876:228-230 - BRAZIL: Amazonas (north bank, Rio Solimões; right bank Rio Iça).

Absolument semblable au Pithecia calva, mais au pelage d'un rouge brunâtre vif, excessivement pâle sur la nuque et passant au blanchâtre sur le dessus de la tête.

Observé, par Castelnau et Deville, sur la rive septentrionale du Solimoëns, dans les bois en face de San-Paulo (Olivença) jusqu'à la rive droite ou méridionale de l'Iça, qu'il ne paraît pas franchir (Schlegel, 1876:228-230).

Absolutely similar to Pithecia calva, but with the coat of a bright brownish red, excessively pale on the nape and whitish on the top of the head. Observed, by Castelnau and Deville, on the northern bank of the Solimões, in the forests opposite San-Paulo (Olivença) to the right or southern bank of Içá, which it does not seem to cross (Schlegel, 1876:228-230)

C. rubicundus, Cabrera, 1912:27 - BRAZIL: Amazonas, São Paulo de Olivença. "*Olivença, alto Amazonas*" (Cabrera, 1912:27); Thomas, 1928:253 - BRAZIL: Amazonas (Auati-Paraná, opposite Fonte Boa).

The Museum has recently received from Herr Ehrhardt two excellent specimens of C. rubicundus from the Auty-Parana, close to Fonte Boa, precisely agreeing with the various figures and descriptions of that animal (Thomas, 1928:253).

Cacajao rubicundus, Elliot, 1913:304-305 – BRAZIL: Amazonas – taxonomic classification. Coloured plate.

Cacajao rubicundus rubicundus, Cabrera, 1958:146 - classification. See Hershkovitz (1987b).

Cacajao calvus rubicundus, Hershkovitz, 1972:5, 10 - classification; geographic distribution.

C. calvus rubicundus, Mittermeier and Coimbra-Filho, 1977:143 - BRAZIL: Amazonas. Distribution and Habits

The red uakari also occurs north of the Solimões between the Içá and Solimões. We observed it in the Rio Jacurapá, a small black water tributary of the Içá); (*The two groups of C. calvus rubicundus encountered during the 1973 survey were in igapó forest of a small, black water tributary*, p.144).

3.5.2.3 *Cacajao ucayalii* (Thomas, 1928) – Ucayali bald uakari

Cacajao calvus rubicundus, Abordo et al. 1975, - Florida (Monkey Jungle); social grooming with *Saimiri*. Calouro, 1999:195, BRAZIL, Acre - Species list of Serra do Divisor National Park.

Cacajao calvus, Calouro, 1999:200, BRAZIL, Acre - Species list of Serra do Divisor National Park. Lopes and Rehg, 2003:181 (Table 1), BRAZIL, Acre - Species list of Serra do Divisor National Park.

> *Conforme enquete realizada com 25 famílias da Parte Sul (Tab. IV), existem grupos de Cacajao calvus (L Geoffroy, 1847), Ateies chamek (Humboldt, 1812) e Lagothrix lagotricha (Humboldt, 1812) na área do Igarapé Reforma e cabeceiras do Igarapé Aparição* (Calouro, 1999, p.200).

> *According to the interviews with 25 families from the Southern portion (Tab. IV)), there are groups of Cacajao calvus (L Geoffroy, 1847), Ateles chamek (Humboldt, 1812) and Lagothrix lagotricha (Humboldt, 1812) in the region of Igarapé Reforma and the headwaters of Igarapé Aparição* (Calouro, 1999, p.200).

C. c. rubicundus, Fontaine and Dumond, 1977:168, 174 – "The Monkey Jungle ouakari colony".

> *This report describes a program designed to establish a self-perpetuating population of red ouakaris (Cacajao calvus rubicundus = Cacajao rubicundus) in a seminatural environment at Monkey Jungle in Goulds, Florida* (Fontaine and Dumond, 1977, p.168) .

> *The Monkey Jungle ouakari colony consists entirely of representatives of those extreme western populations of Cacajao calvus rubicundus that were formerly classified by Hill (1960) as Cacajao rubicundus ucayali. All the red ouakaris living at Monkey Jungle display the pelage features diagnostic of C. r. ucayali: a nape concolorous with the back and a relatively sharp demarcation between the red of the nape and the grizzled grey hairs of the forepart of the crown* (Fontaine and Dumond, 1977, p.174).

3.5.2.4 *Cacajao novaesi* (Hershkovitz, 1987) – Novaes' bald uakari

Cacajao rubicundus, Lönnberg, 1938:22 – BRAZIL, Amazonas, Rio Eiru, Santo Antônio.

Cacajao rubicundus rubicundus, Vieira, 1948:248 – BRAZIL, Amazonas, Rio Eiru, Santo Antônio, Santa Cruz. Description of the pelage colouration and a comparison with *C. rubicundus ucayalii* and *C. rubicundus rubicundus*.

Cacajao calvus rubicundus, Mittermeier and Coimbra Filho, 1977:143 – BRAZIL, Amazonas, upper Rio Juruá.

During the 1973 survey, several local people told us of "white" uakaris from south of the Solimões. These reports probably originate from areas like the upper Rio Juruá, where populations of the widespread red uakari (C. calvus rubicundus) sometimes have whitish backs. (Mittermeier and Coimbra Filho, 1977, p.143)

3.5.3 MATERIAL EXAMINED (TOTAL 100 VOUCHERS)

Cacajao calvus (N=42): Rio Jutaí Extractive Reserve, AM: IDSM codes JT003, JT022, JT082, JT085, JT088, JT090; Igarape Grande, Sao Romao, right bank of Tarauaca River: IDSM codes FES64, FES70, FES71; Lago Tucuma, right bank of Tarauaca River: IDSM codes FES 095; Mamirauá SDR: IDSM codes Masto_1383, Masto_283; Sacado do Tarauaca: INPA 5241; Pauini River (AM): INPA codes RS062, RS063, RS064; Paraná do Maiana, Mamirauá SDR, AM: MNRJ 1706, MNRJ 1591, MNRJ 1595, MNRJ 1599, MNRJ 1703, MNRJ 1704, MNRJ 1705, MNRJ 2441, MNRJ 2442, MNRJ 2444, MNRJ 2445, MNRJ 2447, MNRJ 2452; Juruá River, Brazil: MPEG 0576; Jurupari River, right bank, AM: MPEG 21861, MPEG 21862, MPEG 21863; Lago Tracaja, Mamirauá SDR: MUZUSP 17535, MUZUSP 17539; Foz do Mamirauá, Mamirauá SDR: MUZUSP 17536, MUZUSP 17537; Vila Alencar, Mamirauá SDR: MUZUSP 17542; Sao Pedro, Japura River: MUZUSP 17545, MUZUSP 17538; INPA 0212; Unknown locality: INPA 0212, MUZUSP 03734

Cacajao rubicundus rubicundus (N=8): Jutaí-Solimões Ecological Station: IDSM codes JT062, JT063, JT078; Jacurapá channel, right bank tributary of Içá River: IDSM codes FES46, FES47, FES48; Buiuçu, Auatí-Paraná: MUZUSP 17552, MUZUSP 17553

Cacajao rubicundus ucayalii (n=30)*:* Alto Yavari Mirim, Loreto, Peru: FMNH 88810, FMNH 88811, FMNH 88812, FMNH 88813, FMNH 88814, FMNH 88815, FMNH 88816, FMNH 88817, FMNH 88818, FMNH 88819, FMNH 88820, FMNH 88821, FMNH 88822, FMNH 88823, FMNH 88824, FMNH 88825; Chimbotes, Peru: MPEG 0461, MPEG 0468; Napo River, Peru: MPEG 0462, MPEG 0049, MPEG 0499, MPEG 0506, MPEG 0511, MPEG 0512; Javari River, Estirao do Ecuador (Brazil?): MPEG 1848, MPEG 1849, MPEG 1850, MPEG 1852, MPEG 1853, MPEG 1854

Cacajao novaesi (N=20): Igarapé Preto, right bank of Jurua River: IDSM codes FES65, FES66, FES67; Igarape Lontra, right bank of Jurua River: IDSM codes FES68, FES69; Santa Cruz, Eiru River: MUZUSP 04149, MUZUSP 04150, MUZUSP 04151, MUZUSP 04330, MUZUSP 04331, MUZUSP 04332, MUZUSP 04333, MUZUSP 04334, MUZUSP 04335, MUZUSP 04336, MUZUSP 04337, MUZUSP 04338, MUZUSP 04339, MUZUSP 05496, MUZUSP 19701.

Table Suppl 3-1 Vouchers examined in this study

Species	Locality	Scientific Collection*	Specimens
Cacajao calvus (N = 42)	Jutaí River Extractive Reserve, AM	IDSM	JT003, JT022, JT082, JT085, JT088, JT090
	Igarapé Grande, São Romão, right bank of Tarauacá River	IDSM	FES64, FES70, FES71
	Lago Tucumã, right bank of Tarauacá River	IDSM	FES 095
	Mamirauá SDR, AM	IDSM	Masto_1383, Masto_283
	Sacado do Tarauacá	INPA	INPA 5241
	Pauini River, AM	INPA	RS062, RS063, RS064
	Paraná do Maiana, Mamirauá SDR, AM	MNRJ	MNRJ 1706, MNRJ 1591, MNRJ 1595, MNRJ 1599, MNRJ 1703, MNRJ 1704, MNRJ 1705 MNRJ 2441, MNRJ 2442, MNRJ 2444, MNRJ 2445, MNRJ 2447, MNRJ 2452
	Juruá River, Brazil	MPEG	MPEG 0576
	Jurupari River, right bank, AM	MPEG	MPEG 21861, MPEG 21862, MPEG 21863
	Lago Tracajá, Mamirauá SDR, AM	MZUSP	MUZUSP 17535, MUZUSP 17539
	Foz do Mamirauá, Mamirauá SDR, AM	MZUSP	MUZUSP 17536, MUZUSP 17537
	Vila Alencar, Mamirauá SDR, AM	MZUSP	MUZUSP 17542
	São Pedro, Japurá River, AM	MZUSP	MUZUSP 17545, MUZUSP 17538
	Unknown	INPA	INPA 0212
		INPA	INPA 0212
		MZUSP	MUZUSP 03734

Cacajao rubicundus (N=8)	Jutaí-Solimões Ecological Station	IDSM	JT062, JT063, JT078
	Jacurapá channel, right bank tributary of Içá River	IDSM	FES46, FES47, FES48
	Buiuçu, Auatí-Paraná	MZUSP	MUZUSP 17552, MUZUSP 17553
Cacajao ucayalii (n=30)	Alto Yavarí Mirí, Loreto, Peru	FMNH	FMNH 88810, FMNH 88811, FMNH 88812, FMNH 88813, FMNH 88814, FMNH 88815, FMNH 88816 FMNH 88817, FMNH 88818, FMNH 88819, FMNH 88820, FMNH 88821, FMNH 88822, FMNH 88823 FMNH 88824, FMNH 88825
	Chimbote, Peru	MPEG	MPEG 0461, MPEG 0468
	Napo River, Peru	MPEG	MPEG 0462, MPEG 0049, MPEG 0499, MPEG 0506, MPEG 0511, MPEG 0512
	Javari River, Estirão do Equador (Brazil?)	MPEG	MPEG 1848, MPEG 1849, MPEG 1850, MPEG 1852, MPEG 1853, MPEG 1854
Cacajao novaesi (N=20))	Igarapé Preto, right bank of Juruá River	IDSM	FES65, FES66, FES67
	Igarapé Lontra, right bank of Juruá River	IDSM	FES68, FES69
	Santa Cruz, Eiru River	MZUSP	MUZUSP 04149, MUZUSP 04150, MUZUSP 04151, MUZUSP 04330, MUZUSP 04331, MUZUSP 04332, MUZUSP 04333, MUZUSP 04334, MUZUSP 04335, MUZUSP 04336, MUZUSP 04337, MUZUSP 04338, MUZUSP 04339, MUZUSP 05496, MUZUSP 19701

*MZUSP = Museu de Zoologia da Universidade de São Paulo; MPEG = Museu Paraense Emilio Goeldi; MNRJ = Museu Nacional do Rio de Janeiro; INPA = Instituto Nacional e Pesquisas da Amazônia; IDSM = Instituto de Desenvolvimento Sustentável Mamirauá; FMNH = Field Museum of Natural History.

Chapter 4. Elucidating the geographic distribution of bald uakaris (*Cacajao* sp.) in Brazilian Amazonia

4.1 INTRODUCTION

Bald uakaris primarily occur in flooded forests and are endemic to western Amazonia across the Ucayali-Solimões-Juruá river systems (Silva-Júnior et al. 2013) (Figure 4.1). Its geographic distribution has been updated in Peru (Ward and Chism 2003; Bowler et al. 2009; Vermeer et al. 2013) and Brazil (Vieira et al. 2008; Cardoso et al. 2014), but its occurrence throughout their range remains poorly known, with few studies reporting on their distribution. Bald uakaris have been little studied hitherto, with only two long-term studies on the ecology and behaviour (Ayres 1986 – *C . calvus* at Mamirauá Sustainable Development Reserve, Brazil; Bowler and Bodmer 2009b, 2011 – *C. ucayalii* at Lago Preto Conservation Concession, Peru). In Brazil, their occurrence and distribution have been overlooked or misidentified, with some reports entirely omitting infraspecific taxonomy, which does ensure accurate identification according to the classification scheme proposed by Hershkovitz (1987a). Here, I am considering the species level when I refer to the bald uakaris – i.e., *C. calvus*, *C. rubicundus*, *C. ucayalii*, and *C. novaesi*.

The white uakaris, *C. calvus*, were known only in the flooded forests of Mamirauá Sustainable Development Reserve (Mamirauá SDR). However, primate surveys confirmed the presence of white uakaris in the Juruá River (Peres 1988, 1997), and Silva Jr and Martins (1999) reported an isolated population of white uakaris from the region of Jurupari River, a right tributary of the Envira River, upper Juruá River basin (Figure 4.1). Further surveys confirmed the presence of white uakaris in the region of the lower Jutaí River (Cardoso et al. 2014; Silva et al. 2017).

Silva Jr and Martins (1999) reported white uakari populations (identified as *C. calvus*) separated by ~700 km from another in the Solimões River "with *C. novaesi* enclaved between them". The report of *C. novaesi* in the middle Juruá River, however, was based on a previous misidentification. Hershkovitz (1987a) mentioned as one of the most remarkable diagnostic characters of the Novaes' uakari (*Cacajao novaesi*) its "*General coloration orange* *with dorsum from nape to tail tip contrastingly paler orange, buffy or whitish…*" (Hershkovitz 1987a, p.42) . The species was described by Hershkovitz (1987a) with limited data available on its occurrence:

"*Known only from between the Rio Tarauacá and Rio Eiru, south bank upper Rio Juruá, Amazonas, Brazil; the range may extend west from the Tarauacá to the Rio Gregôrio or beyond to occupy the entire basin between the Tarauacá and right bank of the Rio Juruá; the genus is unknown to the south in Acre*" (Hershkovitz, 1987a, pp. 38).

Cacajao novaesi was supposedly recorded at Lago Fortuna, left bank of Juruá River, nearby the Carauari city (Figure 4.1), which would extend its occurrence in about 500km to the northeast (Peres 1988). This information has underpinned the geographic distribution of *C. novaesi* ever since with its inclusion in species list of Protected Areas and other publications (Peres 1990; Veiga et al. 2008; Bowler and Bodmer 2009; Barnett et al. 2013; Figueiredo-Ready et al. 2013; Silva-Júnior et al. 2013). However, Peres (1988, pp. 84) referred to the uakaris of that region as the "*recently described species of white uakari* (*Cacajao calvus novaesi*)" – a clear reference to the white uakaris population – therefore, *C. calvus* – from Juruá River basin (see Silva Jr and Martins 1999) and not to the orange-buff uakaris – *C. novaesi* – described by Hershkovitz a year before. A new white uakari population was also reported in Pauini River basin, a left-bank tributary of Purus River (Sampaio et al. 2018).

Another bald uakari species with inaccurate information on its occurrence in Brazil is *Cacajao ucayalii*. This taxon occurs mostly in Peruvian forests, being considered restricted to the Ucayali-Yavarí interfluve (Silva-Júnior et al. 2013). However, additional records have been published beyond this range (Bowler et al. 2009; Vermeer et al. 2013; McHugh et al. 2019). Bowler et al. (2009) reported *C. ucayalii* on the right bank of Río Yanayacu, a small tributary of Río Marañon, within the Pacaya-Samiria National Reserve. Prior to this record, the taxon had been listed only in one protected area: the Tamshiyacu-Tahuayo Communal Reserve (Bowler et al. 2009). The second report is from montane forests in the Cordillera Cahuapanas, San Martin, north-eastern Peru, where Vermeer et al. (2013) found a new isolated population separated by over 365 km to the west of the locality reported by Bowler et al. (2009). McHugh et al. (2019) recorded an isolated population of reddish uakaris in montane areas of southwest Peru, district of Pampa Hermosa, Región Junín (~1287-2015m asl). Hershkovitz (1987) mentioned the presence of *C. ucayalii* in Brazil based on voucher specimens held in the Field Museum of Natural History:

"Four males (1 juv.) and 3 females labelled Estirão do Equador, east bank of lower Javari River, Amazonas, Brazil, agree with C. ucayalii from the opposite bank of the same river but their backs average slightly paler. These specimens of ucayalii are the only ones known to occur east of the Javari River. They almost certainly represent an enclave population cut off from parental stock on the west or Peruvian bank of the Javari River (Yavari)" Hershkovitz (1987a p. 35).

However, there is no field data from the right bank of the Javari River to confirm *C. ucayalii* in Brazil. Bald uakaris were recorded in the Serra do Divisor National Park (SDNP) – Acre State, Brazil (Figure 4.1), but their taxonomic identification in that region is controversial (Calouro 1999; Silva Jr et al. 1999; Lopes and Rehg 2003). Calouro (1999) reported the occurrence of red uakaris, which were identified as "*Cacajao calvus rubicundus*", in a montane region (~600m) in the northern sector of SDNP that is drained by the Moa River, a left-bank tributary of the Juruá River. Some years later, Lopes and Rehg (2003) presented a species list of the primates recorded in the Ouro Preto River, a left-bank tributary of the Juruá River in the southern sector of SDNP and listed *Cacajao calvus*. Therefore, the presence of *C. ucayalii* in Brazilian territory remains unknown.

Although Calouro (1999) identified the red uakaris of SDNP as *C. rubicundus*, this taxon is only known from few localities in the middle Solimões River. Its type locality is the mouth of Içá River, a left (north) bank of Solimões River, opposite the town of São Paulo de Olivença, Amazonas State (Hershkovitz 1987a). The species has a disjunct distribution occurring in the Auati-Paraná channel, in a contact zone with *C. calvus* (Vieira et al. 2008). *Cacajao rubicundus* also occurs in the Jutaí River, at the Jutaí-Solimões Ecological Station (Silva et al. 2017), the southern bank of the Solimões River.

Here, I reviewed the geographic distribution of bald uakaris in Brazil, and present new information on the occurrence of each species based on multi-year surveys. The data presented here were collected during field expeditions organised by the Mamirauá Institute for Sustainable Development to the following areas: Juami-Japurá Ecological Station (JJES), Baixo Juruá Extractive Reserve (BJER), Serra do Divisor National Park (SDNP), Içá River, and Tarauacá-Gregório interfluve. I also include data collected by collaborators in the following areas: Juruá River (Uacari Sustainable Development Reserve (USDR), Médio Juruá Extractive

Reserve (MJER), Deni Indigenous Land (DIL), and Kanamari do Juruá Indigenous Land (KJIL) – data provided by Dr Carlos Peres, Dr Whaldener Endo, and Dr Torbjørn Haugaasen); Rio Gregório Extractive Reserve (RGER) (data provided by Dr André L. Ravetta); and Riozinho da Liberdade Extractive Reserve (RLER) (data provided by Dr Ricardo Sampaio). These data are part of mammals' surveys that included the inventories of Protected Areas (PAs) to compose the species list of their management plans, long-term monitoring programs (e.g. Peres 1980, 1988, 1997, see also www.institutojurua.org), and *ad libitum* information on the presence and absence of bald uakaris. I also used the localities information from the voucher specimens available in six major zoological collections. When taken together, this dataset provides the most accurate and updated information on the geographic distribution range of the four species considered under the scope of this thesis. In addition, it updates the species lists of the management plans of the Protected Areas of that region. This information is the baseline to assess the conservation status of each species and to plan effective strategies for their long-term conservation.

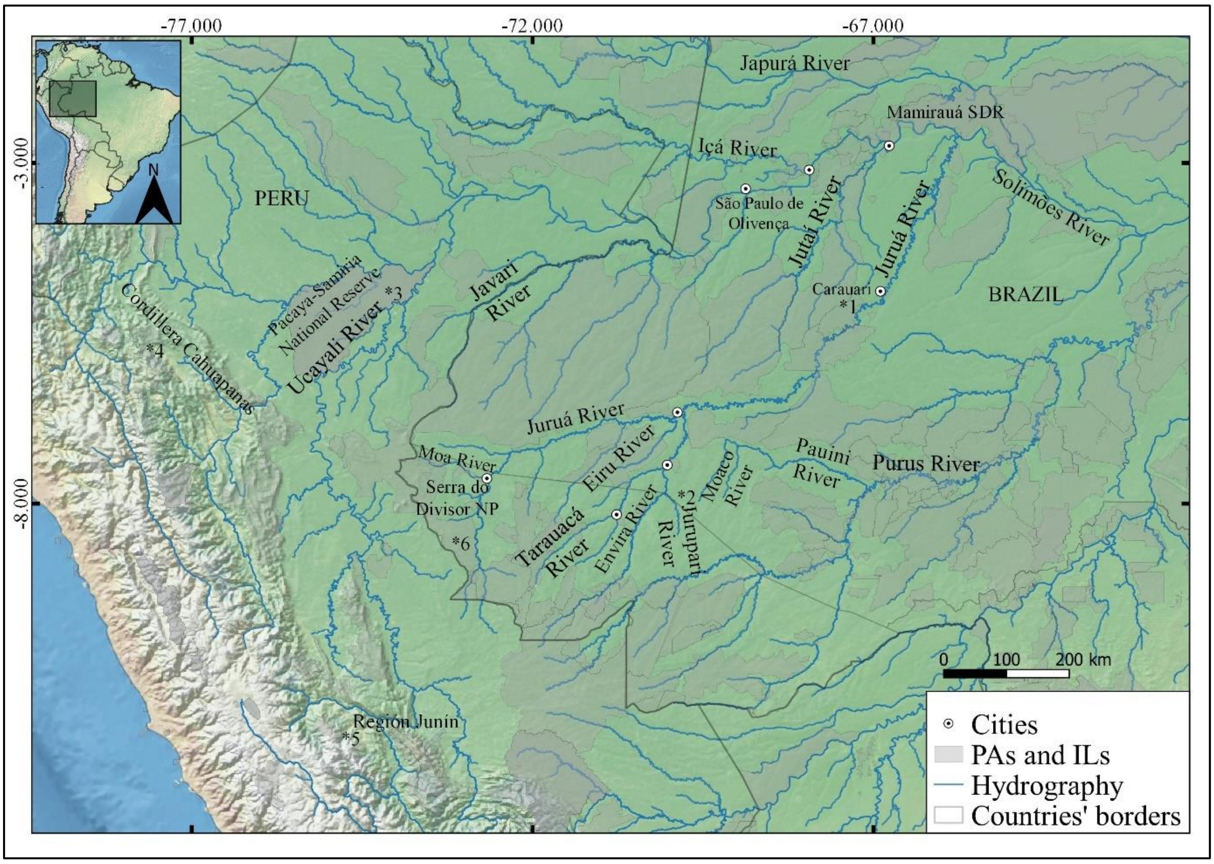

Figure 4.1 The region where bald uakaris occur in the Western Amazonia.*1 – Lago Fortuna where Peres (1988) recorded white uakaris. *2 – Jurupari River, where Silva Júnior and Martins

(1999) recorded an isolated population of white uakaris. *3 Pacaya-Samiria National Reserve, where Bowler et al. (2009) recorded *C. ucayalii*. Isolated populations of *C. ucayalii* were also recorded by Vermeer et al. (2013) (*4), and McHugh et al. (2019) (*5). *6 Red uakaris recorded in Serra do Divisor National Park by Calouro et al. (1999).

4.2 METHODS

Surveys were conducted using pre-existing trails and paths in the upland forest (“*Terra Firme*”), and small canoes in the flooded forest (“*várzeas*”). The surveys were done mostly during the morning and afternoon, any occasional sightings were considered to confirm the presence of uakaris. These surveys were conducted from 2008 to 2018 in the Solimões and Juruá river basins (Figure 4.2, Table 4-1). These areas are known as “*Várzea*”, “*Paleo-várzea*” or “*Igapó*” – according to the level of fertility in the floodplains – and are classified as “wetlands with oscillating water level” with a marked seasonal variation in precipitation the flood pulse (Junk et al. 2011). The soils are composed of sedimentary units from Miocene known as Solimões formation (Rossetti et al. 2005).

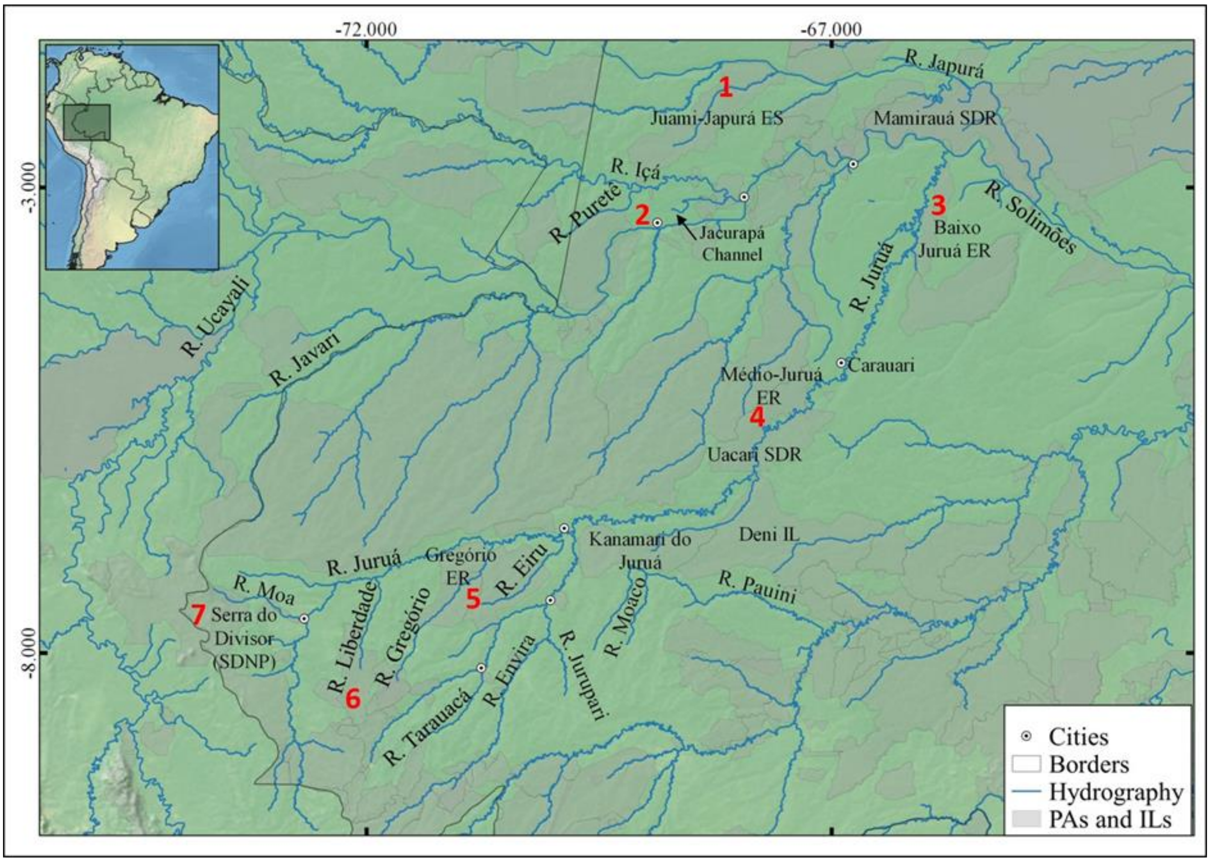

Figure 4.2 The study area where the surveys were conducted. See Table 4-1 for details.

Table 4-1 Areas surveyed in the Solimões and Juruá river basins. JJES – Juami-Japurá Ecological Station; BJER – Baixo Juruá Extractive Reserve; USDR – Uacari Sustainable Development Reserve; MJER – Médio Juruá Extractive Reserve; DIL – Deni Indigenous Land; KJIL – Kanamari do Juruá Indigenous Land; RGER – Rio Gregório Extractive Reserve; RLER – Riozinho da Liberdade Extractive Reserve; SDNP – Serra do Divisor National Park; N/A – Not applicable (non-protected area)

Area	**River**	**Year**	**Legally Protected Land**	**Locality**	**Lat**	**Long**	**Effort (days)**
1	Japurá	2017	JJES	-	-2.1798	-68.3547	14
2	Içá	2015	N/A	Jacurapá channel	-3.2369	-68.6181	5
				Cachoeira e Monte Tabor (Cuiaoá) local villages	-2.8895	-68.3681	5
				Lago Mapuru	-2.9543	-68.4239	5
				São Pedro local village	-3.0294	-68.8823	5
				Pauiri e Nova Esperança local villages (Igarapé Tapuru, Puretê River)	-3.0415	-69.1057	5
3	Juruá	2018	BJER	-	-3.5649	-65.969	17
4	Juruá	2008 - 2010	USDR	Left bank of Juruá River - Anaxiqui, Bauna (LB), Eré, Marari	-5.6243	-67.6504	209
				Right bank of Juruá River - Anaxiqui, Bauna, Eré, Marari	-5.6243	-67.6504	195
			MJER	Riozinho, left bank tributary of Juruá River	-4.4007	-66.8369	347
		2015	USDR	Lago Pupunha, left bank of Juruá River	-5.6243	-67.6504	14
		2011 - 2012	DIL	Xeruã River, right bank tributary of Juruá River	-6.7048	-68.4572	54
			KJIL	Xeruã River, right bank tributary of Juruá River	-6.7485	-68.6881	40
5	Gregório	2015	RGER	Igarapé do Coatá	-7.1577	-70.767	14
	Tarauacá	2017	N/A	Igarapé São Romão	-6.7531	-69.9248	6
	Eiru	2017	N/A	Igarapé Preto	-6.8643	-70.1958	14
6	Liberdade	2018	RLER	Periquito	-8.0667	-72.0642	8
				Alegria	-7.8911	-72.267	4
				Bom Futuro	-7.9037	-72.0654	2
				Morro da Pedra	-7.844	-72.0545	4
				Maurício Mapes	-7.7989	-72.0223	4
				Santa Rita	-7.7059	-71.998	4
				São João	-7.6322	-71.9606	6
				São José	-7.6039	-71.9512	6
				São Luiz	-7.5652	-71.9416	6
7	Moa	2018	SDNP	Pé da Serra local village	-7.4614	-73.668	10

I am also including the literature records, and the information from 100 vouchers that I examined in the following zoological collections: Museu de Zoologia da Universidade de São Paulo (MUZUSP), Museu Paraense Emílio Goeldi (MPEG), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Instituto de Desenvolvimento Sustentável Mamirauá (IDSM) and Field Museum of Natural History (FMNH). I estimated the Extent of Occurrence of each taxon according to the set of occurrence records gathered from field surveys, literature, and Zoological Collections. Therefore, I plotted all records and created polygon layers for each species using the geographic information system in the software QGIS version 3.4.5 (QGIS Development Team 2019). Finally, I drew the boundaries of the geographic distribution range for each species. Each population with disjunct distribution was represented in a separated polygon and areas where the species potentially occur were also represented.

4.3 RESULTS

4.3.1 CACAJAO CALVUS

I registered white uakaris *C. calvus* in the right bank of the Tarauacá River (Figure 4.3, Figure 4.4). The species occurs throughout the right (east) bank of Tarauacá River until its confluence with Juruá River, in the right bank (Figure 4.3). Sampaio et al. (2018) also recorded *Cacajao calvus* in the upper Moaco River, a right-bank tributary of the Pauini River (Figure 4.3). White uakaris, *Cacajao calvus,* also occurs in the left bank of the middle Juruá River, in both Médio-Juruá ER and Uacari SDR (Figure 4.3). Long-term mammals' surveys in this region only recorded the species at the right bank of Juruá on two occasions (Table Suppl. 4-1). Although several mammals' surveys were conducted by different research teams from Carauari to the lower Juruá River, there is no evidence of uakaris in this extension until the confluence with Solimões River. Surveys in the Baixo Juruá Extractive Reserve (RESEX do Baixo Juruá) and the reports of local people also support this information. *Cacajao calvus* also occurs on the right bank of the Jutaí River (Cardoso et al. 2014; Silva et al. 2017).

Therefore, *Cacajao calvus* has three disjunct populations which (Figure 4.3), according to the specimens examined, accrued a geographical variation in the pelage colouration (see session 2.3.6.1 *Cacajao calvus* (I. Geoffroy, 1847) – White bald uakariThe first is entirely encompassed by the Mamirauá SDR, an area of 1,124,000ha of the flooded forest. The second population occurs in the right bank Jutaí – about 100km southwestern to the Mamirauá SDR – and extends up to the middle Juruá river basin. The third population occurs in the right bank of Tarauacá River and in the headwaters of Pauini and Moaco rivers, which is about 200km south to the population from middle Juruá. The white uakaris, *C. calvus*, has an EOO of 153,431 km^2 (Figure 4.10).

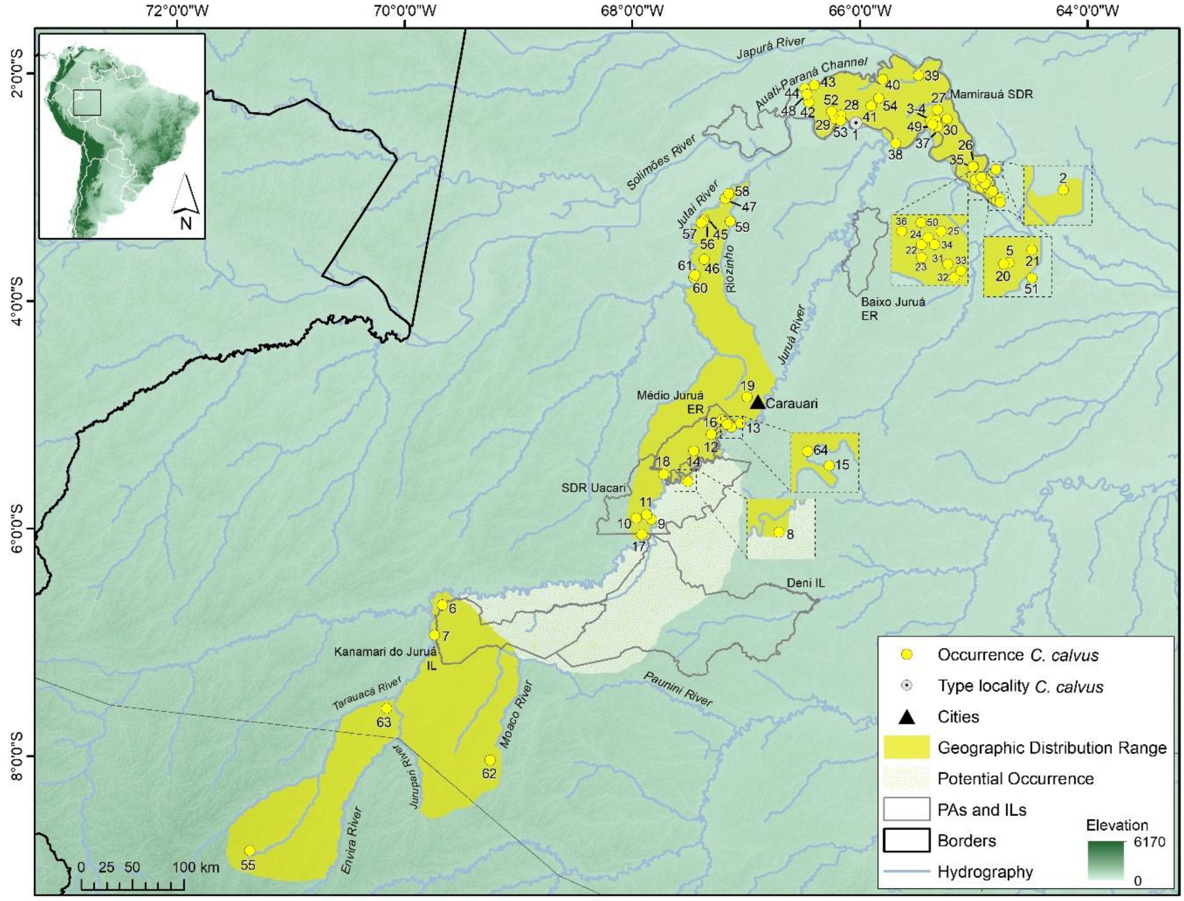

Figure 4.3 The geographic distribution range of *C. calvus*. Numbers are represented in Table Suppl. 4-1.

Figure 4.4 *Cacajao calvus* from right bank of Tarauacá River. Photo: Marcelo I. Santana.

4.3.2 CACAJAO RUBICUNDUS

During the surveys to the Içá-Solimões interfluve, I only recorded *C. rubicundus* in the Jacurapá channel (Figure 4.5, Table Suppl. 4-2). This channel delimits the várzea of Solimões River from the right bank of low Içá River and extends about 150km to the west. I did not register uakaris in any other locality in that region, although the surveys extended from the mouth of Içá River to the Puretê River. Also, bald uakaris do not occur in the Juami-Japurá Ecological Station (Area 1), north bank of Içá River. Local people emphatically reported the Jacurapá channel as the only place with uakaris in that region.

The geographic distribution of *Cacajao rubicundus* is delimited by the flooded forests of the Solimões River. Although with an Extent of Occurrence (EOO) estimated in 17,594km^2, the species occurs in three restricted and disjunct populations (Figure 4.5, Figure 4.10). The first, as I mentioned above, occurs in the flooded forests of Jacurapá channel, north bank of Solimões River. This region, opposite to São Paulo de Olivença city is the type locality. The second population occurs in the left bank of Jutaí River, which is about 40km distant from the Jacurapá channel and in the south bank of Solimões River – a major barrier for the dispersal of terrestrial mammals. The third population of *C. rubicundus* occurs in Auati-Paraná channel, which connects the Solimões River to the Japurá River. This region is about 100km northeast to the one from the left bank of Jutaí River, and about 270km east to that from Jacurapá channel. A contact zone between *C. rubicundus* and *C. calvus* was identified by Vieira et al. (2008) in the Aiupiá channel, a south bank tributary of Auati-Paraná channel Figure 4.6

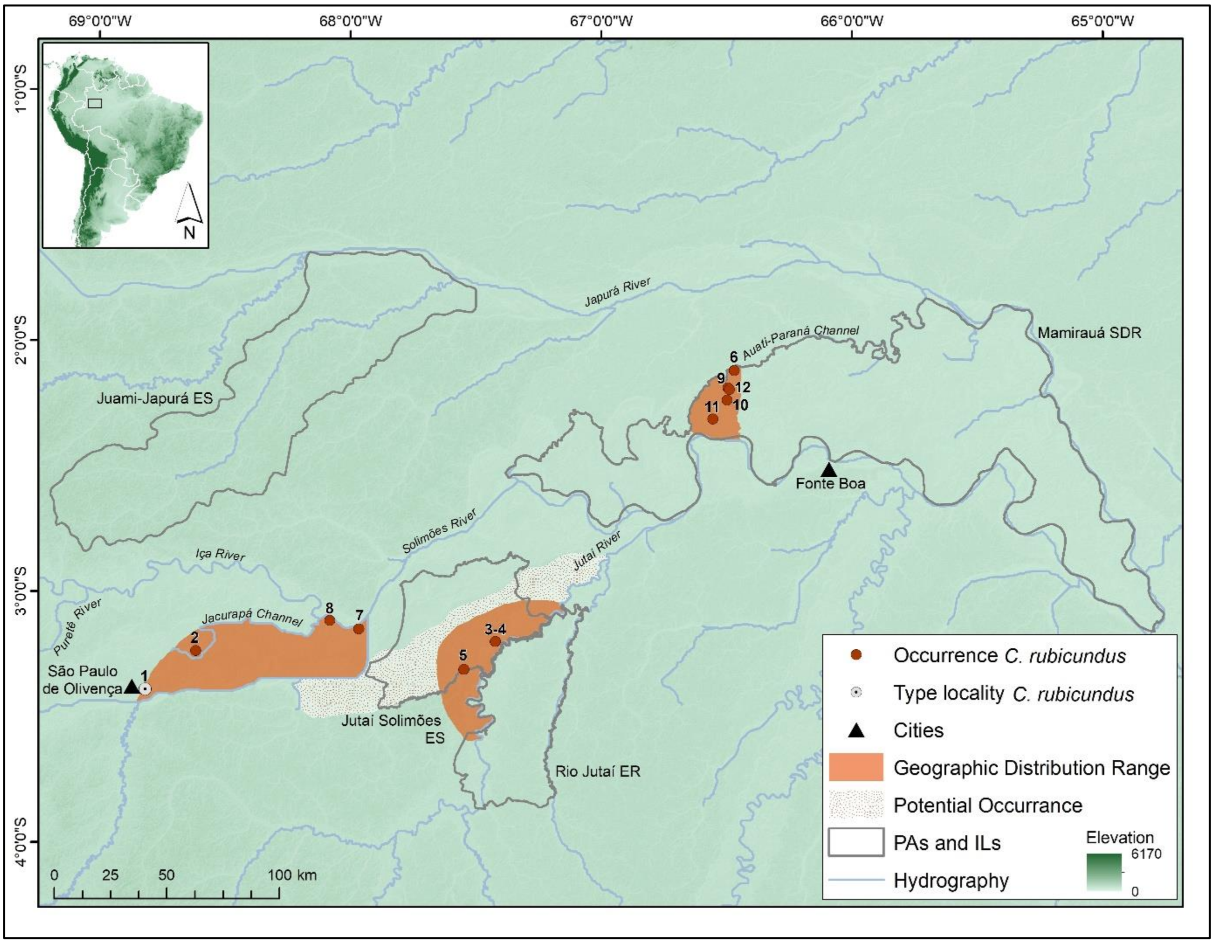

Figure 4.5 The geographic distribution range of *C. rubicundus*. Numbers are represented in Table Suppl. 4-2.

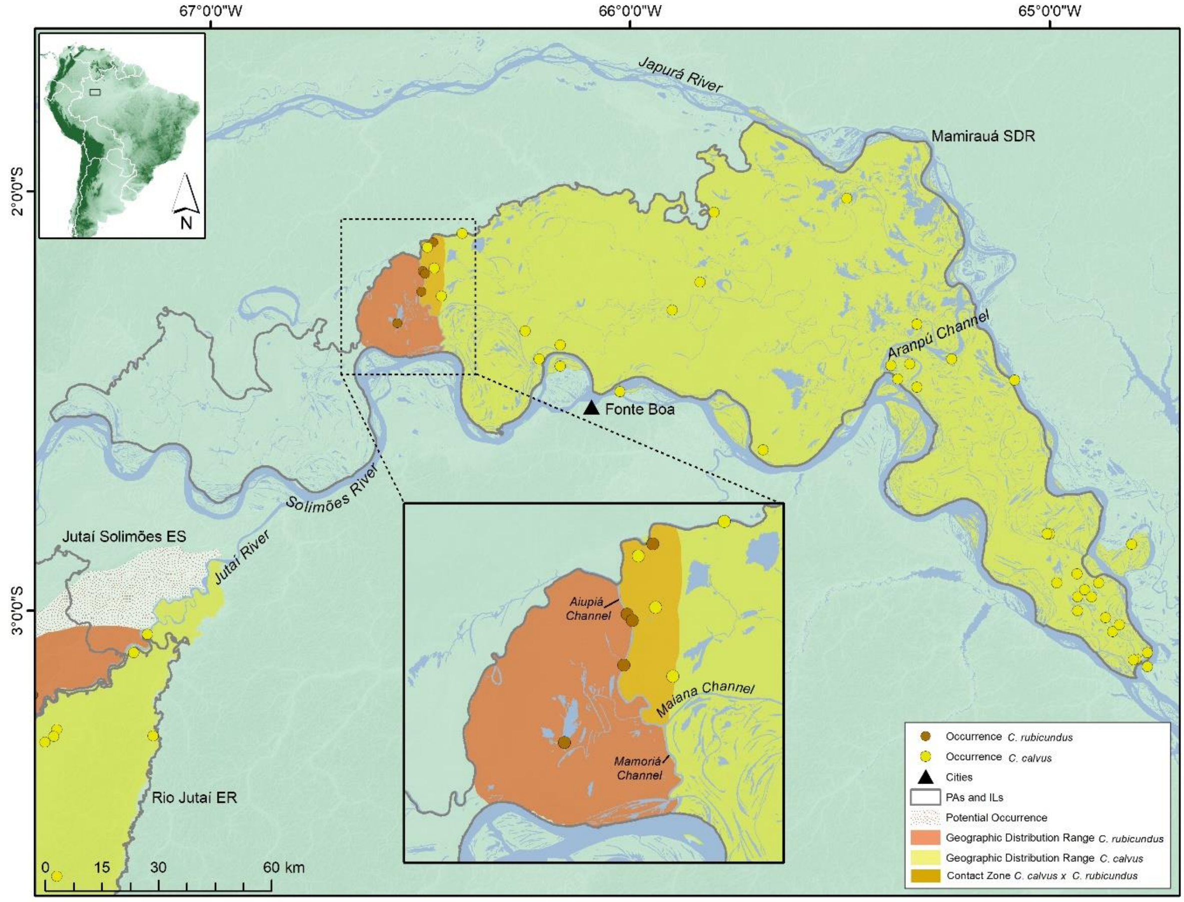

Figure 4.6 Contact zone between *C. calvus* and *C. rubicundus*.

4.3.3 CACAJAO UCAYALII

At the SDNP, I recorded a group of >30 individuals in a *Terra Firme* forest at an altitude of 350 m asl. in the right bank of the upper Moa River (Figure 4.7, Table Suppl. 4-3). The uakaris in that region have the same reddish pattern described by Hershkovitz (1987) for *C. ucayalii*: a "*general coloration entirely reddish orange or reddish golden without sharply contrastingly-coloured nape or midback*". This contrastingly-colored buffy or whitish nape and midback is present only in *C. rubicundus* and *C. novaesi*. Therefore, I confirmed that *Cacajao ucayalii* occur in Brazilian territory at the Serra do Divisor National Park. However, I did not survey the region of Estirão do Equador, where the voucher series MPEG 1848-1854 were collected. Reports from local people indicate that uakaris occur only in the left bank of Javari River – the Peruvian territory – and, possibly, these specimens were collected there and brought to Estirão do Equador – in the Brazilian territory (Mark Bowler, personal communication). *Cacajao ucayalii* has the EOO estimated in 353,507km^2, but also in a disjunct distribution, and with isolated populations found in the Peruvian altitude forests (Vermeer et al. 2013; McHugh et al. 2019) (Figure 4.7, Figure 4.10)

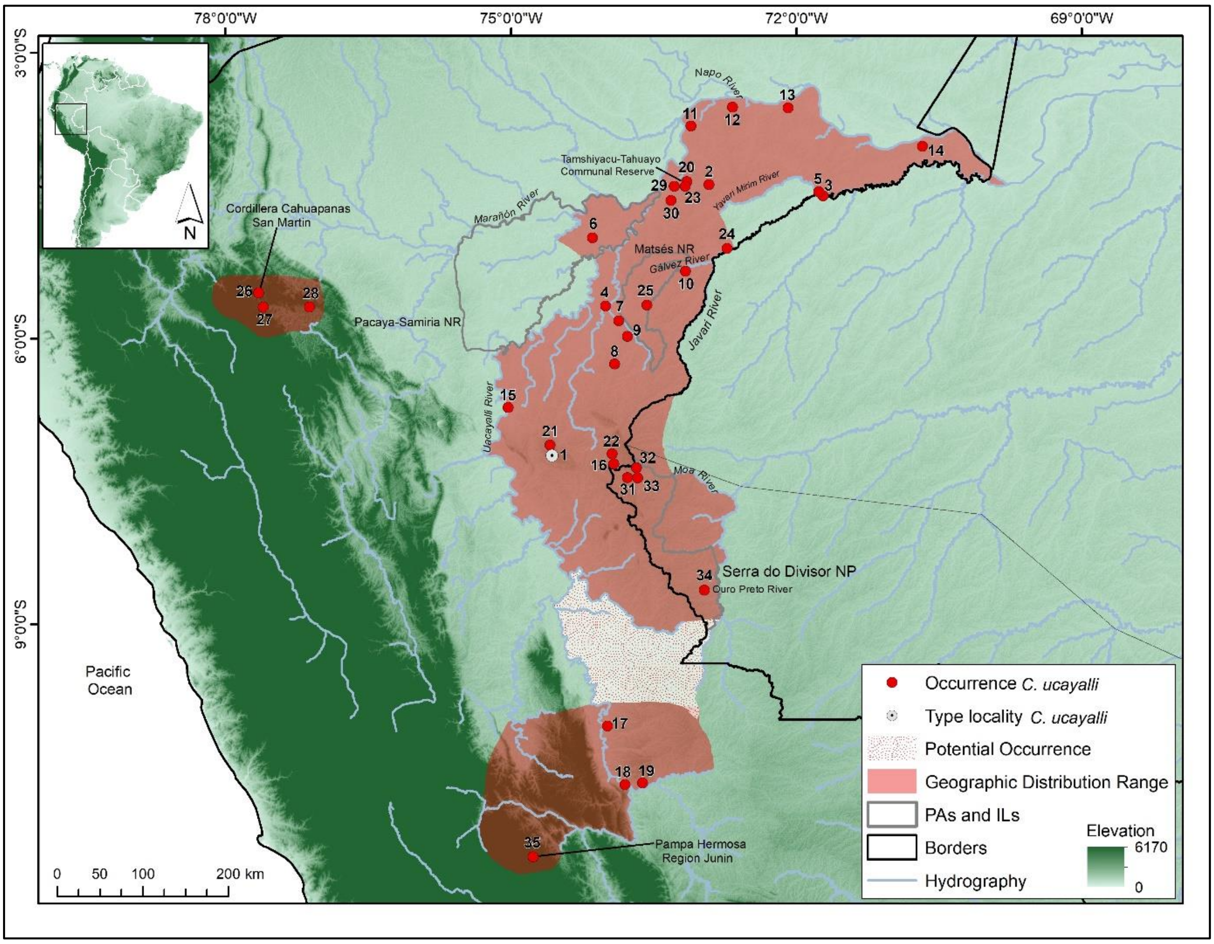

Figure 4.7 The geographic distribution range of *C. ucayalii.* Numbers are represented in Table Suppl. 4-3.

4.3.4 CACAJAO NOVAESI

On the RESEX do Rio Gregório, *C. novaesi* was registered only in the right bank of Gregório River. Also, during the 44 days survey on the Riozinho da Liberdade no bald uakaris were recorded in that area. The Gregório River is the western limit of the geographic range of *C. novaesi* – a finding also supported by the reports of local people. I recorded *C. novaesi* on the left bank of Tarauacá River and at Igarapé Preto (Figure 4.8, Figure 4.9), nearby its type locality (Eiru River), in both *Várzea* and *Terra Firme* forests (Figure 4.8, Table Suppl. 4-4). I did not record this taxon on the right bank of Tarauacá River, but I did record the white uakaris, *C. calvus*, indicating that the Tarauacá River is a significant geographic barrier for bald uakaris.

Cacajao novaesi has the most restricted geographic distribution, limited by the Gregório and Tarauacá rivers, in an estimated EOO of 3,837km^2 (Figure 4.10).

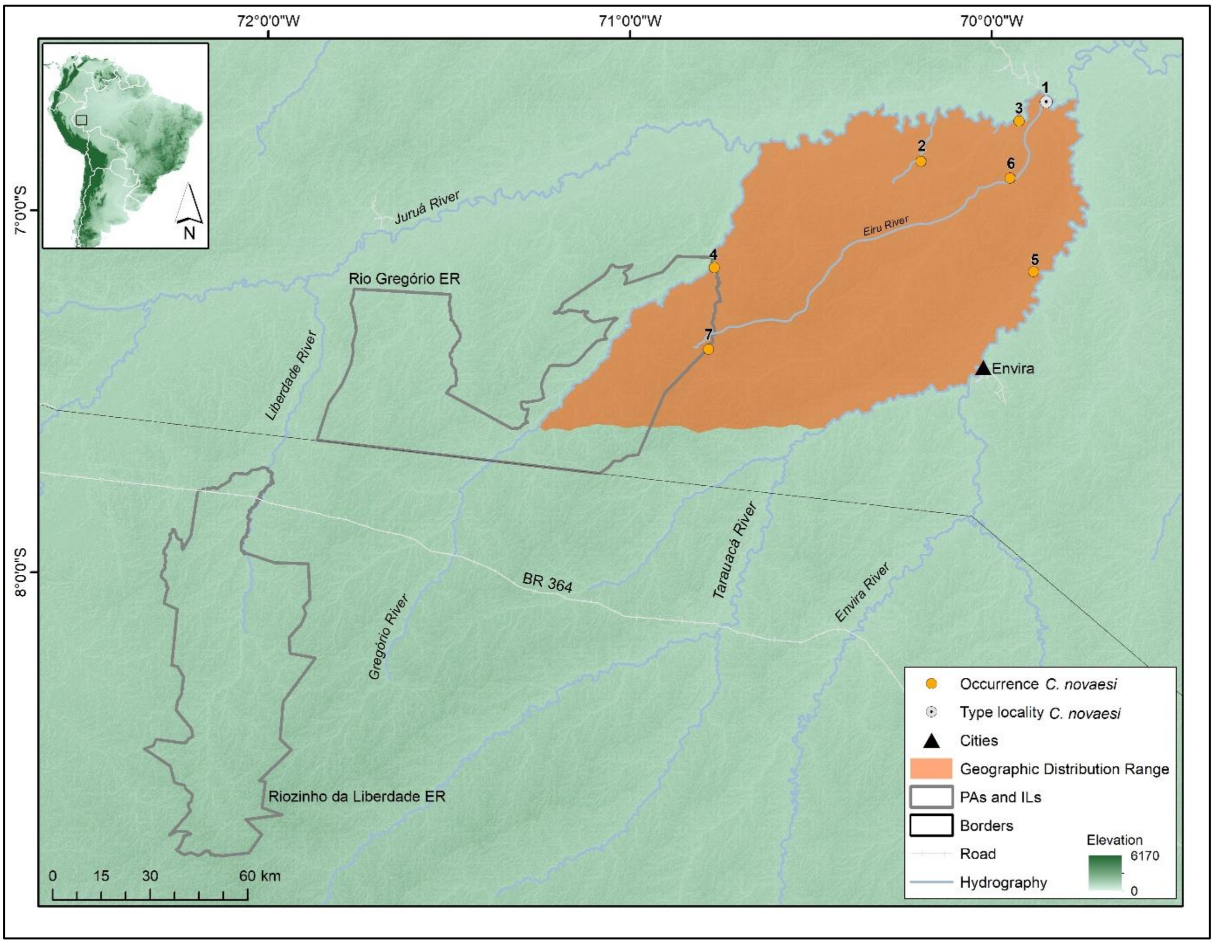

Figure 4.8 The geographic distribution range of *C. novaesi.* Numbers are represented in Table Suppl. 4-4.

Figure 4.9 *Cacajao novaesi* from Igarapé Preto. Photo: Marcelo I. Santana.

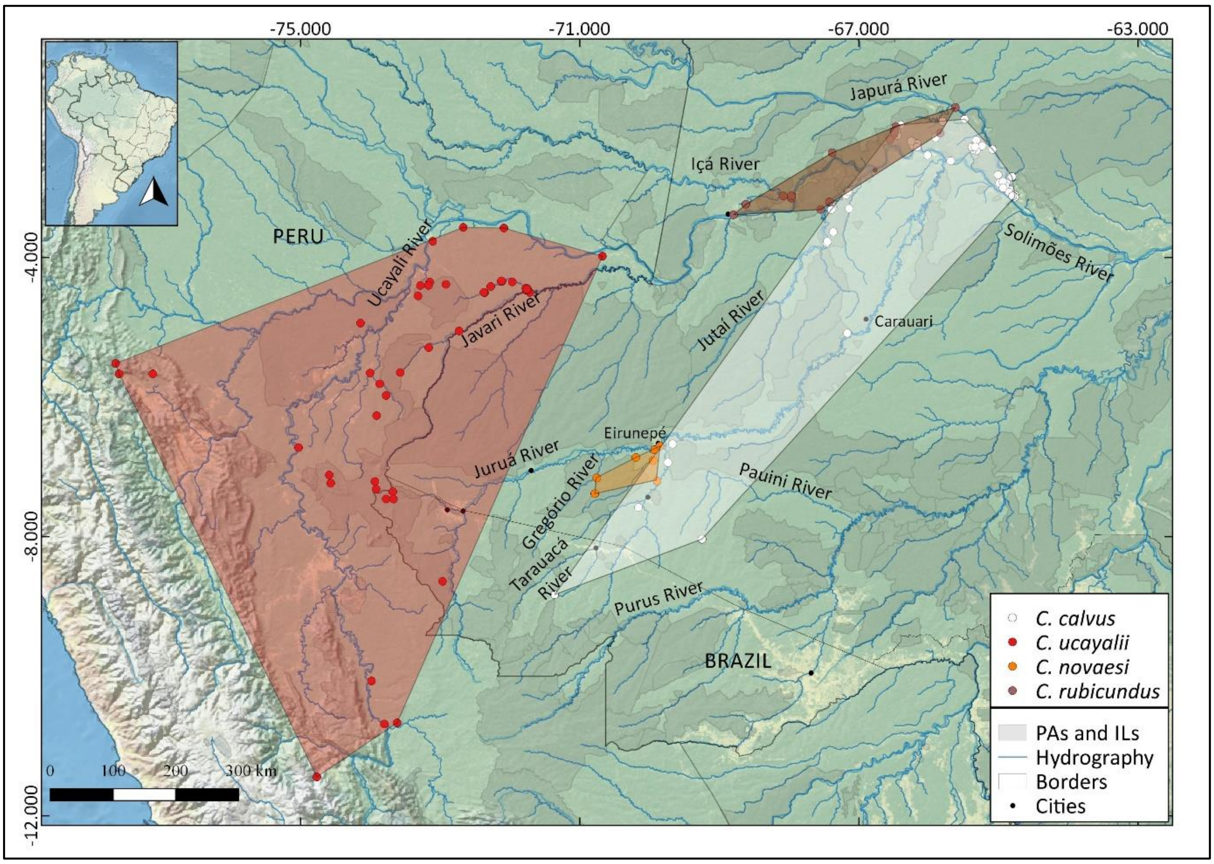

Figure 4.10 The Extent of Occurrence of bald uakaris.

4.4 DISCUSSION

Here I presented an updated dataset on the occurrence and geographic distribution of bald uakaris, and I estimated the EOO for each species. *Cacajao calvus* and *C. ucayalii* have the largest EOO. *Cacajao calvus* is parapatric with *C. novaesi* and has a contact zone with *C. rubicundus* in Mamirauá SDR (Vieira et al. 2008). Although some level of gene flow between these populations could be expected, in all analysis presented in Chapter 3, the white uakaris, *C. calvus*, were very well separated from the clade of the red uakaris. *Cacajao ucayalii* is completely allopatric and occupied a broad range of habitats, rather than mostly flooded forests (Heymann and Aquino, 2010) as found for the bald uakaris in Brazil.

Bald uakaris have a patchy distribution with disjunct populations found in three species. The populations of white uakaris, *C. calvus*, from Mamirauá SDR and right bank of Jutaí River, occur in opposite banks of Solimões River, one of the most significant biogeographic barriers in Amazon Rainforest, and there is a large area between them without any record of bald uakaris. These populations are more than 200km distant from those of the middle Juruá and Tarauacá rivers. Similarly, the three populations of *C. rubicundus* are disjunct, but they are more restricted to the flooded forests of the Solimões River basin. In Brazil, *Cacajao ucayalii* is only confirmed in two localities within the SDNP. The first is the Moa River, a mountain region in the border with Peruvian forests. The second is the Ouro Preto River, a right-bank tributary of Juruá River. Surveys in the Río Yavari are essential to confirm if this taxon occurs in the right bank of this river, in the Brazilian territory. The species was previously recorded in the Sierra del Divisor, in the Peruvian territory (Jorge and Velazco 2006; Heymann and Aquino 2010), a region that is an extension of the geomorphological formation of SDNP. In Peru, isolated populations of *C. ucayalii* have been reported beyond the main known geographic limits. *Cacajao ucayalii* is the only species of bald uakari that occurs in altitude areas and is also recorded in the Sierras de Contamana (~600m asl) (Aquino et al. 2005; Heymann and Aquino 2010) and the mountains of Cordillera Cahuapanas (~1400m asl) (Vermeer et al. 2013). The only species found to occur throughout an interfluve was *Cacajao novaesi*, which has the most restrict Extent of Occurrence (EOO) among bald uakaris. While I did not find evidence of bald uakaris in the left (west) bank of Gregório River– even further to Liberdade River, the Tarauacá River separates the *C. novaesi* and *C. calvus* and is a significant barrier for other primates such as titis and sakis.

Inaccurate information on the occurrence and distribution imply (but are not limited to) in an erroneous list of species of Protected Areas and, therefore, in misguided assessments of species conservation status. Furthermore, problems in the identification of specimens and samples from scientific collections can significantly hinder the understanding of phylogenetic relationships and thus, the evolutionary history of a group. For example, when Figueiredo-Ready et al. (2013) presented their phylogenetic and phylogeographic analysis of *Cacajao*, the authors included the few samples available in scientific collections at the time.

Their phylogenetic analysis, however, had a fundamental problem in the identification of two samples as "*Cacajao calvus novaesi*" (i.e. INPA5241 and UFPA-Ccn1). The first, INPA5241, is stored in the Mammal collection of Instituto Nacional de Pesquisas da Amazonia (INPA), an immature male of white uakari (therefore, *C. calvus*) from the right bank of Tarauacá River (Figure 4.11). This region is nearby that reported by Silva Jr and Martins (1999) (Figure 4.1, Figure 4.11). For the second sample, UFPA-Ccn1, neither skull nor skin was stored in any scientific collection. Figueiredo-Ready et al. (2013), therefore, assumed that this sample would be a *C. novaesi* based on the locality assigned – left bank of Juruá River, nearby Carauari city (Figure 4.1), which in turn is an assumption based on the misidentification of the uakaris from the middle Juruá River years before, as mentioned above.

Figure 4.11 *Cacajao calvus*. A – The specimen INPA5241, an immature male from upper Tarauacá River misidentified as "*novaesi*" by Figueiredo-Ready et al. (2013). B – An adult male from Mamirauá SDR (MNRJ 1705). C – An adult male from Jurupari River, reported by Silva Jr and Martins (1999).

Although the Extent of Occurrence (EOO) represent the area accessible for a species according to its dispersal ability in a certain timeframe, some recent studies have shown that biotic or environmental factors can limit the occupancy within EOO (e.g. *Ateles chamek*, see

Rabelo et al. 2018), which means that the species does not occur throughout its EOO uniformly. For uakaris, some possibilities have been raised to explain the disjunct distribution, but without specific research in this direction. The first explanation for the disjunct distribution is the sampling effect, which sounds reasonable since the few studies on *Cacajao* represent only a small handful of field-sites. Regardless, the evidence presented here support that indeed bald uakaris have disjunct populations; in some situations, hundreds of kilometres distant.

Possibly the most intriguing report is the *C. ucayalii* population found 365km to the west of the known range of the species, in the Cordillera Cahuapanas, San Martin, Peru (Vermeer et al., 2013). *Cacajao ucayalii* has the most extensive distribution and the broadest disjunct populations among the bald uakaris. Also, the species is the only bald uakari occurring in higher elevation away from floodplains. The species' relative flexibility in habitat requirement (Heymann and Aquino, 2010) and its dispersion ability may have been essential to reach these areas. Then, the dynamic changes in the landscape in western Amazonia such as the meandering of the lowland rivers (Rossetti et al. 2015), and the retraction of the flooded forests (várzea) during the late Pleistocene (Pupim et al. 2019) could have influenced the current pattern of occupancy of bald uakaris.

Since disjunct distribution has been reported for other bald uakaris as well, studies on the ecology and behaviour of these different populations will shed light on which key resources are there and may have been crucial to maintaining these isolated populations. For example, one essential plant family in the feeding ecology of the genus *Cacajao* is Lecythidacea (Ayres and Prance 2013). These plants produce fruits with hard husks, and the immature fruits are available in periods of fruit scarcity (especially the dry season) when the uakaris can take some advantage from their adaptation to seed predation (Ayres and Prance 2013). The monitoring of the potential effects of climate change and habitat degradation in Lecythidacea productivity, phenology, and mortality can shed light on how uakaris can adapt to the rapid changes caused by the anthropogenic impacts. The patchy distribution and the isolation of some populations provide a unique opportunity to understand which ecological singularities of each field site may have influenced the evolution of adaptations to the different climatic patterns of the past and which may be essential for future scenarios.

Although the geographic distribution of a species is one of the most basic information underlining conservation actions, many primate species in Amazon Rainforest are still known for only a few records and localities. Species lists are an essential tool for the management of Protected Areas. Only with accurate identification of what are the species legally protected, what are their geographic distribution range, and how sensible they are to habitat alteration caused by deforestation and climate change will be possible to assess their conservation status and plan effective strategies for their long-term Conservation. The Amazonian primates in Brazil require urgent attention to these aspects.

4.5 Supplementary Material – Chapter 4

Table Suppl. 4-1 The occurrence records of *Cacajao calvus*. In bold, the type locality. The localities are represented in Figure 4.3.

	Taxon	Lat	Long	Localidade	Reference
1	***C. calvus***	**-2.5333**	**-66.0167**	**Rio Solimões (left bank), opposite Fonte Boa, Amazonas, Brazil**	**Hershkovitz 1987a**
2	*C. calvus*	-2.8414	-64.8048	Lago Pantaleão, Low Rio Japurá, Amanã Reserve, Amazonas, Brazil	This study
3	*C. calvus*	-2.4156	-65.3781	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	This study
4	*C. calvus*	-2.4113	-65.3337	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	This study
5	*C. calvus*	-3.1150	-64.7936	Comunidade Boca do Mamirauá, Amazonas, Brazil	This study
6	*C. calvus*	-6.6706	-69.6673	Comunidade São Romão, Igarapé Grande, Rio Tarauacá (right bank) , Amazonas, Brazil	This study
7	*C. calvus*	-6.9351	-69.7379	Lago Tucumã, Rio Tarauacá (right bank), Amazonas, Brazil	This study
8	*C. calvus*	-5.5857	-67.5098	Comunidade Santo Antônio do Brito, Uacari SDR (right bank), Amazonas, Brazil	This study
9	*C. calvus*	-5.9170	-67.8309	Comunidade Mandioca, Uacari SDR, Amazonas, Brazil	This study
10	*C. calvus*	-5.9095	-67.9654	Comunidade Sorocaba, Uacari SDR, Amazonas, Brazil	This study
11	*C. calvus*	-5.8767	-67.8731	Comunidade Xibaua, Uacari SDR, Amazonas, Brazil	This study
12	*C. calvus*	-5.1695	-67.3061	Comunidade Fortuna, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
13	*C. calvus*	-5.0760	-67.0518	Comunidade Goiabal, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
14	*C. calvus*	-5.3162	-67.4598	Comunidade Nova União, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
15	*C. calvus*	-5.1082	-67.1287	Comunidade Novo Horizonte, Médio Juruá Extractive Reserve, Juruá River (right bank), Amazonas, Brazil	This study
16	*C. calvus*	-5.0422	-67.2107	Comunidade Roque, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
17	*C. calvus*	-6.0526	-67.9170	Comunidade São Sebastião, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
18	*C. calvus*	-5.5228	-67.7245	Comunidade Tabuleiro, Uacari SDR, Amazonas, Brazil	This study

19	*C. calvus*	-4.8428	-66.9905	Riozinho, Amazonas, Brazil	This study
20	*C. calvus*	-3.1167	-64.8000	Vila Alencar, Amazonas, Brazil	Ayres 1986, MZUSP 17536, 17537, 17542
21	*C. calvus*	-3.1000	-64.7667	Lago Tracajá, Amazonas, Brazil	Ayres 1986, MZUSP 17535, 17539
22	*C. calvus*	-2.9667	-64.9333	Lago Acácio, Amazonas, Brazil	Ayres 1986
23	*C. calvus*	-3.0000	-64.9333	Lago Mamirauá, Amazonas, Brazil	Ayres 1986 IDSM/FES102
24	*C. calvus*	-2.9500	-64.9167	Lago Teiú, Amazonas, Brazil	Ayres 1986
25	*C. calvus*	-2.9333	-64.8833	Lago Jacitara, Amazonas, Brazil	Ayres 1986
26	*C. calvus*	-2.8167	-65.0000	Lago da Campina, Paraná do Jarauá, Amazonas, Brazil	Ayres 1986
27	*C. calvus*	-2.3167	-65.3167	Lago Viola, Paraná do Panauã, Amazonas, Brazil	Ayres 1986
28	*C. calvus*	-2.3667	-66.1667	São José, opposite to Fonte Boa, Amazonas, Brazil	Ayres 1986
29	*C. calvus*	-2.4000	-66.2167	Paraná do Maiana, opposite to Fonte Boa, Amazonas, Brazil	Ayres 1986
30	*C. calvus*	-2.4000	-65.2333	Lago Fortuna, Paraná do Aranapú, Amazonas, Brazil	Cardoso et al. 2014/Ayres 1986
31	*C. calvus*	-3.0167	-64.8667	Setor Mamirauá, Amazonas, Brazil	Cardoso et al. 2014
32	*C. calvus*	-3.0500	-64.8500	Setor Mamirauá, Amazonas, Brazil	Cardoso et al. 2014
33	*C. calvus*	-3.0333	-64.8333	Setor Mamirauá, Amazonas, Brazil	Cardoso et al. 2014
34	*C. calvus*	-2.9667	-64.9000	Setor Mamirauá, Amazonas, Brazil	Cardoso et al. 2014
35	*C. calvus*	-2.8167	-65.0067	São Raimundo do Jarauá, Amazonas, Brazil	Cardoso et al. 2014
36	*C. calvus*	-2.9333	-64.9833	Cauaçú, Amazonas, Brazil	Cardoso et al. 2014
37	*C. calvus*	-2.4667	-65.3167	Comunidade Barroso, Paraná do Aranapu, Amazonas, Brazil	Cardoso et al. 2014
38	*C. calvus*	-2.6167	-65.6833	Comunidade Batalha de Baixo, Amazonas, Brazil	Cardoso et al. 2014
39	*C. calvus*	-2.0167	-65.4833	Paraná Itaúba, Amazonas, Brazil	Cardoso et al. 2014
40	*C. calvus*	-2.0500	-65.8000	Paraná Itaúba, Amazonas, Brazil	Cardoso et al. 2014
41	*C. calvus*	-2.2833	-65.9000	Santa Maria da Agua Branca, Paraná do Panauã, Rio Japurá, Amazonas, Brazil	Cardoso et al. 2014
42	*C. calvus*	-2.2500	-66.4500	Lago Coatá, Paraná Maiana, Amazonas, Brazil	Cardoso et al. 2014
43	*C. calvus*	-2.1000	-66.4000	Igarapé Lua, Paraná Maiana, Amazonas, Brazil	Cardoso et al. 2014

44	*C. calvus*	-2.1333	-66.4833	Igarapé Zefinha, Paraná Aiupiá, Amazonas, Brazil	Cardoso et al. 2014
45	*C. calvus*	-3.2833	-67.3667	Comunidade Cazuza, Paraná do Acural, Rio Jutaí, Amazonas, Brazil	Cardoso et al. 2014
46	*C. calvus*	-3.6333	-67.3667	Paraná Oitero, Rio Jutaí, Amazonas, Brazil	Cardoso et al. 2014
47	*C. calvus*	-3.1000	-67.1833	Comunidade Bordalé, Rio Jutaí, Amazonas, Brazil	Cardoso et al. 2014
48	*C. calvus*	-2.1833	-66.4667	Igarapé Matias, Paraná do Aiupiá, Amazonas, Brazil	Vieira et al. 2008; Cardoso et al. 2014
49	*C. calvus*	-2.4473	-65.3620	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	IDSM/Masto 1383
50	*C. calvus*	-2.9118	-64.9346	Lago Mamirauá, Amazonas, Brazil	IDSM/Masto 283
51	*C. calvus*	-3.1333	-64.7667	Rio Japurá (mouth), Amazonas, Brazil	Hershkovitz 1987a
52	*C. calvus*	-2.3333	-66.2500	Paraná Maiana, Series Lako – MNRJ, Amazonas, Brazil	Hershkovitz 1987a
53	*C. calvus*	-2.4167	-66.1667	Sitio São José, Paraná do Maraui, Amazonas, Brazil	Hershkovitz 1987a
54	*C. calvus*	-2.2167	-65.8333	Panauã (Refuge), Amazonas, Brazil	Rylands and Mittermeier 1983
55	*C. calvus*	-8.8300	-71.3600	Sacado do Tarauacá, Acre, Brazil	INPA/CCM112
56	*C. calvus*	-3.2995	-67.3739	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva et al. 2017
57	*C. calvus*	-3.3130	-67.3946	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva et al. 2017
58	*C. calvus*	-3.0561	-67.1506	Left bank of Riozinho (right-bank tributary of Rio Jutaí)	Silva et al. 2017
59	*C. calvus*	-3.2981	-67.1371	Left bank of Riozinho (right-bank tributary of Rio Jutaí)	Silva et al. 2017
60	*C. calvus*	-3.7919	-67.4583	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva et al. 2017
61	*C. calvus*	-3.7713	-67.4502	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva et al. 2017
62	*C. calvus*	-8.0339	-69.2481	Rio Moaco (right bank tributary of Rio Pauini), Amazonas, Brazil	Sampaio et al. 2018
63	*C. calvus*	-7.5792	-70.1588	Rio Jurupari (right bank tributary of Rio Envira, Acre, Brazil	Silva Jr & Martins 1999
64	*C. calvus*	-5.0833	-67.1667	Lago Fortuna (left bank of Rio Juruá), Carauari, Amazonas, Brazil	Peres 1988; 1997

Table Suppl. 4-2. The occurrence records of *Cacajao rubicundus*. In bold, the type locality. The localities are represented in Figure 4.5

Map Code	Taxon	Lat	Long	Locality	Reference
1	***C. rubicundus***	**-3.3920**	**-68.8250**	**São Paulo de Olivença, opposite, north bank Rio Solimões, Amazonas, Brazil**	**Hershkovitz 1987a**
2	*C. rubicundus*	-3.2369	-68.6181	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	This study
3	*C. rubicundus*	-3.2009	-67.4227	Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva et al. 2017
4	*C. rubicundus*	-3.2008	-67.4226	Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva et al. 2017
5	*C. rubicundus*	-3.3116	-67.5476	Rio Pati (left bank) Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva et al. 2017
6	*C. rubicundus*	-2.1216	-66.4693	Buiussú, Auati-Paraná, Amazonas, Brazil	Ayres 1986, MUZUSP 17552 17553
7	*C. rubicundus*	-3.1500	-67.9667	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	Hershkovitz 1987a
8	*C. rubicundus*	-3.1167	-68.0833	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	Hershkovitz 1987a
9	*C. rubicundus*	-2.1900	-66.4942	Igarapé Preto, Paraná do Aiupiá, Amazonas, Brazil	Vieira et al. 2008
10	*C. rubicundus*	-2.2392	-66.4975	Igarapé do Itaúba, Paraná do Aiupiá, Amazonas, Brazil	Vieira et al. 2008
11	*C. rubicundus*	-2.3142	-66.5550	Lago do Sapateiro, Paraná do Aiupiá, Amazonas, Brazil	Vieira et al. 2008
12	*C. rubicundus*	-2.1961	-66.4892	Igarapé Matias, Paraná do Aiupiá, Amazonas, Brazil	Vieira et al. 2008

Table Suppl. 4-3. The occurrence records of *Cacajao ucayalii*. In bold, the type locality. The localities are represented in Figure 4.7.

Map Code	Taxon	Lat	Long	Locality	Reference
1	***C. ucayalii***	**-7.2333**	**-74.5667**	**Cerro Azul, Contamana, Río Ucayali, Peru**	**Hershkovitz 1987a**
2	*C. ucayalii*	-4.3833	-72.9167	Quebrada Blanco, Peru	Aquino and Encarnacion 1999
3	*C. ucayalii*	-4.5000	-71.7167	Agua Negra-Carolina, Río Yavarí, Peru	Aquino 1998; Aquino and Encarnacion 1999
4	*C. ucayalii*	-5.6550	-74.0036	Río Tapiche, Peru	Bennett et al. 2001
5	*C. ucayalii*	-4.4583	-71.7650	Lago Preto Conservation Concession, Peru	Bowler and Bodmer 2009
6	*C. ucayalii*	-4.9389	-74.1406	Quebrada Ahuara, Río Yanayacu, Pacaya-Samiria National Reserve, Peru	Bowler et al. 2009
7	*C. ucayalii*	-5.8100	-73.8656	Wiswincho, Río Blanco, Peru	Escobedo Torres 2015
8	*C. ucayalii*	-6.2650	-73.9100	Anguila, Trapiche-Blanco interfluve, Peru	Escobedo Torres 2005
9	*C. ucayalii*	-5.9767	-73.7736	Quebrada Pobreza, Trapiche-Blanco interfluve, Peru	Escobedo Torres 2005
10	*C. ucayalii*	-5.2917	-73.1639	Matsés village of Nuevo San Juan, Río Galvez, Peru	Fleck and Harder 2000
11	*C. ucayalii*	-3.7670	-73.1060	Iquitos (opposite), Río Amazonas, Peru	Hershkovitz 1987a
12	*C. ucayalii*	-3.5678	-72.6692	Rio Napo, opposite mouth at Río Amazonas, Peru	Hershkovitz 1987a
13	*C. ucayalii*	-3.5776	-72.0867	Rio Orosa, Río Amazonas, Peru	Hershkovitz 1987a
14	*C. ucayalii*	-3.9802	-70.6743	Chimbote, Río Amazonas, Peru	Hershkovitz 1987a
15	*C. ucayalii*	-6.7225	-75.0289	Sarayacu, opposite, right bank, Río Ucayali, Peru	Hershkovitz 1987a
16	*C. ucayalii*	-7.3167	-73.9167	Rio Bambo, mouth of Río Tapiche, Peru	Hershkovitz 1987a
17	*C. ucayalii*	-10.0667	-73.9833	Rio Tahuania, Río *Ucayalii*, Peru	Hershkovitz 1987a
18	*C. ucayalii*	-10.6833	-73.8000	Lagarto, Alto Río Ucayali, Peru	Hershkovitz 1987a
19	*C. ucayalii*	-10.6667	-73.6167	Rio Inuya, Río Urubamba, Peru	Hershkovitz 1987a
20	*C. ucayalii*	-4.3500	-73.1500	Reserva Comunal Tamshiyacu-Tahuayo (RCTT), Peru	Heymann and Aquino 1994
21	*C. ucayalii*	-7.1160	-74.5885	Ojo de Contaya, Serra del Divisor, Peru	Jorge and Velazco 2006

22	*C. ucayalii*	-7.2085	-73.9345	Tapiche, Serra del Divisor, Peru	Jorge & Velazco 2006
23	*C. ucayalii*	-4.4000	-73.1667	Communal Reserve Tamshiyacu-Tahuayo, Quebrada Cuchara, Peru	Leonard and Bennett 1996; Aquino 1998
24	*C. ucayalii*	-5.0514	-72.7283	Quebrada Curacinha, Río Yavari, Peru	Salovaara et al. 2003
25	*C. ucayalii*	-5.6464	-73.5707	Reserva Nacional Matsés, Alto Río Gálvez, Peru	Torres-Oyarce et al. 2017
26	*C. ucayalii*	-5.5167	-77.6500	Candamo, Cordillera Cahuapanas, Peru	Vermeer et al. 2013
27	*C. ucayalii*	-5.6667	-77.6000	Aguas Verdes Cordillera Cahuapanas, Peru	Vermeer et al. 2013
28	*C. ucayalii*	-5.6667	-77.1167	Kusu Cordillera Cahuapanas, Peru	Vermeer et al. 2013
29	*C. ucayalii*	-4.4000	-73.2833	Quebrada Tangarana, Río Tahuayo, Peru	Ward and Chism 2003
30	*C. ucayalii*	-4.5500	-73.3167	Quebrada Tahuaillo, Río Tahuayo, Peru	Ward and Chism 2003
31	*C. ucayalii*	-7.4589	-73.7744	SDNP - Sítio Norte 5, Brazil	Calouro 1999
32	*C. ucayalii*	-7.3564	-73.6781	SDNP - Sítio Norte 6, Brazil	Calouro 1999
33	*C. ucayalii*	-7.4614	-73.6679	SDNP – Rio Moa, Brazil	This study
34	*C. ucayalii*	-8.6398	-72.9660	SDNP – Rio Ouro Preto, Brazil	Lopes and Rehg 2003
35	*C. ucayalii*	-11.4415	-74.7649	San Antonio village, Región Junín, Peru	McHugh et al. 2019

Table Suppl. 4-4. The occurrence records of *Cacajao novaesi*. In bold, the type locality. The localities are represented in Figure 4.8 The geographic distribution range of *C. novaesi.*Figure 4.8.

Map Code	Taxon	Lat	Long	Locality	Reference
1	***C. novaesi***	**-6.7000**	**-69.8500**	**Santo Antonio, Rio Eiru, Amazonas, Brazil**	**Hershkovitz 1987a**
2	*C. novaesi*	-6.8643	-70.1958	Igarapé Preto, Rio Juruá (right bank), Amazonas, Brazil	This study
3	*C. novaesi*	-6.7532	-69.9248	Igarapé Lontra, Rio Juruá (right bank) , Amazonas, Brazil	This study
4	*C. novaesi*	-7.1577	-70.7670	Igarapé Coatá, Rio Gregório (right bank), Amazonas, Brazil	This study
5	*C. novaesi*	-7,1699	-69,8858	Comunidade Sobral, Rio Tarauacá (right bank)	This study
6	*C. novaesi*	-6.9109	-69.9488	Santa Cruz, Rio Eiru, Amazonas, Brazil	MUZUSP series
7	*C. novaesi*	-7.3833	-70.7833	Santa Cruz, Rio Eiru, Amazonas, Brazil	Hershkovitz 1987a

Chapter 5. Predicting the Effects of Climate Change and Deforestation in the for the Bald Uakaris in Western Amazonia

5.1 INTRODUCTION

5.1.1 – CLIMATE CHANGE, TROPICAL RAINFORESTS AND PRIMATES

Anthropogenic climate change is considered one of the primary threats to biodiversity (Lambers 2015; Mantyka-Pringle et al. 2015; Urban 2015; González-Orozco et al. 2016; Nunez et al. 2019). The scientific community has presented data and discussed the implication of anthropogenic climate change (hereafter, climate change) to the survival of different taxonomic groups (Parmesan and Hanley 2015; Ribeiro et al. 2016; Queirós et al. 2018; Carvalho et al. 2019), with an increasing number of publications warning for the need to have more effective policies for the environment at the national and global levels.

Climate change is expected to affect rainfall regime in tropical ecosystems, (O'Gorman 2015), altering their seasonal rhythms with a significant impact on forest structure and composition (Feng et al. 2013; Greve et al. 2014; Bonal et al. 2016; Allen et al. 2017; Lyra et al. 2017). For example, it is now well established that extreme drought events are directly correlated with forest fires (Alencar et al. 2015; Silva et al. 2018a; da Silva Júnior et al. 2019; Silva Junior et al. 2019), resulting in significant pulse in carbon emission (Aragão et al. 2018). While these extreme droughts are getting worse due the climate change, these effects are aggravated by the increasing deforestation (Staal et al. 2015; Khanna et al. 2017), which in turn is also linked to the forest fires (Alencar et al. 2015; Condé et al. 2019) as observed in the Brazilian Amazon Rainforest in 2019 (MAAP, 2019).

These synergistic effects of climate change and other threats such as deforestation, habitat degradation, in addition to hunting, are the main drivers of Biodiversity loss in Tropical forests. How will species cope with the rapidly shifting conditions will depend on their ability to adapt, disperse, but also on the quantity and quality of remaining suitable habitat available in the future. These questions are mostly unanswered for many groups, although it is suggested that, in general, endemism and lower dispersal capacity are two factors to increase the risk of extinction (Urban 2015).

Non-human Primates are excellent models to investigate the impact of these threats on biodiversity loss. In addition to being a charismatic group and have an essential role in conservation as a flagship species (Mittermeier 1988), they are intrinsically related to tropical rainforest in a sophisticated ecological and evolutionary way (Sussman 1995; Chapman and Onderdonk 1998; Estrada et al. 2017a). The impacts of climate change in primates have been discussed in the literature (Campos et al., 2017; Korstjens and Hillyer, 2016; Nunn et al., 2005; Wiederholt and Post, 2011; Wright, 2006), although some taxa remain particularly poorly studied in this matter (Korstjens and Hillyer, 2016).

Using climatic variables and predicted Land Use/Cover (LUC) scenarios, two recent publications assessed the combined effects of climate change and habitat loss in Primates (Carvalho et al. 2019; Sales et al. 2019). Carvalho et al. (2019) presented a global assessment of 426 primate species using the Land Use/Cover (LUC) and an updated database from the Intergovernmental Panel on Climate Change (IPCC) for climate emission under different scenarios by 2050. For LUC, the scenarios used varied from primary land (best case scenario) to cropland (worst case scenario), with secondary land considered as an intermediate scenario (Carvalho et al. 2019). The authors adopted the climatic scenarios from the IPCC Fifth Assessment Report (IPCC 2014), which combines the general circulation models (GCMs) with mitigation policies for gas emission (Representative Concentration Pathways – RCP) by 2050. According to the predicted level of mitigation on the greenhouse gas emissions, the scenario RCP 4.5 represents the best case, RCP 6.0 the intermediate, and RCP 8.5 the worst-case scenario (Carvalho et al. 2019, see also IPCC, 2014).

Therefore, Carvalho et al. (2019) predicted that Primates would be strongly affected by the increase in the maximum and minimum temperatures and by the decrease in the precipitation in the wettest month (Carvalho et al. 2019). In addition, crop expansion, the increasing of secondary lands into the primate ranges, and the drastic reduction of primary lands (undisturbed habitat), were predicted to expose primates to extinction risk significantly. (Carvalho et al. 2019).

Sales et al. (2019) tested the predicted effects of climate change and deforestation under different scenarios on habitat suitability and dispersal capacity of 80 Amazonian primate species by 2050. The authors used Bioclimatic variables (www.world clim.org, see Hijmans et al., 2005) to estimate habitat suitability considering two scenarios for greenhouse gas emissions (best case scenario – RCP 4.5; and worst-case scenario – RCP 8.5) and combined this information with the predicted effects of deforestation in the following scenarios (Soares-Filho et al., 2006; see also the description of each scenario in Methods session below)

The authors found that, when taking into account the climate change and the dispersal barriers such as rivers or those barriers caused by anthropogenic influence (e.g. deforestation and forest fragmentation), the Amazonian primate would all lose about 90% of the suitable habitat by 2050 (Sales et al. 2019). These findings are essential to assess how the dynamic anthropogenic changes in the ecosystems can synergistically impact primate populations in Amazon Rainforest in the near future. For example, when the barriers for dispersal (natural or anthropogenic) are not considered, most species would find conditions to disperse and expand their ranges into a new area with suitable habitat (Sales et al. 2019). However, in the more realistic prediction, when considered both climate change and deforestation, the ability to disperse would be highly limited and, consequently, would imply in the reduction of the geographic distribution of the species (Sales et al., 2019).

5.1.3 – A BASELINE TO ASSESS THE CONSERVATION STATUS OF BALD UAKARIS

In the last assessment of the IUCN Red List, bald uakaris were listed as “Vulnerable”, a category assigned *Cacajao calvus* ssp. (Veiga et al. 2008); therefore, including the four subspecies of Hershkovitz’ taxonomic proposal. From 2012 to 2014, the Brazilian government – through Chico Mendes Institute for Biodiversity Conservation (ICMBio) – promoted several meetings with taxa specialists to discuss the conservation status of the Brazilian Fauna. Following the same parameters of the IUCN, the ICMBio invited about 1,270 researchers from over 250 institutions across Brazil and overseas (http://www.icmbio.gov.br/portal/faunabrasileira). This multi-institutional and collaborative effort resulted in the expressive number of 12,254 taxa of the Brazilian fauna evaluated, providing a base for the global assessment of many taxa.

In this assessment, each bald uakaris subspecies was considered separately. Accordingly, *Cacajao c. calvus,* and *C. c. rubicundus* were listed as “Least Concern” under the justification that these taxa occur in a low human density region, are well covered by Protected Areas, and there is no evidence of any threat that could imply in population reduction (Azevedo 2015; Paim et al. 2015). While this justification sounds reasonable for the populations of white uakaris (*C. calvus*) from middle Solimões River, those population from Tarauacá River are in a region with increasing human activity. For *C. rubicundus*, it is important to bear in mind that the lack of evidence of threats is mainly because the taxon is the less studied between the bald-headed uakaris. Under a similar justification – the paucity of information on the distribution and threats – *C.c. ucayalii* and *C. c. novaesi* were listed as "Data Deficient" (Calouro 2015; Ravetta 2015), which is the most cautious option when there is no data to assess the conservation status.

In this chapter, I used the Geographic Information System to estimate the amount of forest loss that lies within the Extent of Occurrence (EOO) of each bald uakaris species. I provide an estimate of the species' habitat loss by 2050 using different deforestation scenarios, according to Soares-Filho et al. (2006). I also used three Ecological Niche Modelling algorithms to evaluate the habitat suitability of bald uakaris using climatic variables in two scenarios following the recent publication on the effects of climate change in primates (Carvalho et al. 2019; Sales et al. 2019): 2050 (Mitigation), and 2050 (Business As Usual). The future scenarios indicate the potential effects of climate change in the habitat of bald uakaris. Habitat loss caused by deforestation and/or by climate change can be used as a baseline to assess the conservation status of bald uakari. The thirty years' time window represents three uakari generation time, which is a period indicated to evaluate how the threats will impact the species and, therefore, determine their conservation status (IUCN 2012). Here, I am considering each taxon at the species level, according to the analysis presented in Chapter 3.

5.2 METHODS

5.2.2 – DEFORESTATION SCENARIOS

I used QGIS version 3.4.5 (QGIS Development Team 2019) to overlay the polygon of each species' geographic range, the Protected Areas (PAs) and Indigenous lands (ILs) (UNEP-WCMC 2017), and the following deforestation scenarios modelled for the Amazon Rainforest (Soares-Filho et al. 2006):

1. Business-As-Usual (BAU): where the deforestation trends will continue, with the implementation of the roads and highways (road paving) as scheduled, the legislation related to the forest reserves on private lands will remain ineffective and without the creation of new Protected Areas.

2. Governance: where the environmental legislation is effectively implemented in the Amazon Rainforest, with the enforcement of mandatory reserves on private properties, and where the expansion of the Protected Areas network will play a fundamental role in suppressing the deforestation.

I applied these scenarios to assess how much habitat of each species will be lost by 2050 (in 30 years). This period represents three-generation time estimated for *Cacajao*, a criterion adopted by IUCN to assess the population decline (IUCN/SSC 2007). Similar approaches have been used in other studies as a baseline for the assessment of the Conservation Status of Amazonian primates (Ochoa-Quintero et al. 2017; Rabelo et al. 2018; Silva et al. 2018d, c; Boubli et al. 2019).

5.2.3 ECOLOGICAL NICHE MODELLING (ENM)

The density of records is higher in some field sites with long-term researches (e.g. Mamirauá SDR), which may imply in a biased analysis of habitat suitability. Therefore, I randomly removed duplicate records within a 5 km radius to control for sampling bias (Boria et al. 2014). After filtering, I got 95-point locations for bald uakaris, including 39 *C. calvus*, 12 *C. rubicundus*, 38 *C. ucayalii*, and 6 *C. novaesi*.

I selected 19 Bioclimatic variables derived from the monthly temperature and rainfall values, which are expected to influence the species distributions in the Western Amazonia (Table 5-1). The bioclimatic variables represent annual and seasonal trends and extreme or limiting environmental conditions (Hijmans et al. 2005). After the cropping of the variables in the study area, I performed a pair-wise correlation test and removed those highly correlated, avoiding collinearity (Figure Suppl. *5-1*, Table Suppl. *5-1*).

I used three presence-only algorithms widely used in Ecological Niche Modelling (Elith et al. 2006; Tsoar et al. 2007; Ren-Yan et al. 2014): BIOCLIM, DOMAIN, MAXENT (maximum entropy). The BIOCLIM model uses the environmental variables and the species presence records to indicate habitat suitability for the species (Tsoar et al. 2007; Ren-Yan et al. 2014). The DOMAIN model is based on the Grower metric to provide a point-to-point similarity between two sites (Carpenter et al. 1993). MAXENT is based on the maximum entropy algorithm, which enables the predictions using only presence records and background samples that represent information on the habitat availability (Phillips et al. 2006). For all analysis, I used the package *Dismo* 1.1-4 (RStudio Team 2019).

For all models, I used 5,000 background points, and I set the data to 30% of testing and 70% of training. For the model evaluation and comparison, I used the AUC statistic, which is defined as the area under the receiver operating characteristic curve (ROC). I followed the same parameters presented in Ren-Yan et al. (2014), where the AUC statistic values between 0.90 and 1.0 are considering “excellent”; 0.8 and 0.9 “very good”; 0.7 and 0.8 “good”; 0.6 and 0.7 “fair” and below 0.6 “poor”. Considering that each model has a different mathematical algorithm and thus can retrieve a different prediction based on the set of variables, conditions, and data available (Guisan et al. 2017), I used an ensemble of the models to derive a final general prediction. Accordingly, the final model was derived from the mean of the three algorithms weighted by the AUC values.

Table 5-1 Climatic variables (https://www.worldclim.org/bioclim; (Hijmans et al. 2005) expected to influence the distribution of the bald uakaris. Variables used in the final model are in bold.

Code	Variable
BIO1	**Annual Mean Temperature**
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	**Isothermality (BIO2/BIO7) (* 100)**
BIO4	**Temperature Seasonality (standard deviation *100)**
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	**Temperature Annual Range (BIO5-BIO6)**
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	**Annual Precipitation**
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	**Precipitation of Driest Quarter**
BIO18	**Precipitation of Warmest Quarter**
BIO19	**Precipitation of Coldest Quarter**

5.3 RESULTS

5.3.2 –DEFORESTATION

In terms of forest cover, I calculated a loss of 73,123km² or 11% of habitat within the bald uakaris ranges under the Governance scenario in the next 30 years. Under the BAU scenario, I estimated a loss of 123,448 km² or 18% of the habitat within the range of bald uakaris for the same period (Figure 5.1, Table 5-2). Considering the Governance scenario, the deforestation within the EOO of each species is relatively low, reaching more than 10% only for *C. ucayalii* (Figure 5.1, Table 5-2). Under the BAU scenario, however, the deforestation is more intense in the south due to the highway BR 364, with *C. ucayalii* and *C. novaesi* presenting the higher level of habitat loss (20% and 45%, respectively) (Figure 5.1, Table 5-2). *Cacajao rubicundus* and *C. calvus* presented the lower deforestation level.

However, the populations of *C. calvus* from the south and north will be affected differently since the deforestation in the region of the upper Juruá will be more intense due to the highway BR 364.

Table 5-2 The Extent of Occurrence (EOO) and the deforestation for each bald uakari species under two scenarios of deforestation for Amazon Rainforest by 2050.

	EOO	Deforestation (Km2)		Deforestation (%)	
Species	(Km^2)	Governance	BAU	Governance	BAU
C. calvus	151,777	9886	19976	0.07	0.13
C. rubicundus	15,864	314	728	0.02	0.05
C. ucayalii	300,650	45197	59616	0.15	0.20
C. novaesi	3,852	113	1732	0.03	0.45

5.3.3 ECOLOGICAL NICHE MODELLING (ENM)

Considering the three algorithms used here, DOMAIN had a lower performance when compared with BIOCLIM and MAXENT. Even so, the statistical performance of this model (AUC=0.778) is considered “good” (see Ren-Yan et al. 2014). BIOCLM and MAXENT presented an AUC value considered “very good” for the model evaluation (0.802 and 0.861, respectively) (Ren-Yan et al., 2014), with MAXENT performing better (Figure *5.2*). The most significant variables were Precipitation of Warmest Quarter (Bio18) and Precipitation in the Driest Quarter (Bio17), which, together, contribute to 71.71% to the MAXENT model gain (Table 5-3). Accordingly, the precipitation variation may influence the conditions required for the habitat suitability of bald uakaris in the Western Amazon.

Although all models were consistent to show a reduction in the habitat suitability for the bald uakaris, they differed in how the climatic variables could affect the habitat. The three algorithms indicated a reduction in the area of suitable habitat by 2050 under both mitigation and BAU scenarios. BIOCLIM was the most restrictive algorithm and showed almost inadequate habitat suitability in the future scenarios (Figure Suppl. *5-2*). The DOMAIN model indicated a decrease in the area of suitable habitat, but this reduction seems to affect mainly the southern populations (Figure Suppl. *5-3*). MAXENT indicated higher habitat suitability but in a smaller area (Figure Suppl. *5-4*). The ensemble model indicated how this reduction in the habitat suitability in the next 30 years would affect the four species of bald uakaris (Figure *5.3*).

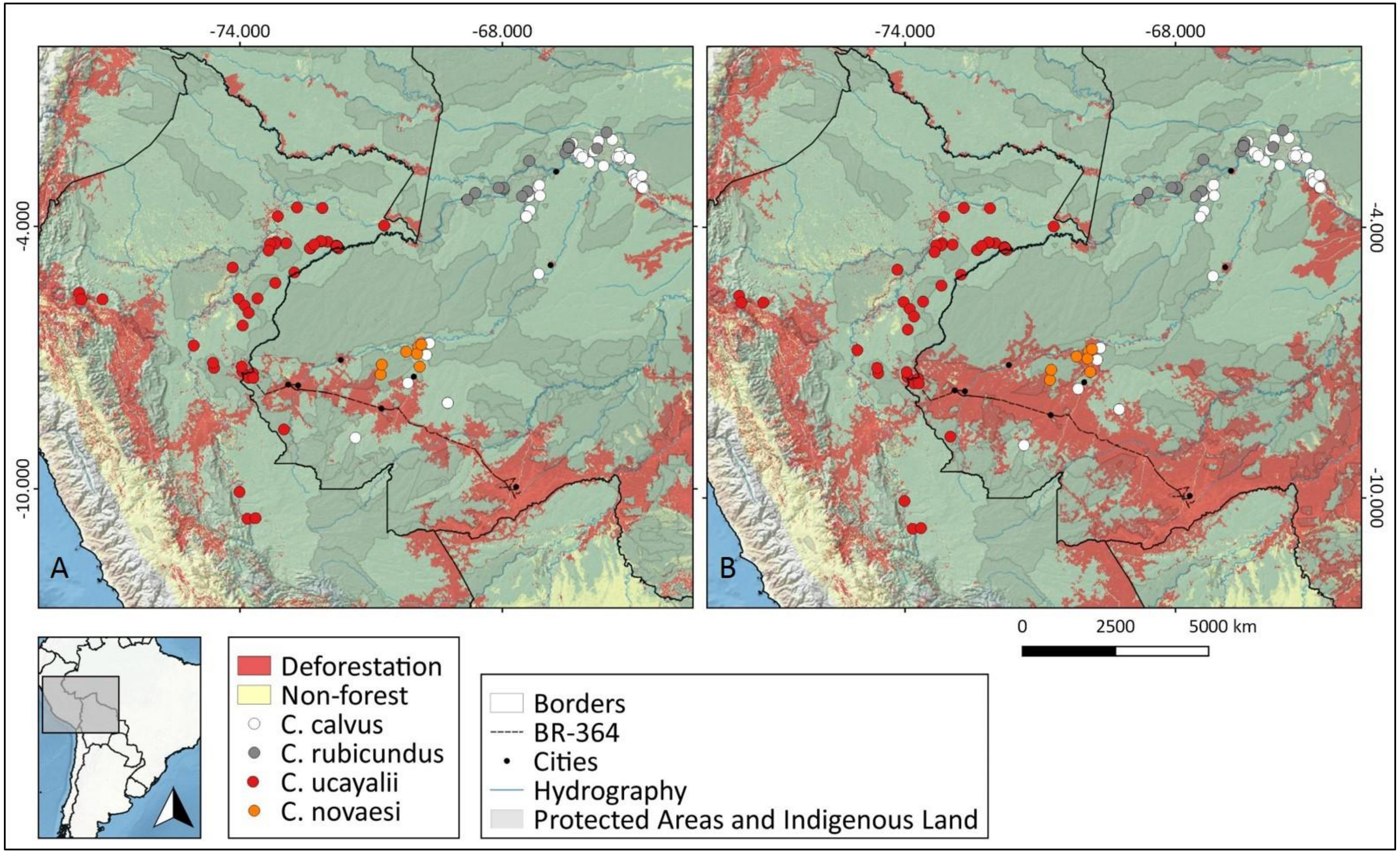

Figure 5.1 The predicted habitat loss within the geographic range of the four bald uakari species under the "Governance" (B) and "Business as Usual" (C) scenarios by 2050.

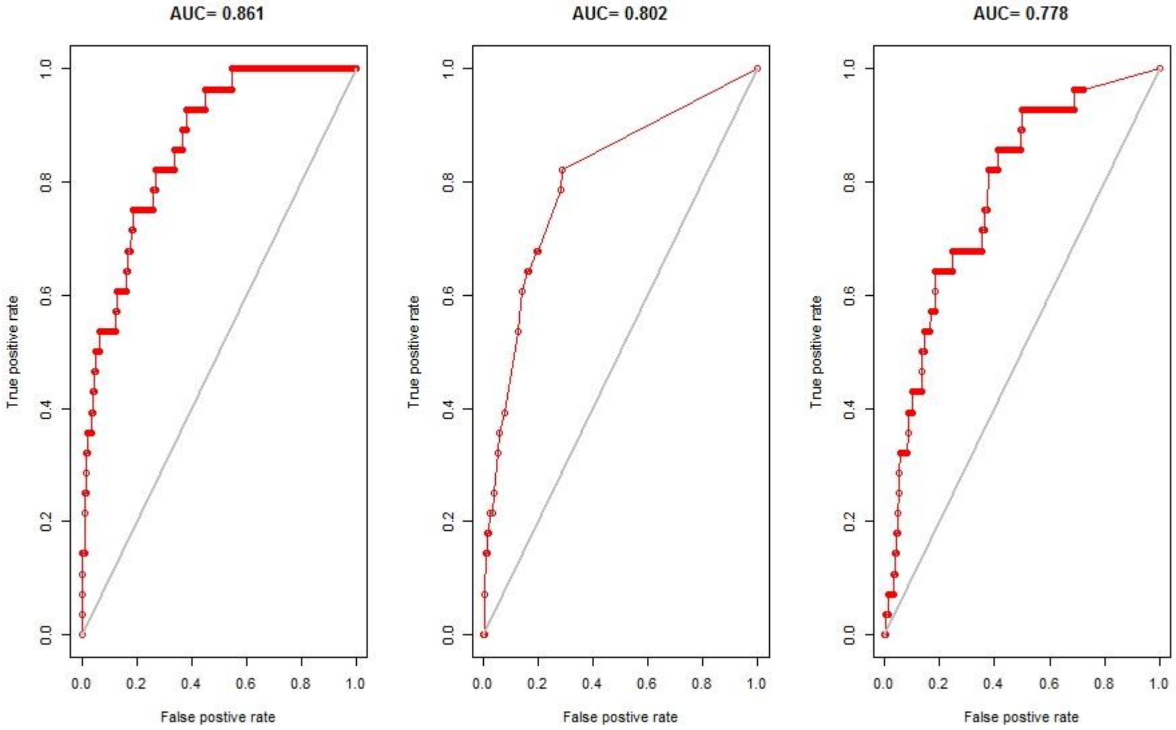

Figure 5.2 The AUC statistic value for the MAXENT (left), BIOCLIM (center) and DOMAIN (right) models.

Table 5-3 The mean values of the percentage of variable contribution and permutation importance to the MaxEnt Model.

	Percent Contribution	Permutation Importance
Bio18	50.99	11.59
Bio17	20.72	35.67
bio03	9.73	10.74
bio19	6.64	15.99
Bio04	5.67	12.65
Bio01	2.74	3.68
Bio07	1.80	3.80
Bio12	1.72	5.88

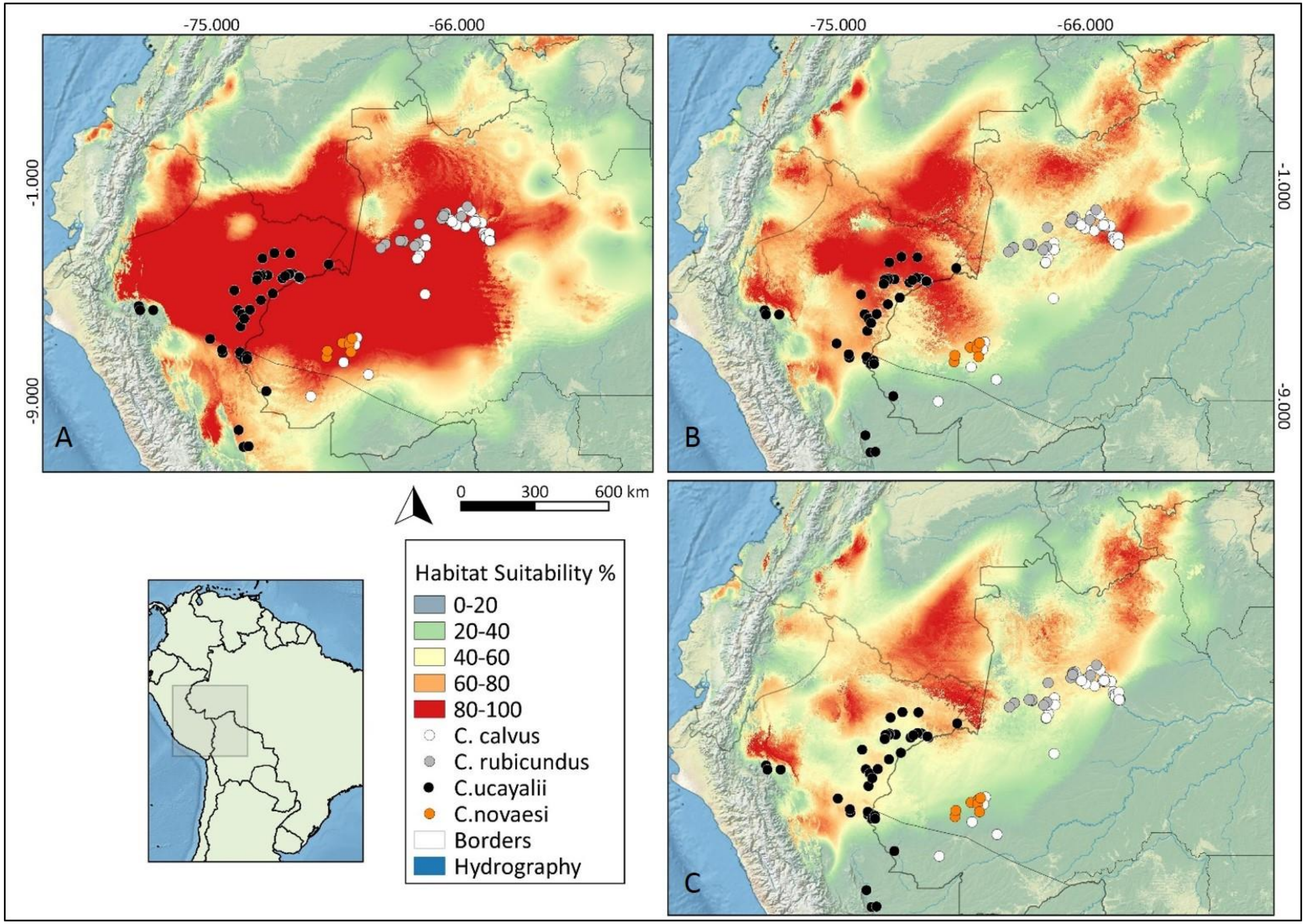

Figure 5.3 The Ensemble Modelling (Bioclim+Domain+MaxEnt) weighted by the AUC values for the current (A) and future scenarios (B – Mitigation; C – BAU).

5.4 DISCUSSION

Here I presented how bald uakaris will be affected by habitat loss and climate change in the next 30 years (by 2050). Under the Governance scenario of deforestation, the habitat loss for all species will be relatively low. However, the BAU scenario pointed out an evident habitat reduction for the southern populations, which include *C. ucayalii*, *C. novaesi* and the populations of *C. calvus* from Tarauacá River. The three algorithms of ENM varied in representing how the climatic variables would affect the occurrence of the species in the future, with DOMAIN and BIOCLIM showing lower habitat suitability in a smaller area; and MAXENT indicating higher suitability but concentrated in a well-delimitated and reduced area. The most significant variables to estimate the habitat suitability were related to precipitation, which is essential to drive the flood pulse in the periodically inundated forests (Junk et al. 2011). The periodic flood and droughts will, in turn, affect the organisms living in these areas, not only the bald uakaris.

5.4.2 – THREATS AND FUTURE SCENARIOS FOR BALD UAKARIS CONSERVATION

Deforestation will affect the four species of bald uakaris in different proportion. The populations of *C. calvus* and *C. rubicundus* from Solimões and Jutaí river basin mostly occur within Protected Areas, in a region with a low rate of deforestation and human population densities. Therefore, the predicted deforestation in this region will represent a small amount of habitat loss for these populations. Furthermore, although hunting is essential for the subsistence of traditional communities in Amazon Rainforest, bald uakaris were not listed as a target species in a long-term hunting monitoring program in middle Solimões River (Pereira et al. 2019b). Considering 4,218 hunting events for 11 years (2003-2013), Pereira et al. (2019b) registered 10,992 animals hunted, including 541 primates individuals of nine species, and without any records of bald uakaris.

However, the scenario is different for those populations from the Tarauacá River. The highway BR-364 cut through the main rivers (i.e. Gregório, Envira, Eiru and Tarauacá rivers) where *C. novaesi* and *C. calvus* occur. This area is a hotspot of deforestation in Acre State connecting the largest cities of Acre State (such as Cruzeiro do Sul and Rio Branco) to

Rondônia State – where the deforestation rate is one of the highest of the Amazon Rainforest. In Peru, the populations of *C. ucayalii* are more exposed to the risk of habitat loss due to the deforestation in the south region (MAAP 2018).

Although bald uakaris are not hunted in the region of Solimões River (Pereira et al., 2019b), there are reports of hunting in Tarauacá and Gregório rivers. The proximity of the areas where I recorded *C. novaesi* to cities such as Eirunepé, Envira, Tarauacá and Feijó seems to increase hunting pressure. Aside from intensifying economic and cultural changes, the roads that interconnect these cities may provide hunters access to deeper parts of the forest, resulting in the overexploitation of source areas of wildlife (Ayres et al. 1991; Espinosa et al. 2014). For instance, hunting events of *C. novaesi* were reported by locals in the border of BR-364 highway, near Feijó city; and, nearby the Eiru River, it was reported by locals the hunting of about 15 individuals of *C. novaesi* during one single event – a strategy commonly adopted to hunt large herds of peccaries (*Tayassu pecari*). *Cacajao novaesi* was also listed as the third most hunted primate at the Gregório Extractive Reserve (Amazonas 2010). At Igarapé Preto and low Tarauacá River, I did not record atelids, the largest Neotropical primates usually consumed by local communities (Peres 1990; Rosin and Swamy 2014). However, these primates were reported to have its abundance decreased in the recent past decades. According to locals from these areas, medium-bodied primates such as *Cebus* and *Cacajao* are an important protein source, possibly a mechanism to compensate their foraging returns on the absence of large-sized overhunted terrestrial mammals. A similar situation is reported in Peru, and the overhunting may be responsible for the population reduction of *C. ucayalii* in some areas (Puertas and Bodmer 1993; Bodmer 1995; Ward and Chism 2003; Benessaiah 2007; Vermeer et al. 2013). These reports and records provide essential information on the threats for bald uakaris, although a systematic data set in these areas is still required. An evaluation of hunting pressure on these populations, especially in areas close to the roads and cities, is urgently needed.

The middle Solimões River, especially the region of Mamirauá SDR, will stand the last suitable habitat for bald uakaris in Brazil in the future scenarios of gas emission (RCP 4.5). While the ensemble model shows an area of habitat suitability in the north of Brazil, is highly unlikely that they reach that region since the two significant biogeographic barriers (Japurá and Negro rivers) and the presence of the black uakaris in these areas would hamper the dispersion of bald uakaris into the newly suitable areas.

Although there are only two long term studies on the ecology of bald uakaris (*C. calvus* - Ayres, 1986; *C. ucayalii* - Bowler and Bodmer, 2011), they pointed to the importance of the seasonal availability of key resources in the diet of bald uakaris. The temporal variation in the diet of bald uakaris is related to the seasonal variation in the water regime (flood pulse, rainfall) (Ayres 1986). Although an increase in forest productivity as a response of the higher CO2 levels has been suggested (Phillips et al. 2009; Korstjens and Hillyer 2016), there is no evidence on how Amazonian primates will cope with possible changes in the availability of key resources. The adaptation for seed predation allows uakaris to access an essential item – seeds of unripe fruits – that is not accessed by other primates (Barnett et al. 2013). However, the ripening of key resources is essential in periods of seasonal shortage. For example, in Lago Preto, Peru, Bowler and Bodmer (2011) found that the ripening of one key resource – the palm tree *Mauritia flexuosa* – was essential in *C. ucayalii* diet during four months per year (from May to August), which was a period of fruit scarcity. The balance in forest productivity and uakari food selection also implies in a range of behavioural adaptations such as foraging strategies, group size, use of space and reproduction. How the uakaris will cope with the changes in the temporal availability of resources is an unanswered question and will significantly influence their long-term survival.

Since disjunct distribution has been reported for bald uakaris, studies on the ecology and behaviour of these different populations will shed light on which key resources are there and may have been crucial to maintaining these isolated population under different future scenarios. For example, one essential plant family in the feeding ecology of the genus *Cacajao* is Lecythidacea (Ayres and Prance 2013). These plants produce fruits with hard husks, and the immature fruits are available in periods of fruit scarcity (especially the dry season) when the uakaris can take some advantage from their adaptation to seed predation (Ayres and Prance 2013). The monitoring of the potential effects of climate change and habitat degradation in Lecythidacea productivity, phenology, and mortality can shed light on how uakaris can adapt to the rapid changes caused by the anthropogenic impacts.

Considering the vulnerability of species to Climate Change, Foden et al. (2013) developed a framework that includes three dimensions: “Sensitivity”, “Exposure”, and “Low Adaptative Capacity”. Accordingly, a high “Sensitivity” species has a low potential for long-term survival (in situ) because they have strict ecological conditions (Foden et al. 2013). While there is no information on the effects of climate change in the ecology of uakaris, the isolated populations are potentially more exposed to local extinction, have a smaller proportion of individuals reproducing, and, in some cases, are under the synergistic effects of threats such as deforestation and hunting (especially for *C. ucayalii* and *C. novaesi*). Therefore, a critical component of the "Sensitivity" to be considered for some populations of bald uakaris is "rarity", which according to Foden et al. (2013):

"The inherent vulnerability of small populations to allee effects and catastrophic events, as well as their generally reduced capacity to recover quickly following local extinction events, suggest that many rare species will face greater impacts from climate change than more common and/or widespread species" (Foden et al. 2013, p. 7)

The second component of the vulnerability to the Climate Change considered by Foden et al. (2013) was the "Exposure", which measures the level of changes of the species' physical environment, i.e. the environmental variables used in the Ecological Niche Modelling. In this sense, according to the analysis presented in this chapter, the precipitation was identified as the main variable for the habitat suitability of bald uakaris in all scenarios and is essential in the dynamic of the flood pulse and rainfall in the Western Amazonia. Finally, the component "low adaptive capacity" primarily reflects the capacity of the species to cope with the relatively rapid changes in the environment through dispersal or adaptation. In the case of bald uakaris, the models indicate a shift in the area of habitat suitability to the north of Brazil and Colombia. As mentioned above, it is highly unlikely that bald uakaris will be able to disperse to this area in a relatively short time due to significant biogeographic barriers and the presence of other *Cacajao* species in those areas.

In summary, bald uakaris are highly vulnerable to climate change, although information on the habitat characteristics and use for the different populations are urgently needed to assess the sensitivity of each species, i.e. Ecological response. The patchy distribution and the isolation of some populations provide a unique opportunity to understand which ecological singularities of each field site may have influenced the evolution of adaptations to the different climatic patterns of the past and which may be essential for future scenarios.

5.5 Supplementary Material - Chapter 5

Table Suppl. 5-1 Pair-wise matrix of correlation coefficients between environmental variables. In bold, the Correlation coefficients > 0.75.

	bio01	bio02	bio04	bio05	bio06	bio07	bio08	bio09	bio10	bio11	bio12	bio13	bio16	bio17	bio18	bio19
bio01	1.0000															
bio02	-0.4422	1.0000														
bio04	-0.1274	0.2134	1.0000													
bio05	**0.9644**	-0.2431	-0.0001	1.0000												
bio06	**0.9551**	-0.6576	-0.2065	**0.8569**	1.0000											
bio07	-0.2901	**0.8811**	0.4003	-0.0422	-0.5511	1.0000										
bio08	**0.9939**	-0.4157	-0.1003	**0.9610**	**0.9366**	-0.2598	1.0000									
bio09	**0.9912**	-0.5013	-0.1341	**0.9463**	**0.9730**	-0.3541	**0.9745**	1.0000								
bio10	**0.9972**	-0.4376	-0.0588	**0.9706**	**0.9491**	-0.2685	**0.9923**	**0.9896**	1.0000							
bio11	**0.9974**	-0.4562	-0.1930	**0.9548**	**0.9595**	-0.3140	**0.9893**	**0.9902**	**0.9907**	1.0000						
bio12	0.4542	-0.4754	-0.3449	0.3461	0.5374	-0.4815	0.4249	0.4854	0.4317	0.4687	1.0000					
bio13	0.5027	-0.3386	-0.2054	0.4776	0.5302	-0.2544	0.4599	0.5420	0.4944	0.5130	**0.8073**	1.0000				
bio16	0.5177	-0.3427	-0.2132	0.4907	0.5381	-0.2486	0.4776	0.5513	0.5082	0.5273	**0.8411**	**0.9850**	1.0000			
bio17	0.2116	-0.4988	-0.3952	0.0301	0.3721	-0.6724	0.1975	0.2466	0.1824	0.2301	**0.7833**	0.3716	0.3893	1.0000		
bio18	0.0695	-0.1583	-0.3496	-0.0507	0.1071	-0.2898	0.1014	0.0304	0.0362	0.0838	0.6245	0.2981	0.3414	0.6685	1.0000	
bio19	0.3437	-0.5746	-0.1803	0.2226	0.5146	-0.6372	0.2762	0.4292	0.3378	0.3528	0.6757	0.6179	0.6123	0.5954	0.1158	1.0000

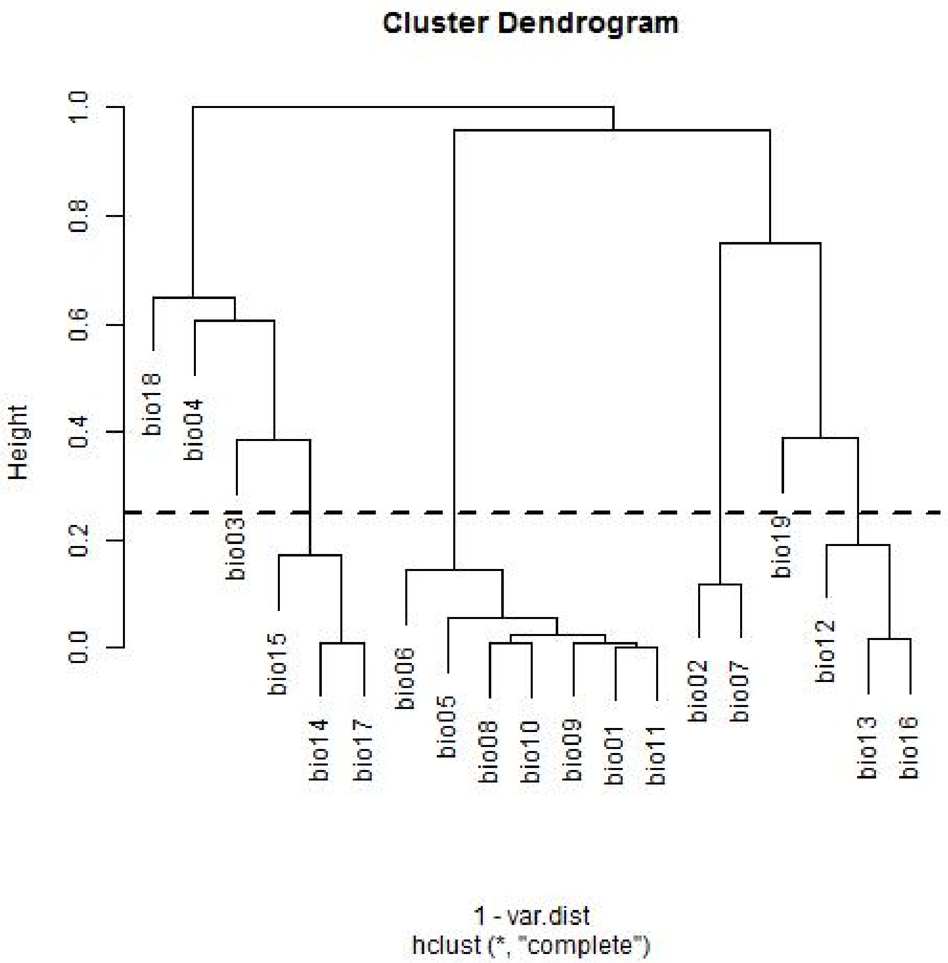

Figure Suppl. 5-1 Pearson’s correlation coefficients of the 19 environmental variables.

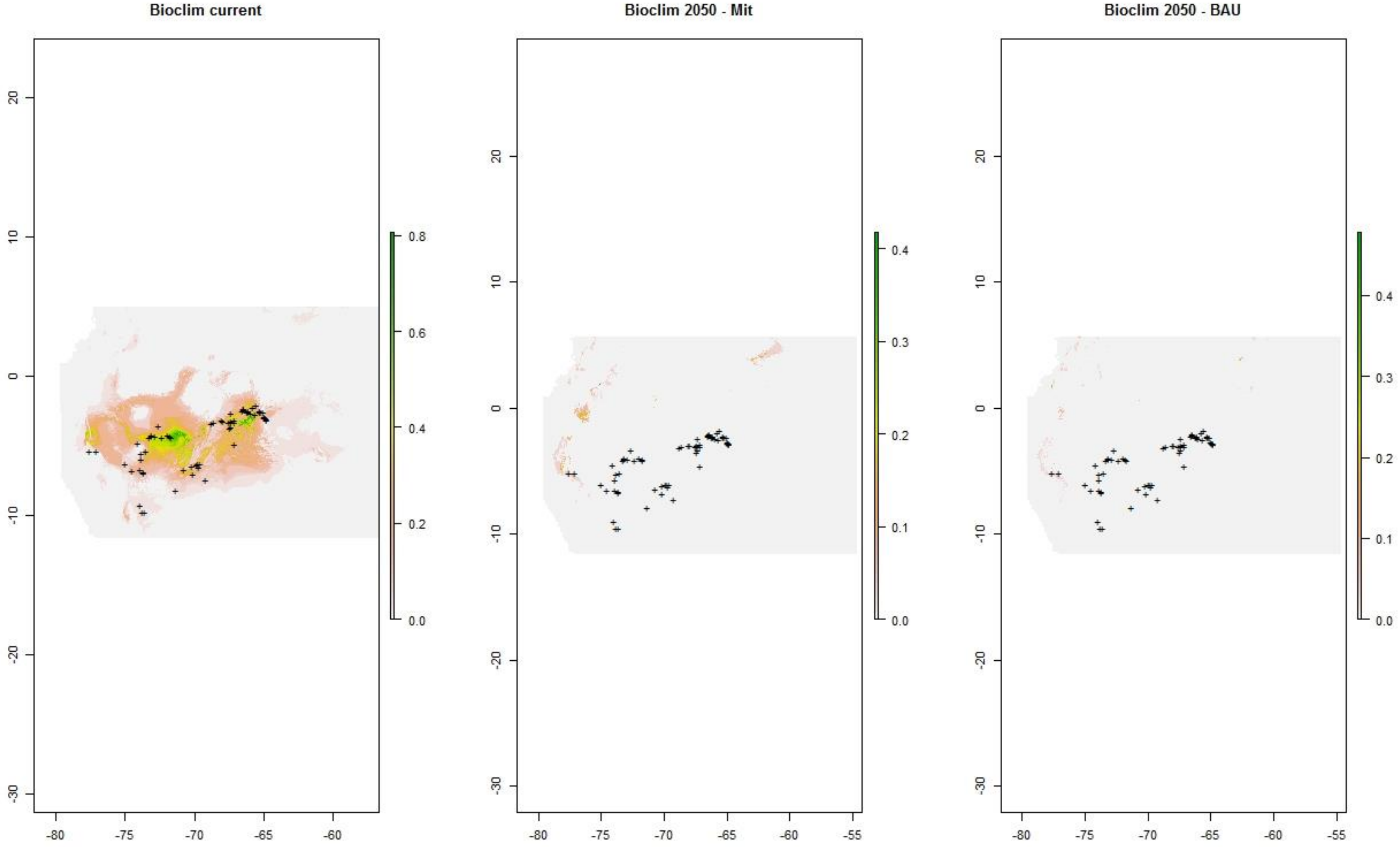

Figure Suppl. 5-2 The habitat suitability for bald uakaris in the current and future scenarios under the BIOCLIM algorithm.

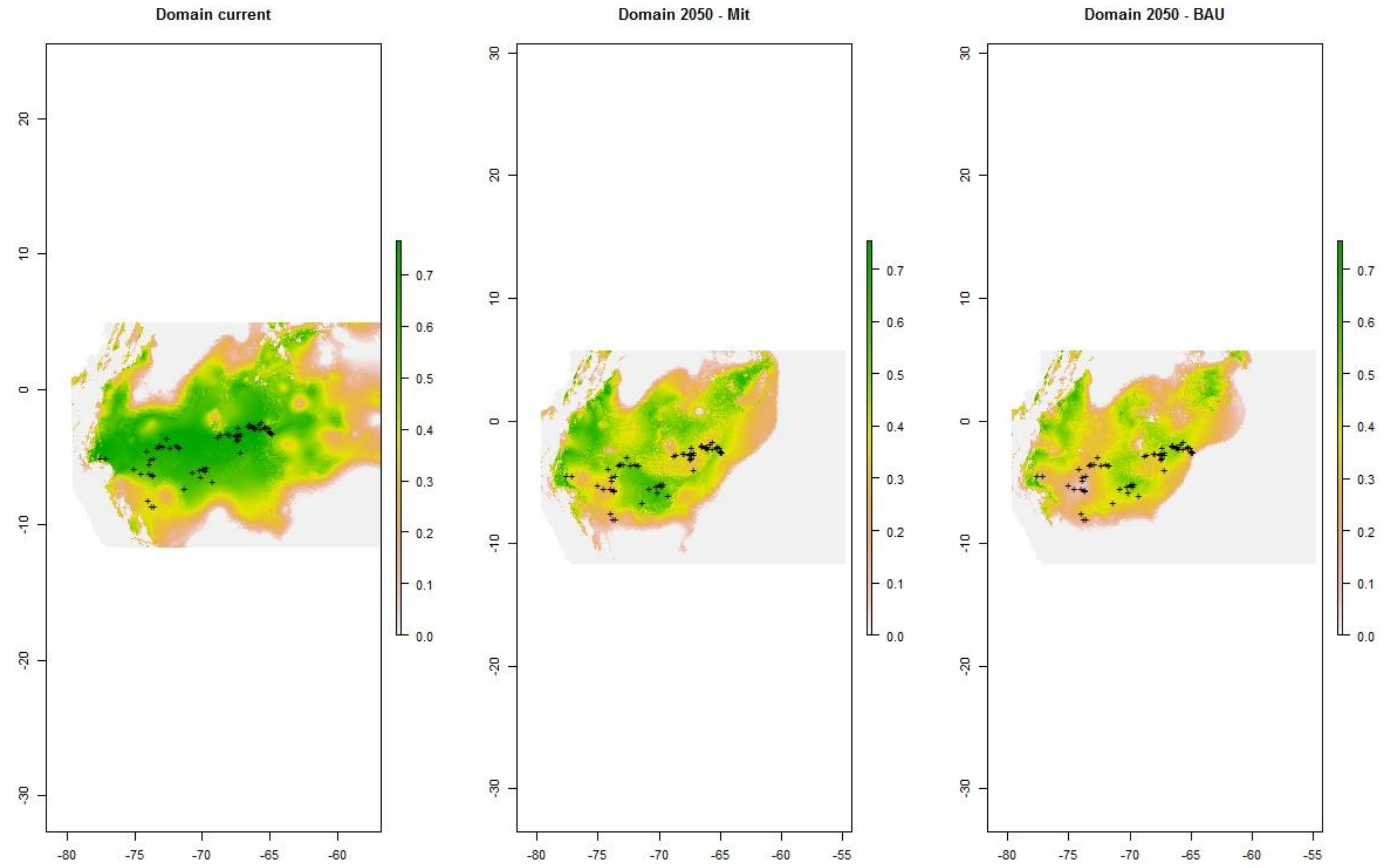

Figure Suppl. 5-3 The habitat suitability for bald uakaris in the current and future scenarios under the DOMAIN algorithm.

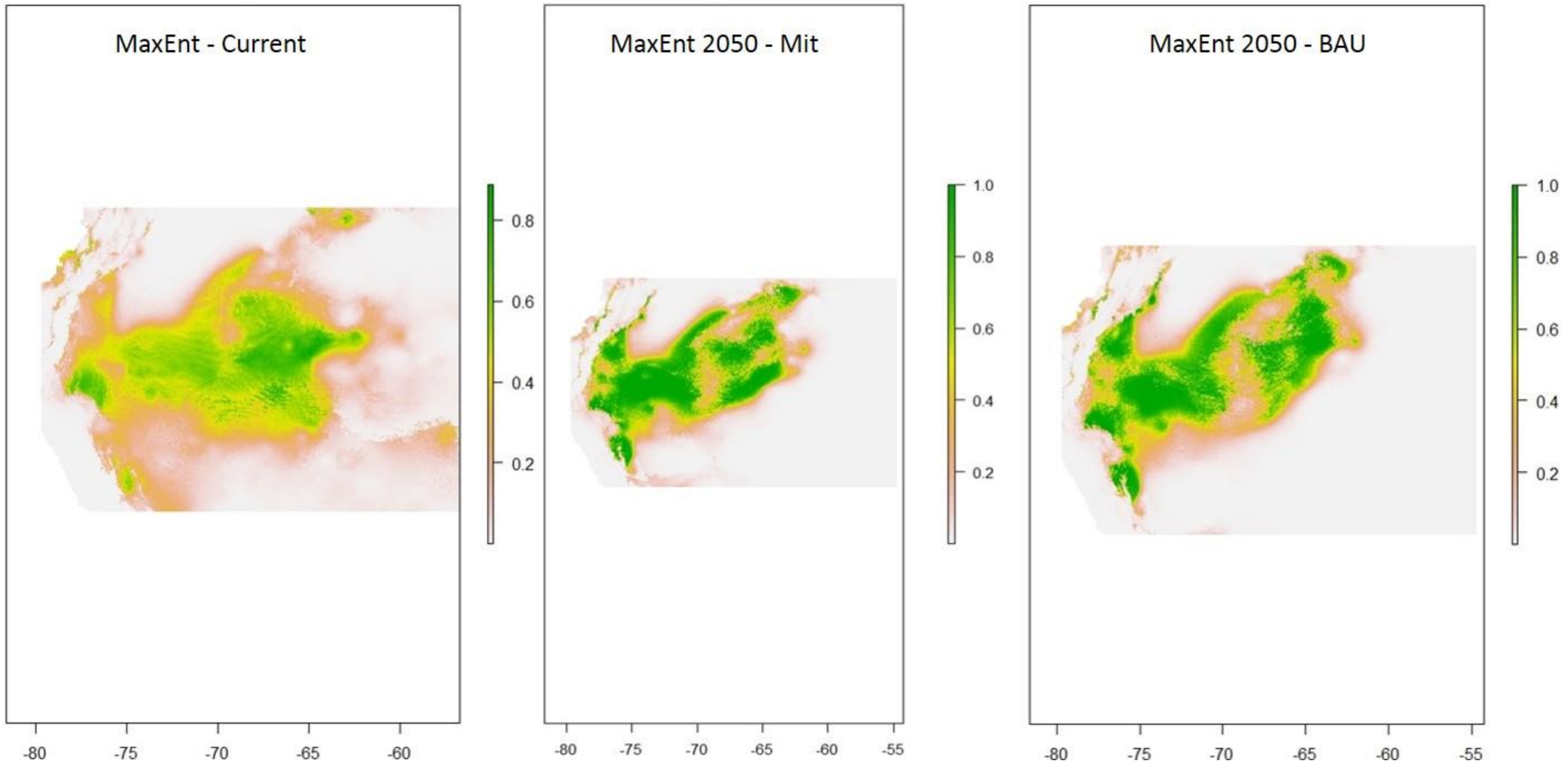

Figure Suppl. 5-4 The habitat suitability for bald uakaris in the current and future scenarios under the MaxEnt algorithm.

Chapter 6. CONCLUSIONS

Since the taxonomic revision of *Cacajao* (Hershkovitz 1987a) and the first study on the ecology and behaviour of uakaris (Ayres, 1986), the new evidence on the occurrence and distribution (Silva Jr et al. 1999; Boubli 2002; Ward and Chism 2003; Vieira et al. 2008; Bowler et al. 2009; Vermeer et al. 2013; Cardoso et al. 2014) and the first molecular studies based on cytochrome *b* (Boubli et al. 2008; Figueiredo-Ready et al. 2013) provided the foundation for the reassessment of the diversity of uakaris from an evolutionary perspective. While an explicit taxonomic hypothesis was proposed for the black uakaris based on new evidence gathered in fieldwork and scientific collections (Boubli et al. 2008), the misidentification of samples and the inaccuracy of occurrence records of bald uakaris are the primary reason why we knew so little about this group. This thesis was only possible due to a collaborative effort that involved different institutions and researchers from Brazil, Peru, and other countries, representing more than 30 years of accumulative information involving genetic material, unpublished records, and my efforts to understand the geographic range of each species of bald uakaris based on the field trips and Museum analysis. This dataset allowed to give some more steps in the uakari research, although we have a long road ahead.

6.1 Main findings

The overall goal of this study was to investigate the evolutionary history of *Cacajao* using molecular data and to propose a taxonomic classification for the bald uakaris based on a robust molecular phylogenomic analysis. I provided the most updated information on the geographic distribution of each species and how climate change and deforestation can potentially pose them in the risk of extinction in the future scenarios.

In Chapter 2, I used the cytochrome *b* sequences of all Pithecidae genera (which included all *Cacajao* species) to get a time tree and to test if the *Cacajao* is a lowland (Western Amazonia) or an upland (Guiana and Brazilian shields) affiliated group. I found that the Pitheciinae clade diverged from the clade of titi monkeys – *Plecturocebus*, *Cheracebus*, and *Callicebus* – at 16.7 Mya, originating *Pithecia* and the ancestral of *Chiropotes* and *Cacajao*. The divergence time between *Pithecia* and *Chiropotes*/*Cacajao* occurred in the mid-Miocene, at 14.4Mya, with the split between *Chiropotes* and *Cacajao* estimated at 9.0Mya. The phylogeographic analysis showed that *Cacajao* started its diversification about 5Mya and that the clade *Cacajao/Chiropotes* had a common ancestor that was a lowland water-affiliated taxon, with *Cacajao* occupying the floodplain of Negro–Branco and Ucayali–Solimões–Juruá river systems, in western Amazonia; and *Chiropotes* dispersing to the Brazilian and Guiana shields.

In Chapter 3, I use the ddRAD to investigate the population structure of bald uakaris using the software pipeline STACKS (Catchen et al. 2011, 2013). I applied a parametric (STRUCTURE) and a non-parametric approach (PCA) to analyse the population data. The most evident structure occurs between the red uakaris (*C. rubicundus, C. ucayalii,* and *C. novaesi*) and the white ones (*C. calvus*). The program STRUCTURE did not retrieve the genetic difference between the red uakari species, but it showed two well-delimitated clusters of white uakaris (representing the populations from Jutaí and upper Juruá rivers) and a third cluster with admixture individuals from Mamirauá SDR. When analysing these data through the PCA, all populations were well-delimitated, with the primary separation between white and red uakaris.

Then, to get a phylogenomic perspective of the *Cacajao* and verify the consistency in the phylogenetic relationship of the main lineages throughout the genus, I use the software pipeline IPYRAD (Eaton 2014). I tested the combination of twenty-five parameter settings to check how the parametrisation influenced the analysis. Considering the overall statistical support of the trees, I identified the main lineages of bald uakaris. The two main clades of bald uakaris include the reds and white ones, and this separation is consistent with the split between black uakaris from North and South bank of Negro River. The white uakaris included two main clades. The first grouped the populations from the Tarauacá and Pauini rivers, and the second grouped those from Mamirauá SDR and Jutaí River. The clade including the red uakaris showed that *C. ucayalii* is a sister group of *C. rubicundus*, and both are sister groups of *C. novaesi*, i.e. *novaesi*, *rubicundus* and *ucayalii* are reciprocally monophyletic.

Finally, I reassess the taxonomy of the bald uakaris according to the main results of the phylogenomic analysis. I considered the monophyly and the diagnostic characters of pelage colouration, which were mostly presented in Hershkovitz (1987), to apply the Phylogenetic Species Concept and proposed the taxonomic classification of bald uakaris as follow: *Cacajao calvus* (Geoffroy, 1947), *Cacajao rubicundus* (Geoffroy and Deville, 1948), *Cacajao ucayalii* (Thomas, 1928), and *Cacajao novaesi* (Hershkovitz, 1987).

In Chapter 4, I estimated the Extent of Occurrence and the geographic distribution range for each species based on new information and, in Chapter 5, I analysed the amount of habitat loss for each species of bald uakaris based on the predicted deforestation by 2050. *Cacajao calvus* and *C. rubicundus* inhabit a region with low rates of deforestation, in the middle Solimões River, and have a large part of their range within Protected Areas. However, the deforestation will probably impact the Peruvian populations of *C. ucayalii* from the southern portion of its distribution. For *C. novaesi*, the assessment of the deforestation impact will depend on the scenario considered. Under Governance scenario, the species will not have a significant reduction in their habitat. However, under the BAU scenario, 45% of the habitat the species will be lost by 2050, which qualify the species as Vulnerable according to the IUCN criteria. In addition, the species is hunted and has the smaller EOO among bald uakaris, which are two essential variables to be considered in the assessment of its Conservation Status.

When considered the effects of climate-changing in the habitat suitability, the models provided a valuable insight into how impacted bald uakaris will be in near future scenarios. Areas with suitable habitat will be restricted to some spots in the Western Amazonia, and probably in the north of Brazilian and in Colombian Amazonia, where the bald uakaris do not occur. It is quite unlikely they will be able to disperse to the north bank of Japurá and Negro rivers since these are two significant Biogeographic barriers and black uakaris inhabit the forests of this region.

6.2 – Next Steps

The analyses presented here allowed to establish some priorities and future directions for the research and conservation of bald uakaris. Below, I will provide some possibilities, although many other questions may arise in the next few years. Then, I will present the Theory of Change for the Conservation of bald uakaris populations considering their role as a flagship species in the Amazon Rainforest.

6.2.1 – GEOGRAPHIC DISTRIBUTION.

According to the evidence presented in the previous publication (e.g. Vermeer et al., 2013) and supported by this study, bald uakaris have a disjunct distribution with allopatric populations confirmed for *C. calvus*, *C. rubicundus*, and *C. ucayalii*. Surveys within the Extent of Occurrence of these species, but where no information is available, will improve our knowledge on how they occupy these areas. For example, Vermeer et al. (2013) reported an isolated population of *C. ucayalii* in the Cordillera Cahuapanas, a mountain region of San Martin district, Peru, located 365km west of the known range of the species. Surveys between these areas and surround the Cordillera Cahuapanas can provide valuable information on the occurrence of uakaris in Peru. In Brazil, surveys in the right bank of Javari River will confirm if the vouchers of *C. ucayalii* from Estirão do Equador were indeed collected there or if they were brought from the Peruvian territory. It will also clarify if the Serra do Divisor National Park is the only locality where *Cacajao ucayalii* occur in Brazil. For *C. novaesi*, surveys in the upper Taraucá and Gregorio rivers are essential to delimitate the southern portion of its distribution. Surveys in Tonantins River will also confirm if indeed the populations of *C. rubicundus* from Auati-Paraná and Jacurapá channel are allopatric. For all species, field efforts during the dry and rainy season can bring different information since the social and ecological behaviour of bald uakaris will be consistent with the variation in food resource availability throughout the year.

6.2.2 – MOLECULAR ANALYSIS

Although the molecular approach presented in this study provide robust evidence on the phylogenetic relationship of *Cacajao* and number of lineages, some populations were not represented due to the lack of samples available in scientific collections. For example, I did not include samples of *C. ucayalii* from Peru. These populations are essential in the molecular analysis of bald uakaris. *Cacajao ucayalii* has most of its occurrence in the Peruvian forests, has the largest geographic range among bald uakaris, and may have accrued a genetic variation between the populations that are important to be studied. In Brazil, the contact zone of *C. calvus* and *C. rubicundus* from Auati-Paraná channel is essential to investigate the possibility of gene flow, and how these populations are related to their conspecific ones. In addition, surveys in Tarauacá and upper Jutaí rivers will elucidate if there are other contact zones between white and red uakari populations.

6.3 – Theory of Change for the Conservation of bald uakaris

The previous IUCN Red List assessment considered bald uakaris as Vulnerable (Veiga et al. 2008), a category assigned for *Cacajao calvus* ssp. (following the classification of Hershkovitz 1987a). However, according to the analysis that I presented in Chapter 5, the four species are under different levels of threat. In this thesis, I provided a review on the occurrence records and distribution, and I discussed how deforestation and climate change would have an impact on the habitat loss of bald uakaris by 2050. Considering the available evidence, I can conclude that the primary threat for bald uakaris is habitat loss, which was found here as a product of deforestation and climate change.

However, other threats may have been underestimated because no data is available. Although studies focused on the bushmeat consumption and mammals inventories allowed to get information on the Conservation Status of the Peruvian populations of *Cacajao ucayalii* (Aquino 1988, 1998; Aquino and Encarnación 1994; Bodmer 1995; Bodmer et al. 1997; Bennett et al. 2001; Aquino et al. 2005, 2013; Benessaiah 2007), the information on bald uakaris in Brazil were more limited to few field sites (e.g. Mamirauá SDR). Hunting is reported for *C. ucayalii* and *C. novaesi*, although the effects of such activity were mentioned only for Peruvian populations (Aquino 1988; Ward and Chism 2003; Vermeer et al. 2013). Selective logging of tree species that are important in their diet was discussed only for white uakaris in the region of Mamirauá SDR in the late ‘80s (Ayres and Johns 1987). Information on how these threats are influencing the bald uakaris is still missing for most of the populations. Therefore, the assessment of the Conservation status of the four species can be compromised, and wrong strategies for their Conservation may have been adopted if the data are limited to some few field sites.

One possible approach for the Theory of Change (TOC) of bald uakaris conservation is to start from the available knowledge about the following threats: selective logging, deforestation, climate change, habitat loss, and hunting (Figure *6.1*). The first three are related to the habitat loss and will potentially imply in a reduction of the Extent of Occurrence, in a smaller area of habitat suitability, and a reduction of the population size. Therefore, data on these variables are essential for all populations of bald uakaris (Figure *6.1*).

Selective logging can also imply in lower availability of key food resources for bald uakaris. Therefore, studies on the feeding ecology of bald uakaris are urgently needed for all populations, especially because these studies will enable a comparative analysis across field sites. Data on the impact of bushmeat consumption in primate communities are essential in most of the areas where bald uakaris occur. For example, while I got reports of hunting of *C. novaesi* and *C. ucayalii*, Pereira et al. (2019b) did not get any register for *C. calvus* at Mamirauá SDR after 11 years of monitoring. The relevance of hunting and timber extraction for bald uakaris populations will vary depending on the local context of each field site, and this information is missing for most of the fieldsites.

The consistency of data collection will enable us to take actions involving local government, managers of Protected Areas (PAs), schools, and local communities in a long-term Conservation programme. These initiatives will result in the involvement of the stakeholders and the reduction of the impacts in bald uakaris populations (Figure *6.1*). At this point, the reader may find this narrative unrealistic. However, similar initiatives are a reality in Brazil and Peru where the involvement of local communities have been essential for the Conservation in PAs where bald uakaris occur (Queiroz, 2011; Bowler et al., 2013).

Cacajao calvus and *C. rubicundus* have a significant portion of their geographic distribution protected by a network of different categories of PAs. *Cacajao novaesi* is legally protected by the Rio Gregório Extractive Reserve and by the Indigenous Land Kulina do Médio Juruá. The occurrence of *Cacajao ucayalii* in Peruvian Protected Areas and Indigenous Lands has been updated with new records on its occurrence to the west of the Ucayali River (Bowler et al. 2009; Vermeer et al. 2013). In Brazil, the species is only confirmed at the Serra do Divisor National Park (SDNP).

Although the legally protected lands are essential for the conservation of Amazonian primates, its integrity and effectiveness are in risk due to the political instability in Brazil (Bernard et al., 2014; Estrada et al., 2018; Fearnside, 2017; Ferreira et al., 2014; Pack et al., 2016; Pereira et al., 2019). Specifically, the successive cuts in the annual budget for the Ministries of Science, Technology, Innovation and Communication (MCTIC) and Environment (MMA) (Angelo 2017; Fernandes et al. 2017; Overbeck et al. 2018; Magnusson et al. 2018), together with the deliberated initiatives promoted by the Brazilian government (year-base: 2020) and politicians associated to the agribusiness to weakening the environmental regulations regarding the control of the deforestation, are resulting in a new cycle of deforestation in the Amazon (Soares-filho et al. 2014, Fearnside 2016, 2017, Crouzeilles et al. 2017, Magnusson et al. 2018).

A handful of misguided and irresponsible policy decisions can dramatically worsen an already worrying future scenario for Amazonian primates (see Carvalho et al., 2019; Estrada et al., 2018, 2017; Sales et al., 2019). The strengthening of networks that involve different social actors (at national and international level) in initiatives to promote social-environmental improvements in Amazon Rainforest is essential under these circumstances. For example, Mamirauá SDR was explicitly created to protect the white uakaris, *Cacajao calvus*, in an initiative that included researchers, local communities, governmental and non-governmental agencies in the political and social context of the 1980s (Ayres and Johns 1987; Alves 2011; Queiroz 2011). Mamirauá SDR became a model of Conservation in Brazilian Amazon with the scientific base for the management of natural resources resulting in the improvement of the social conditions of local communities. What seems to be a utopian goal in the current political scenario in Brazil (year-base: 2020) is, actually, an urgent priority for researchers, conservationists, local communities, and civil society.

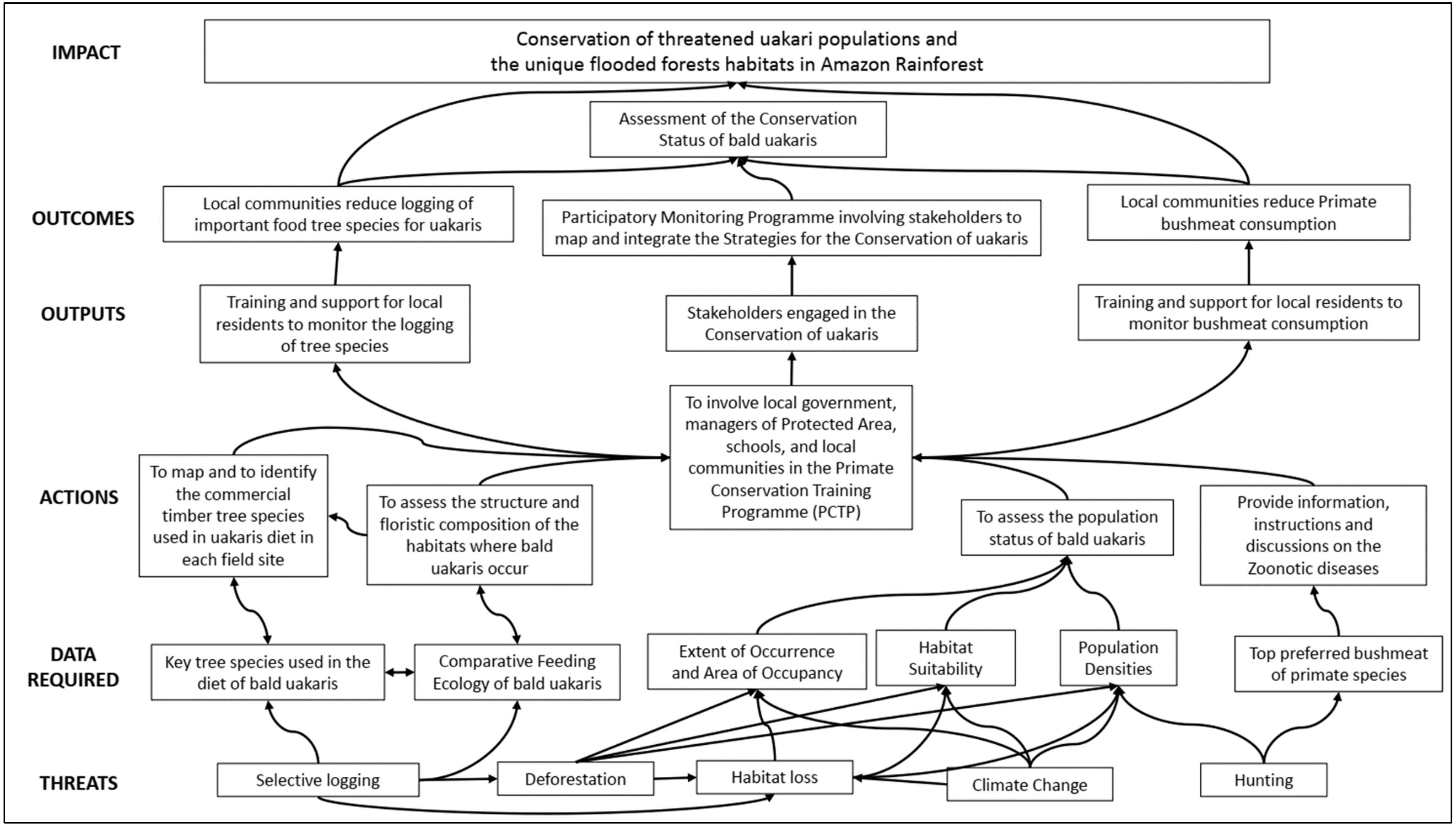

Figure 6.1 Theory of Change for bald uakaris Conservation.

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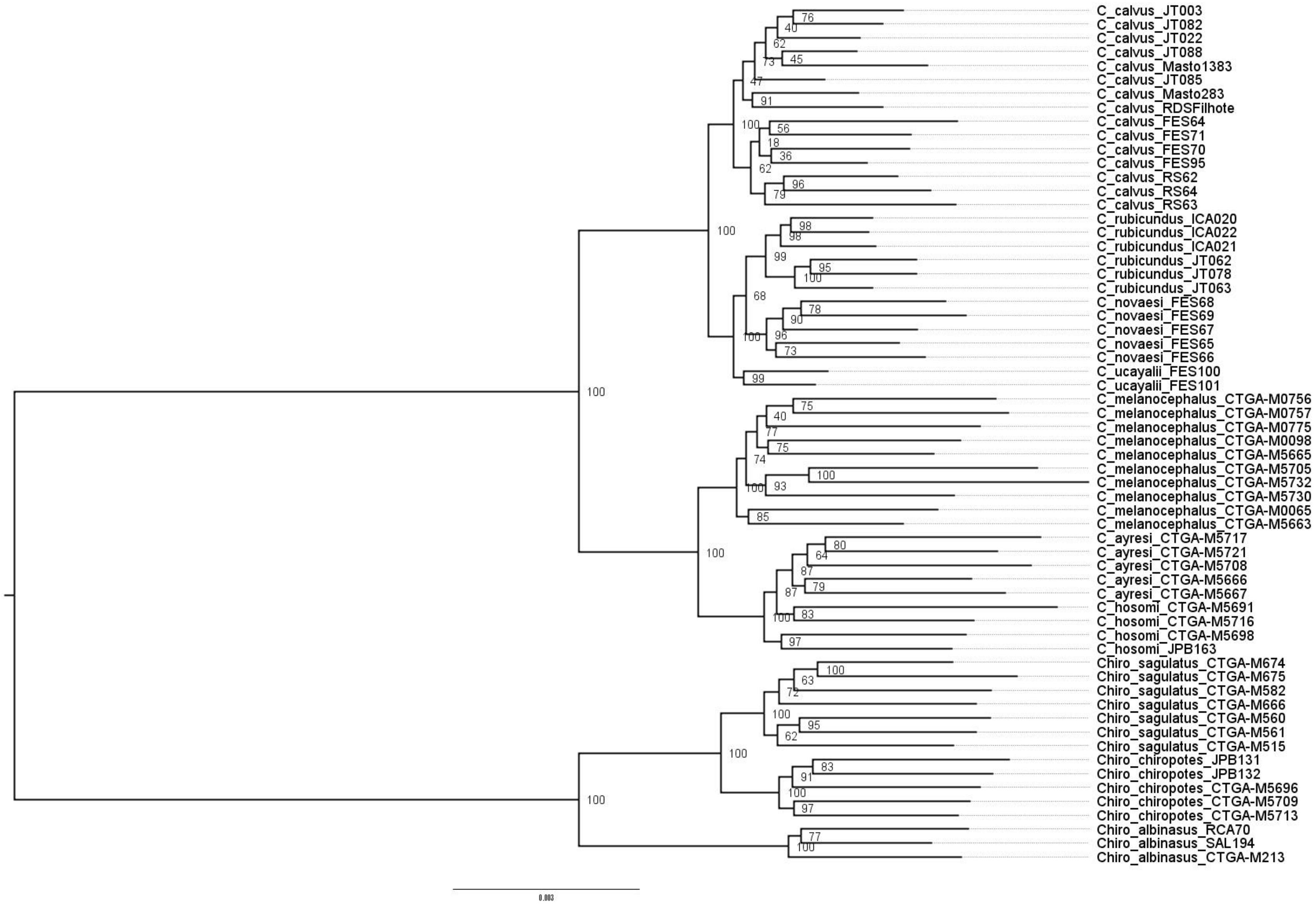
APPENDIX I

Phylogenomic trees retrieved from the parametrisation tests in IPYRAD (Parameter settings according to the Table 3-2, Chapter 3).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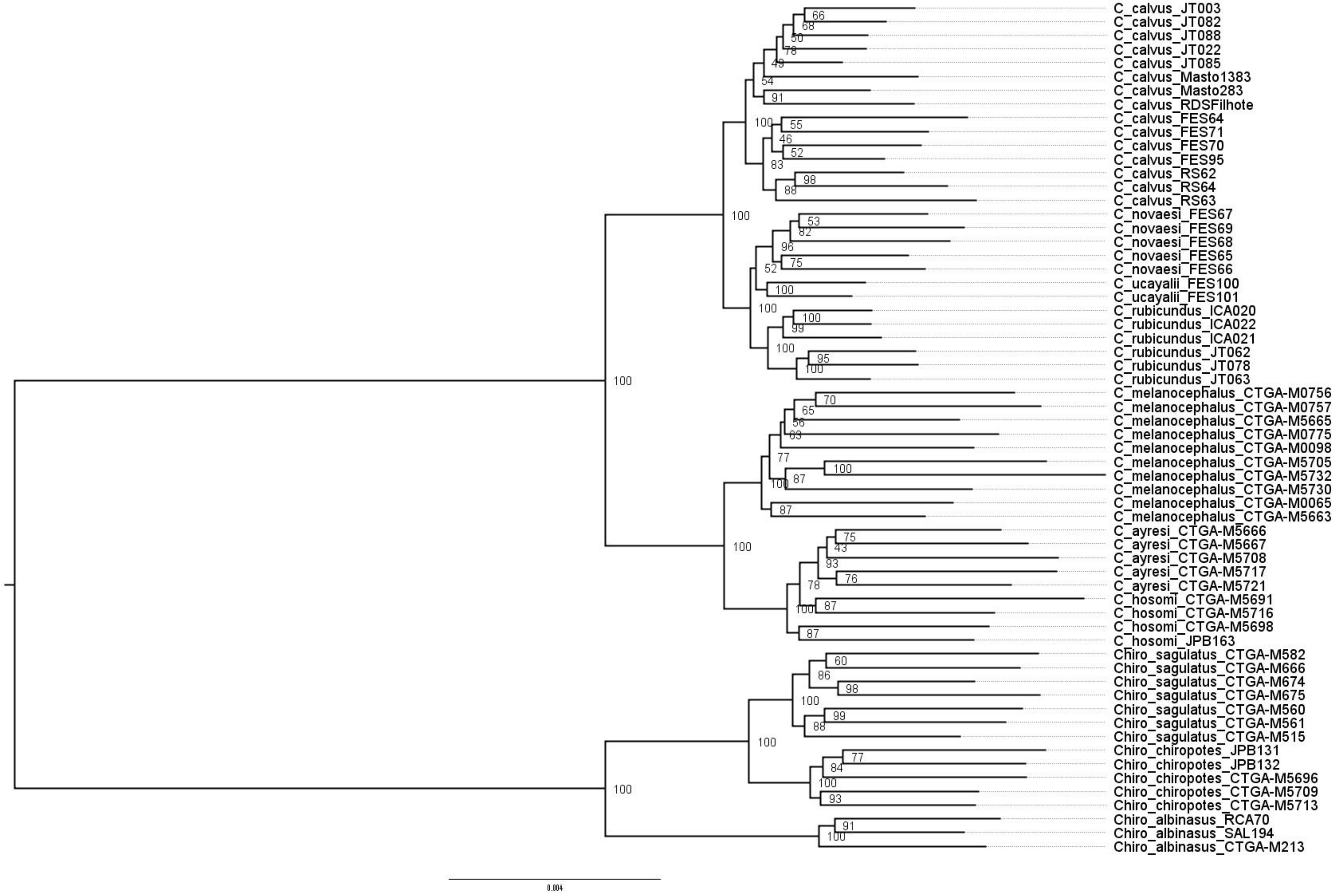
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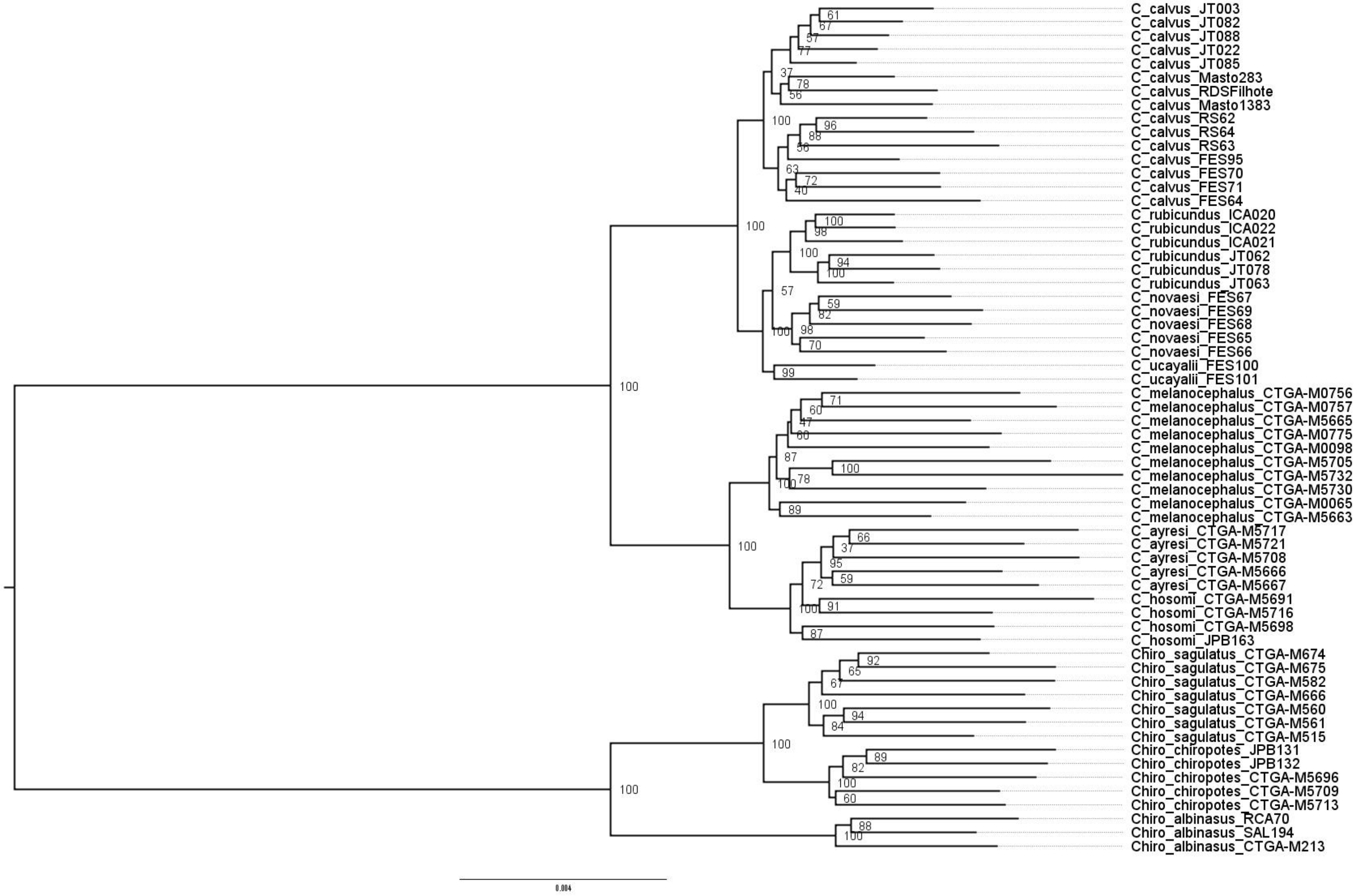
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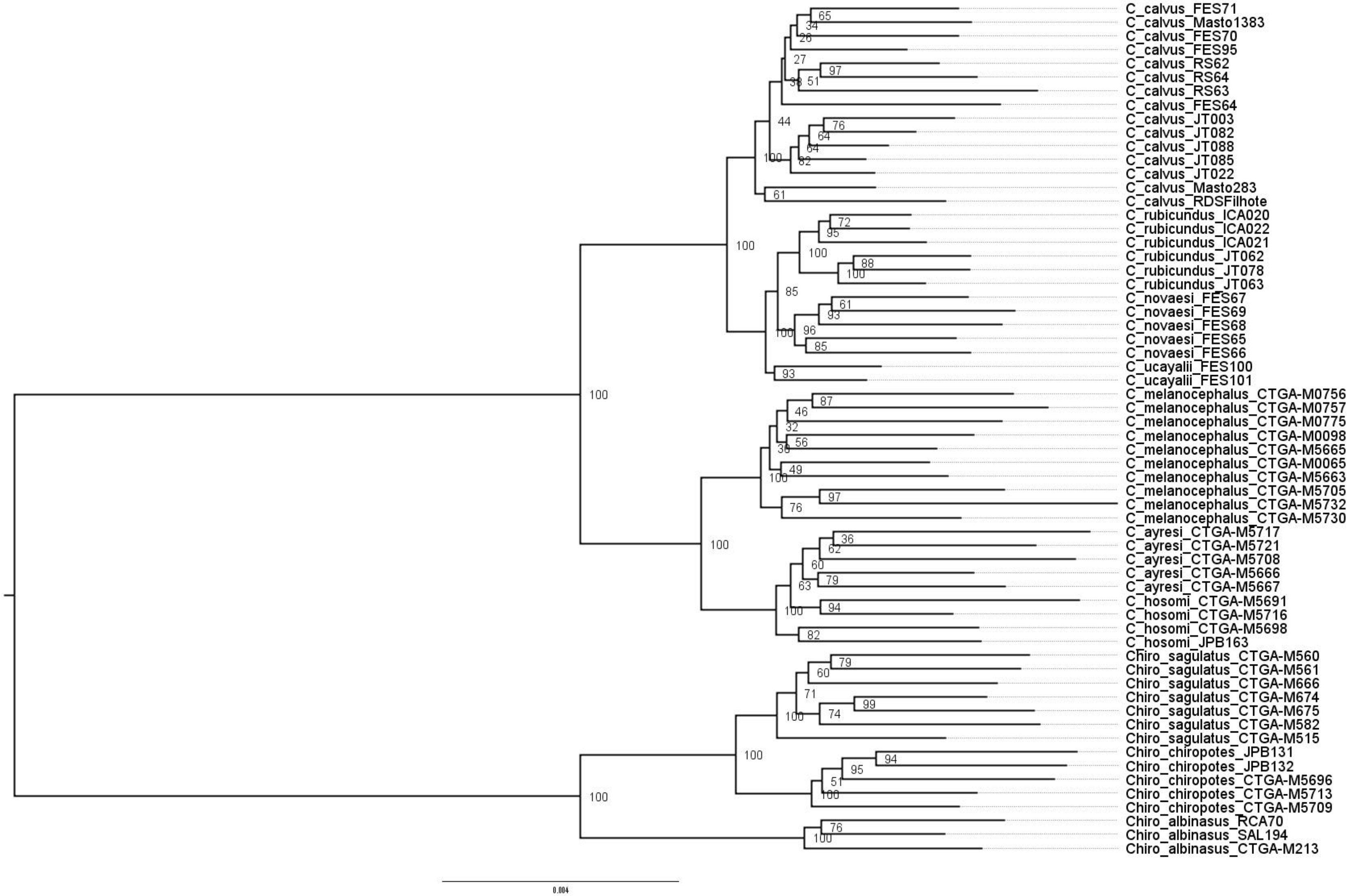
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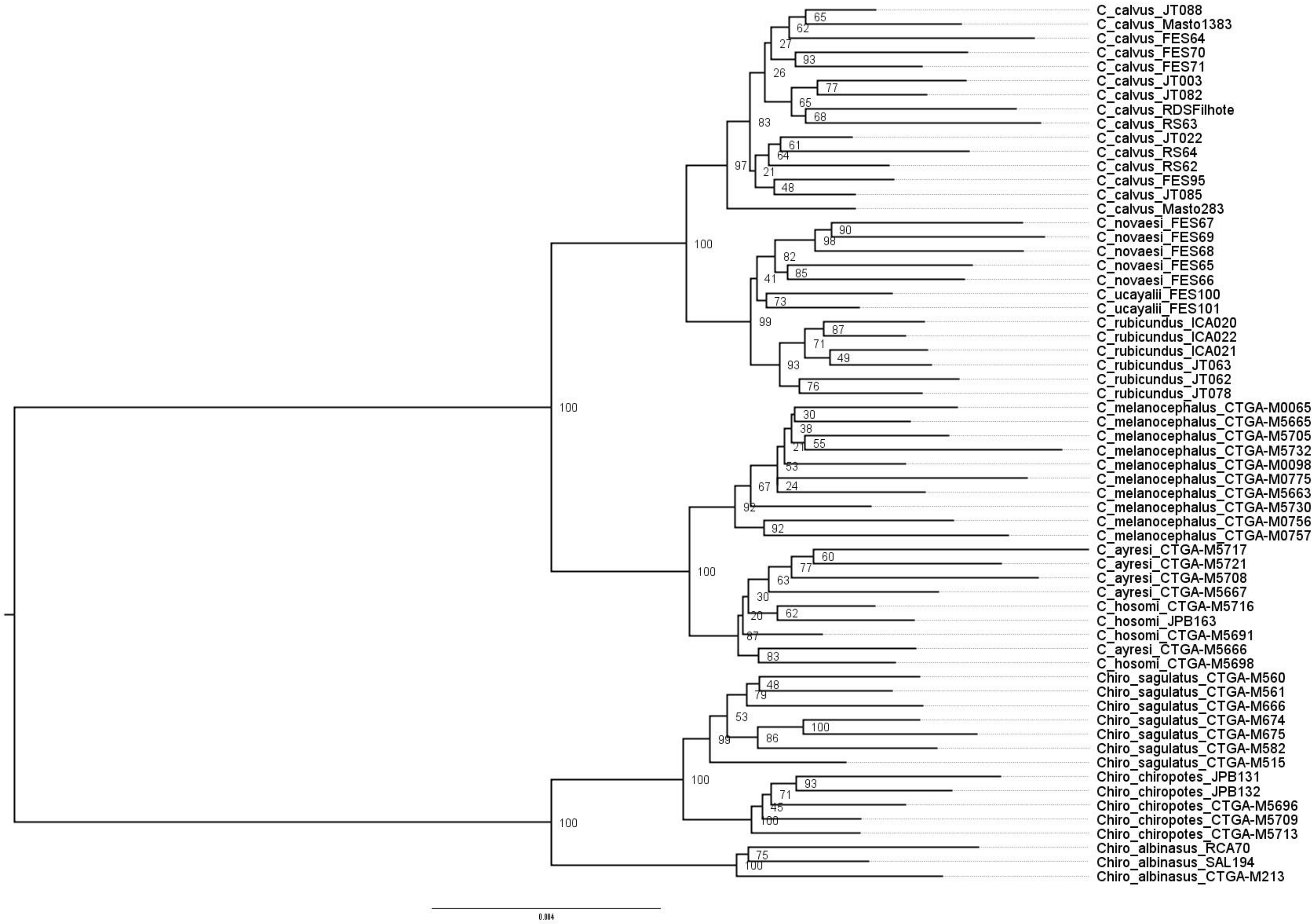
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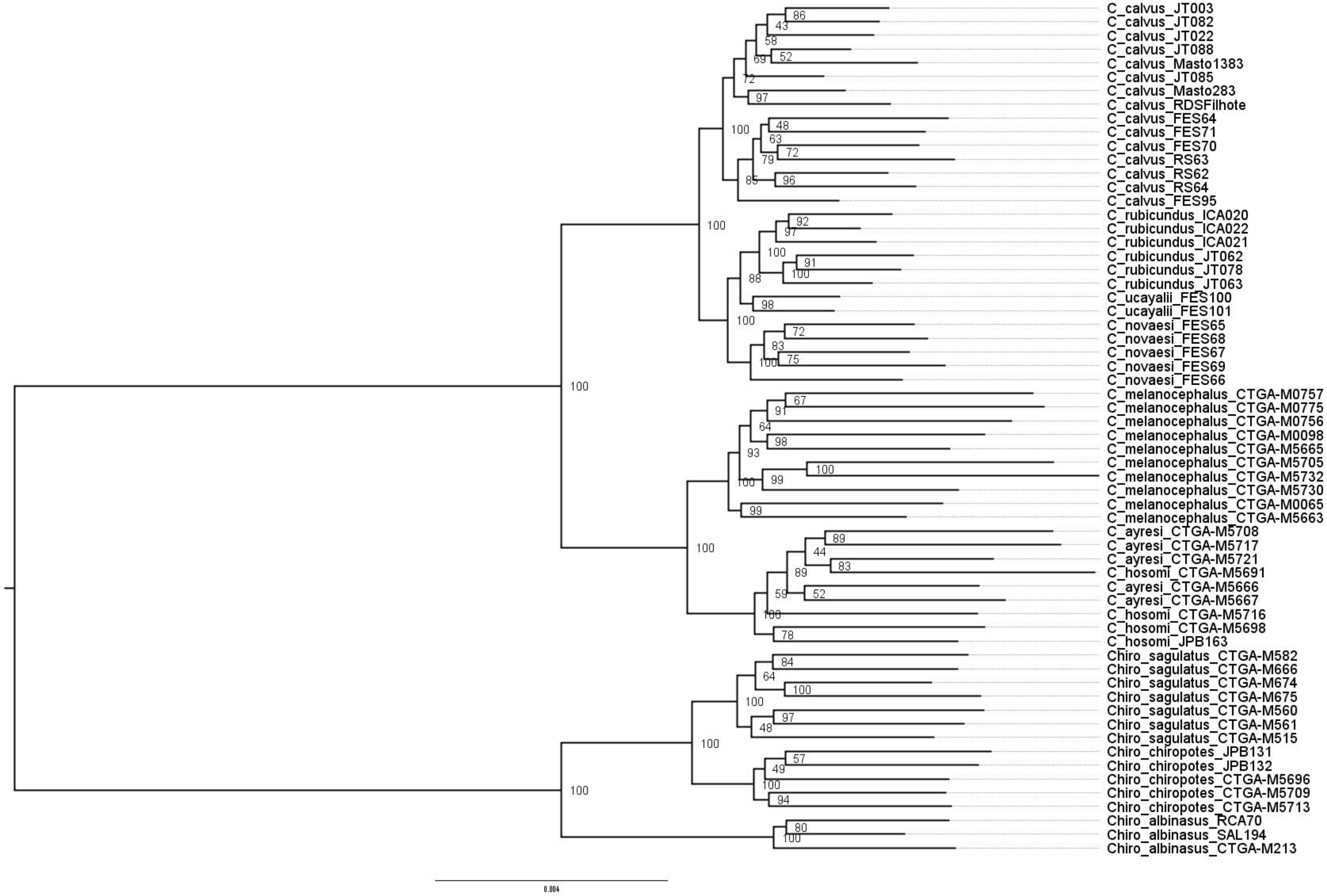
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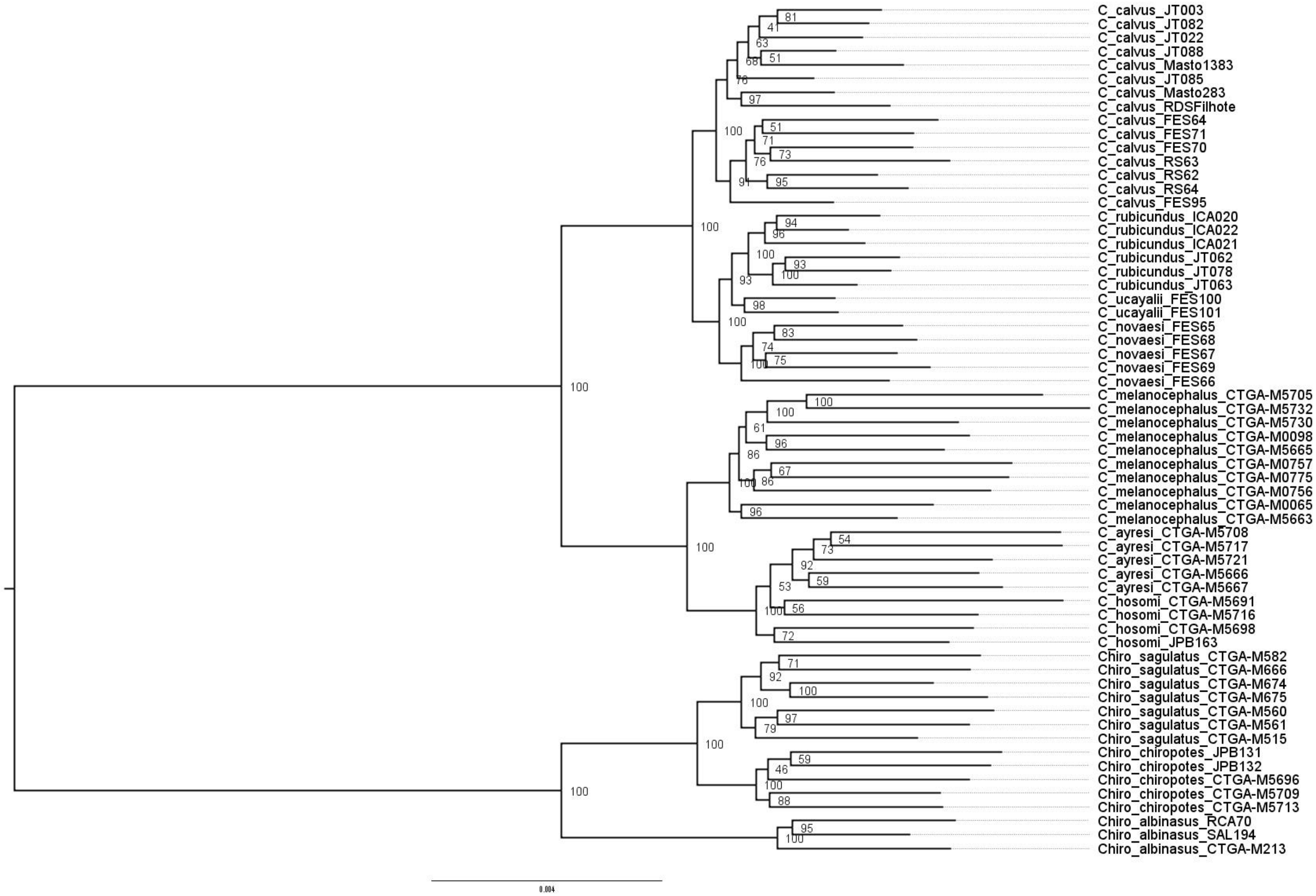
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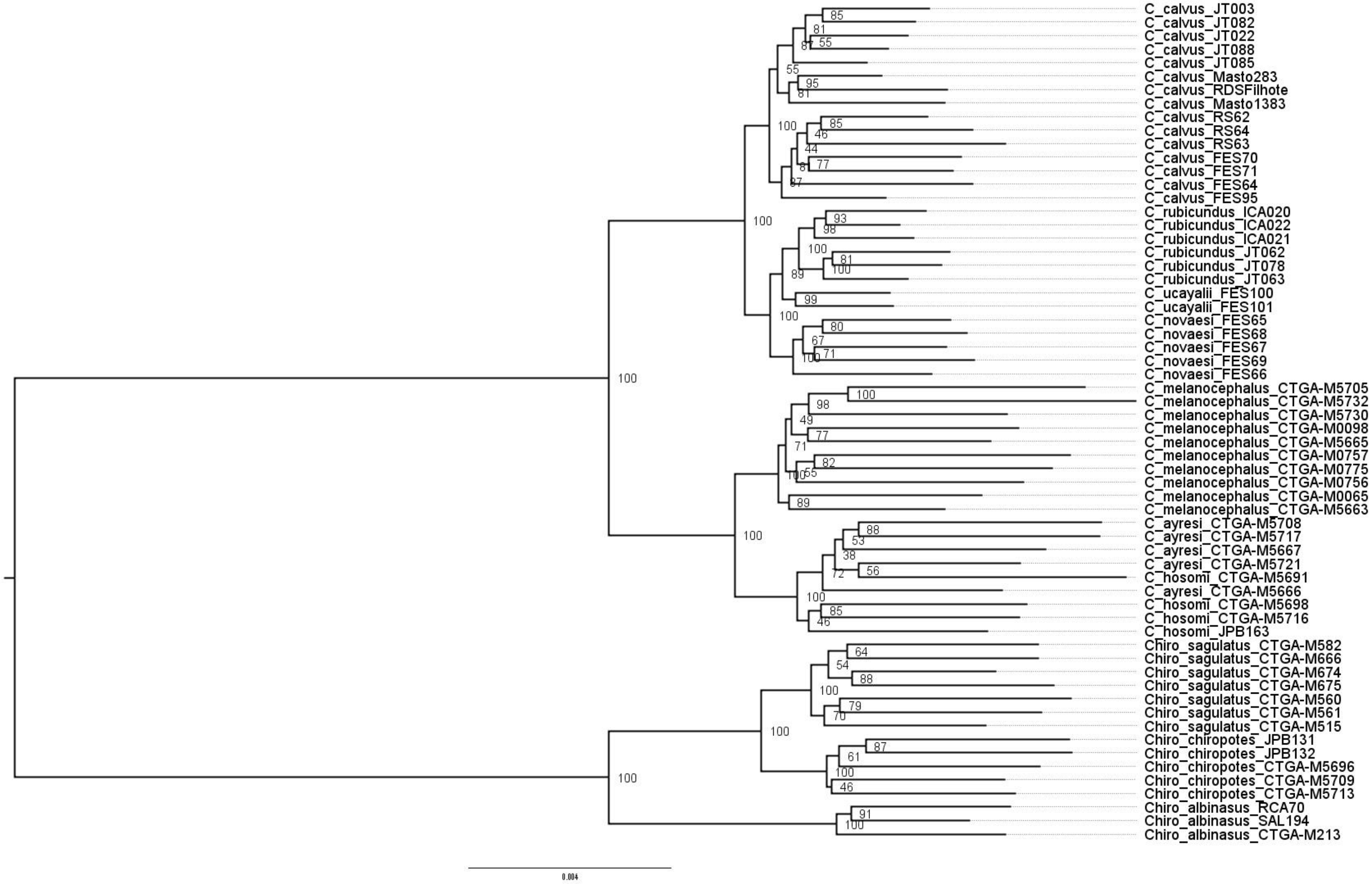
Denovo08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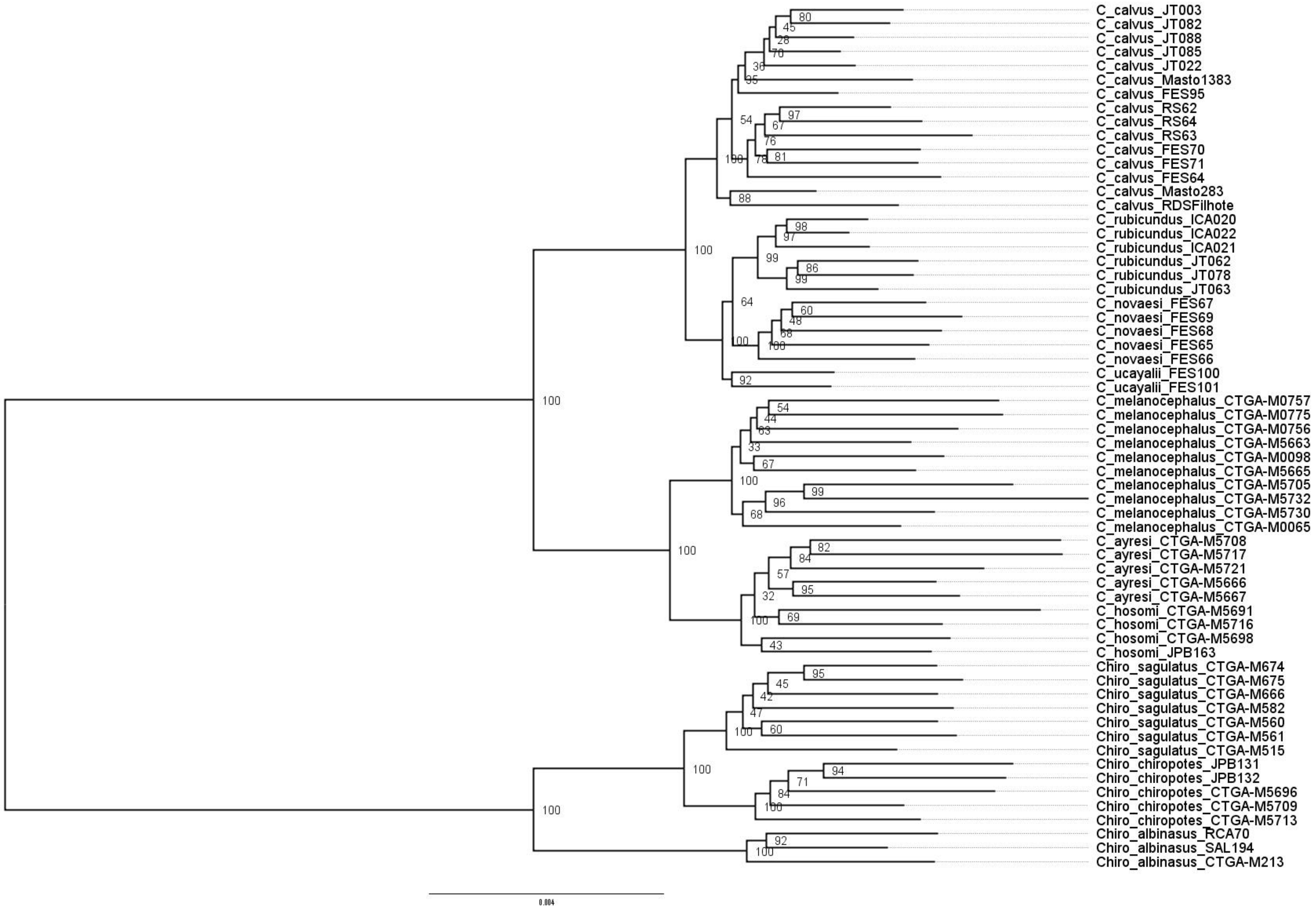
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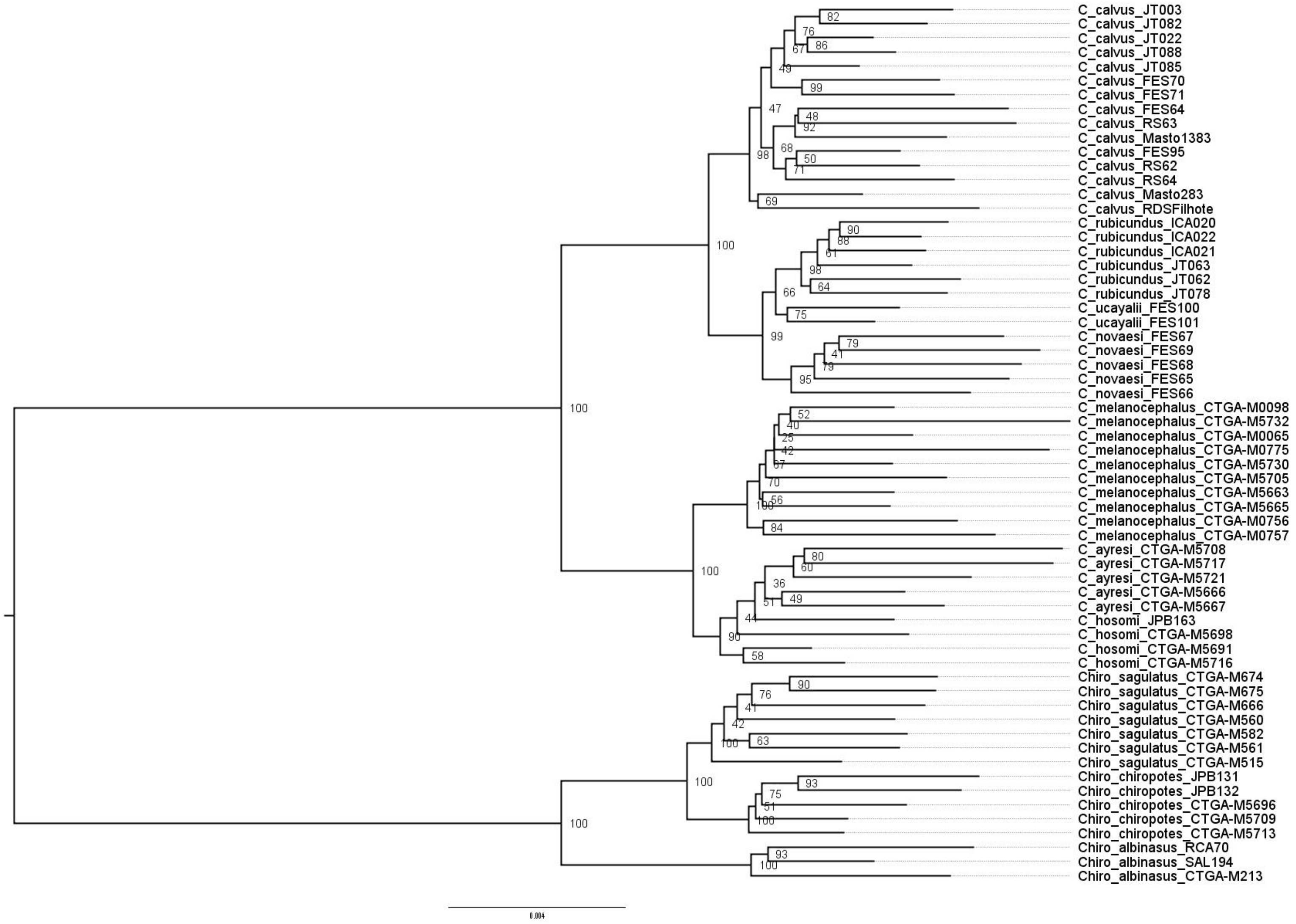
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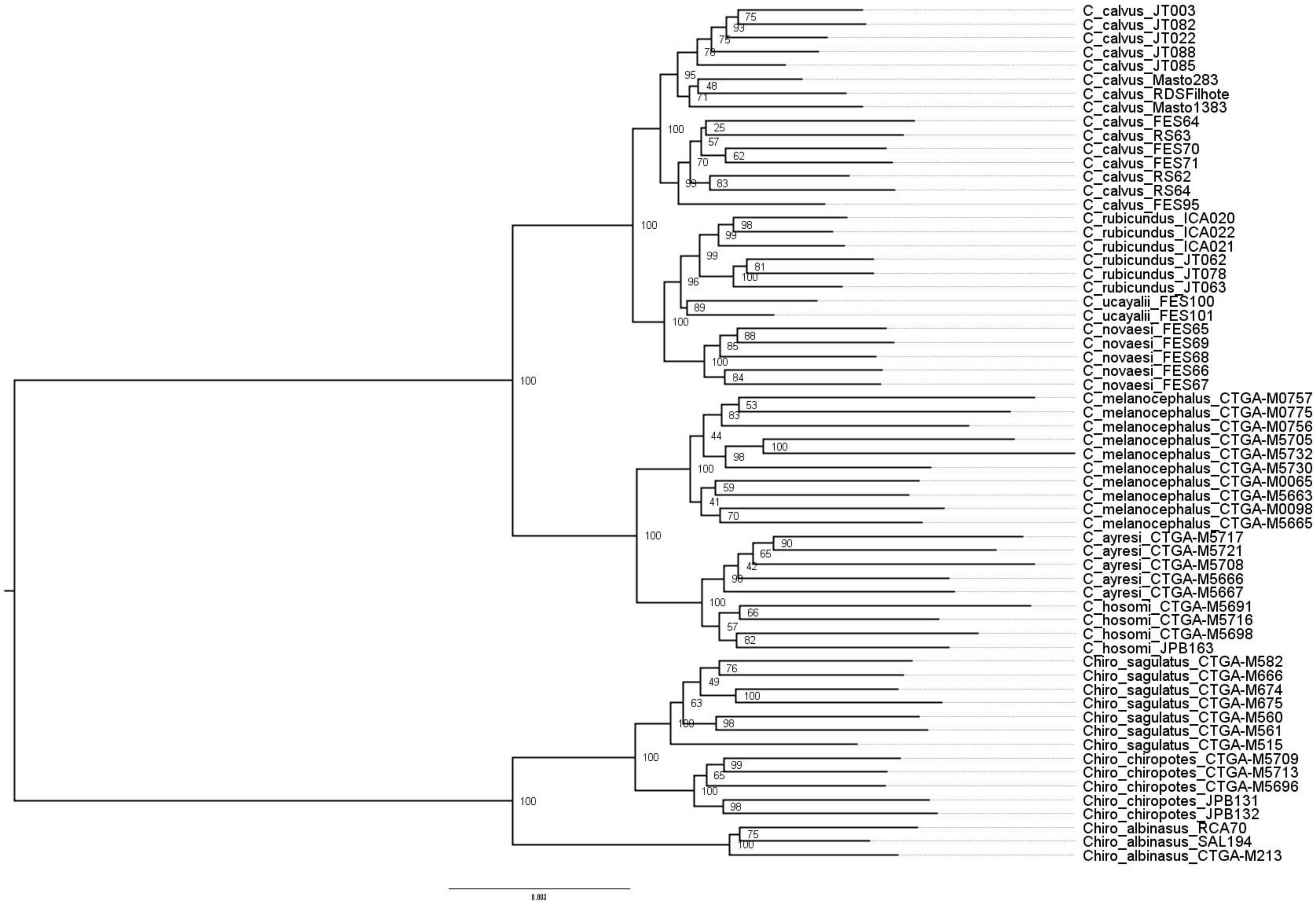
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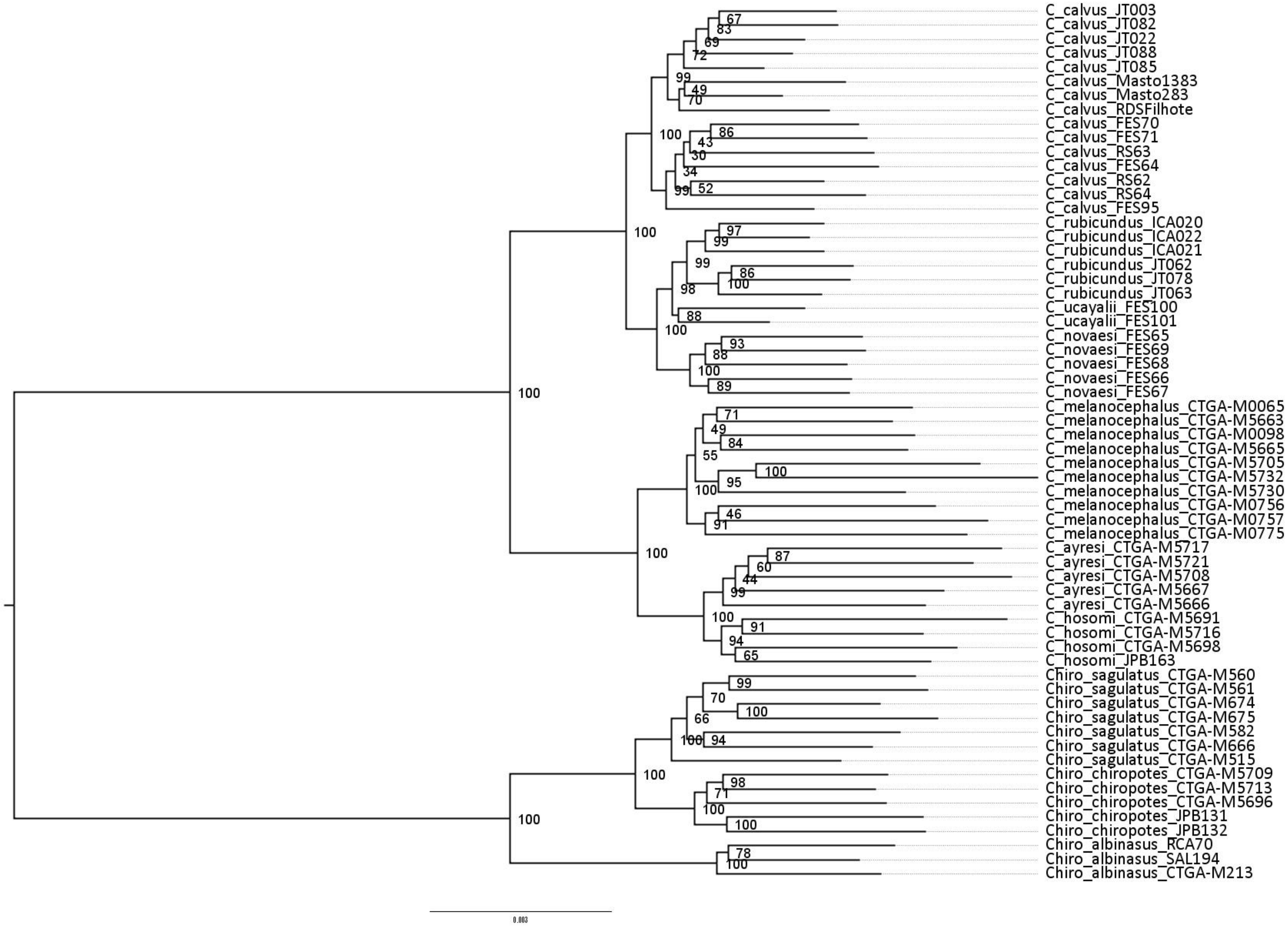
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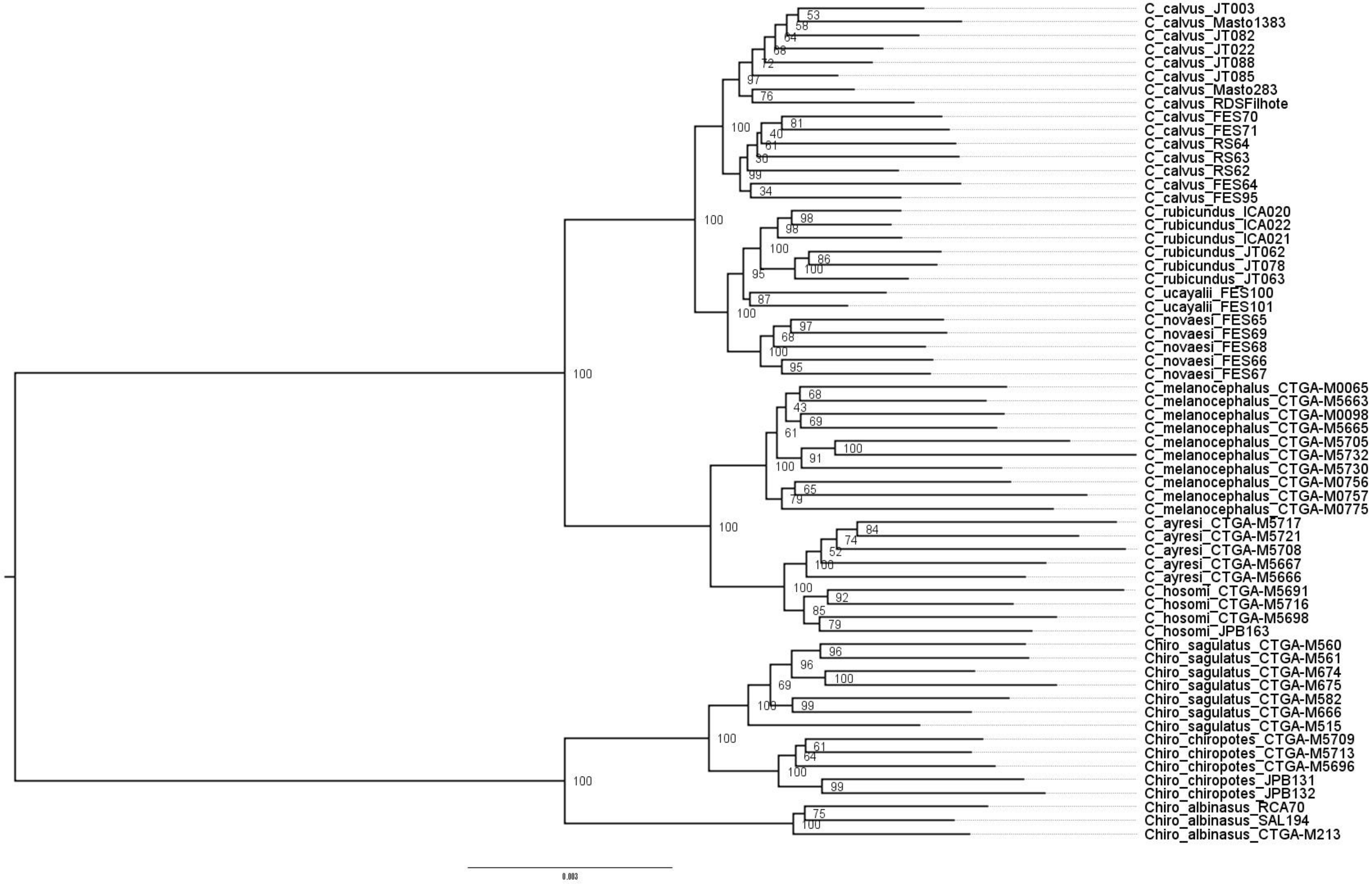
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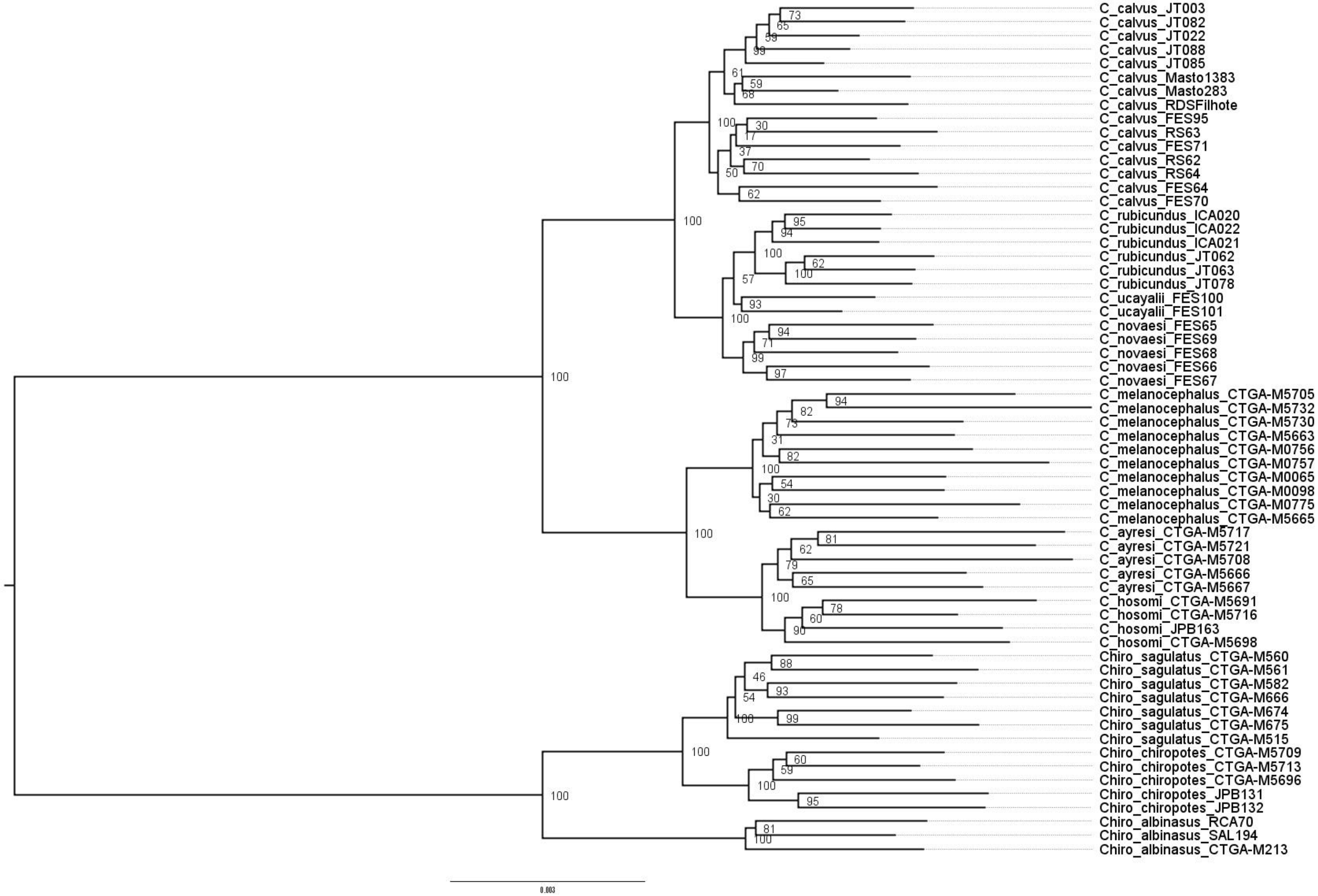
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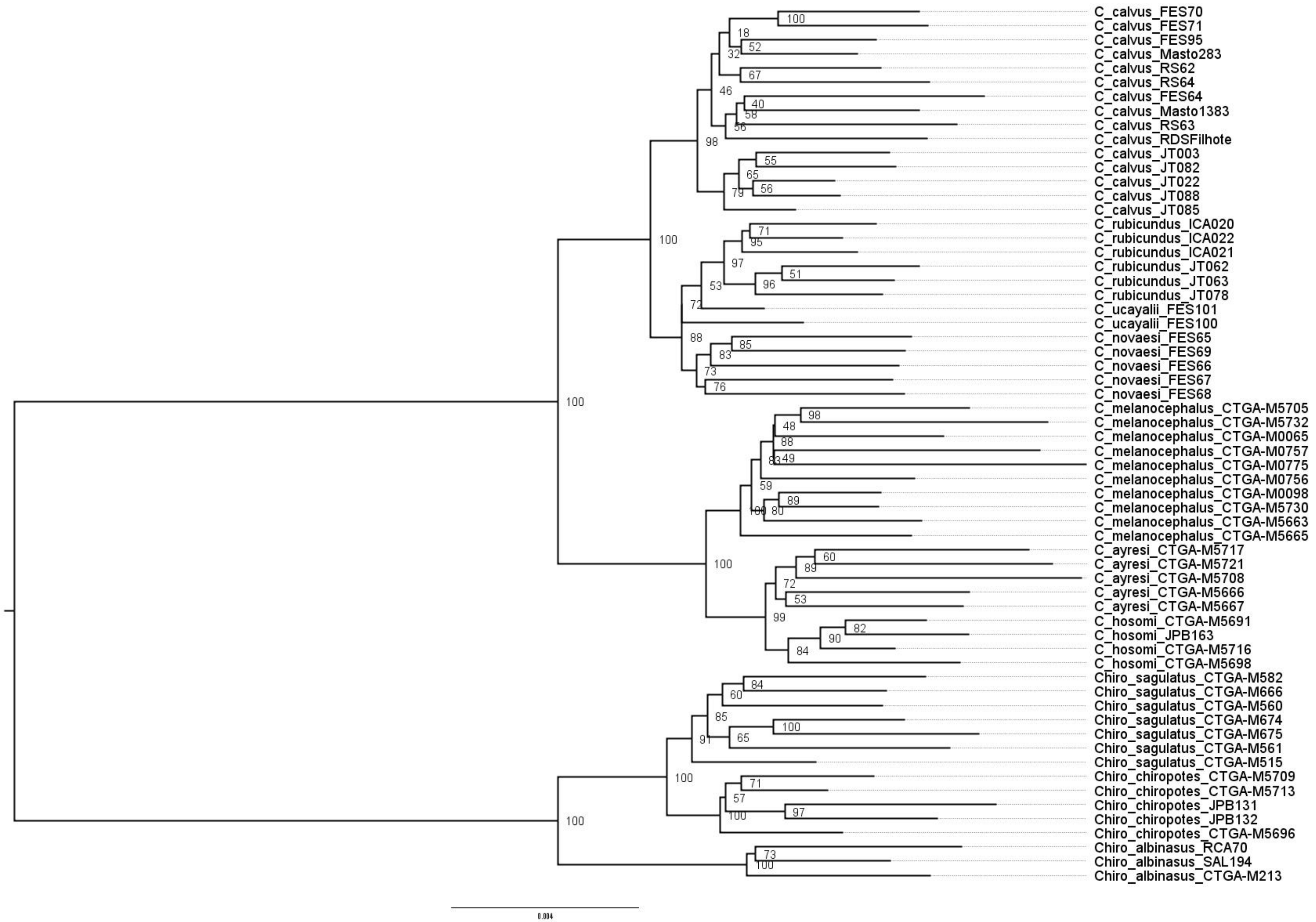
Denovo15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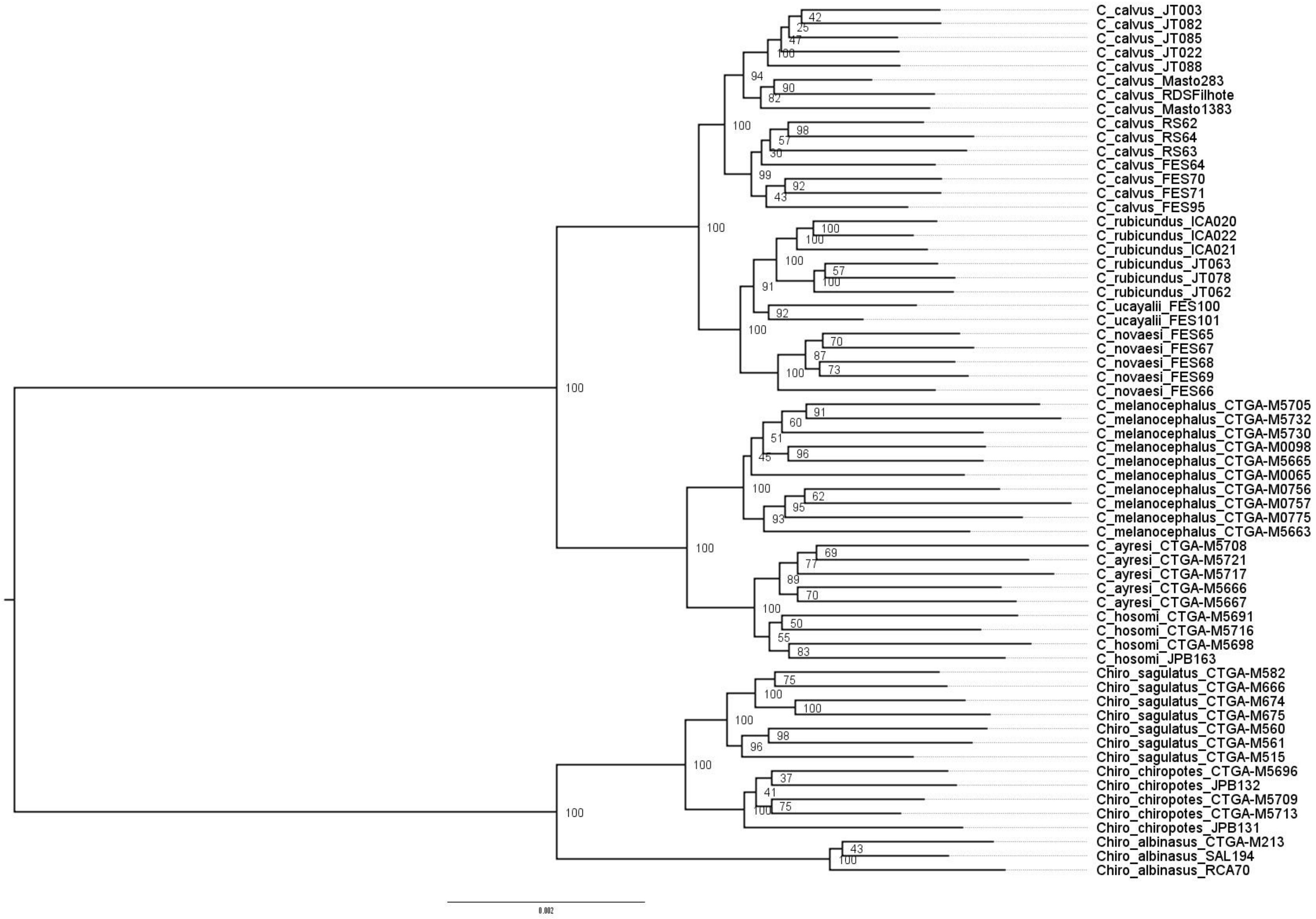
Denovo16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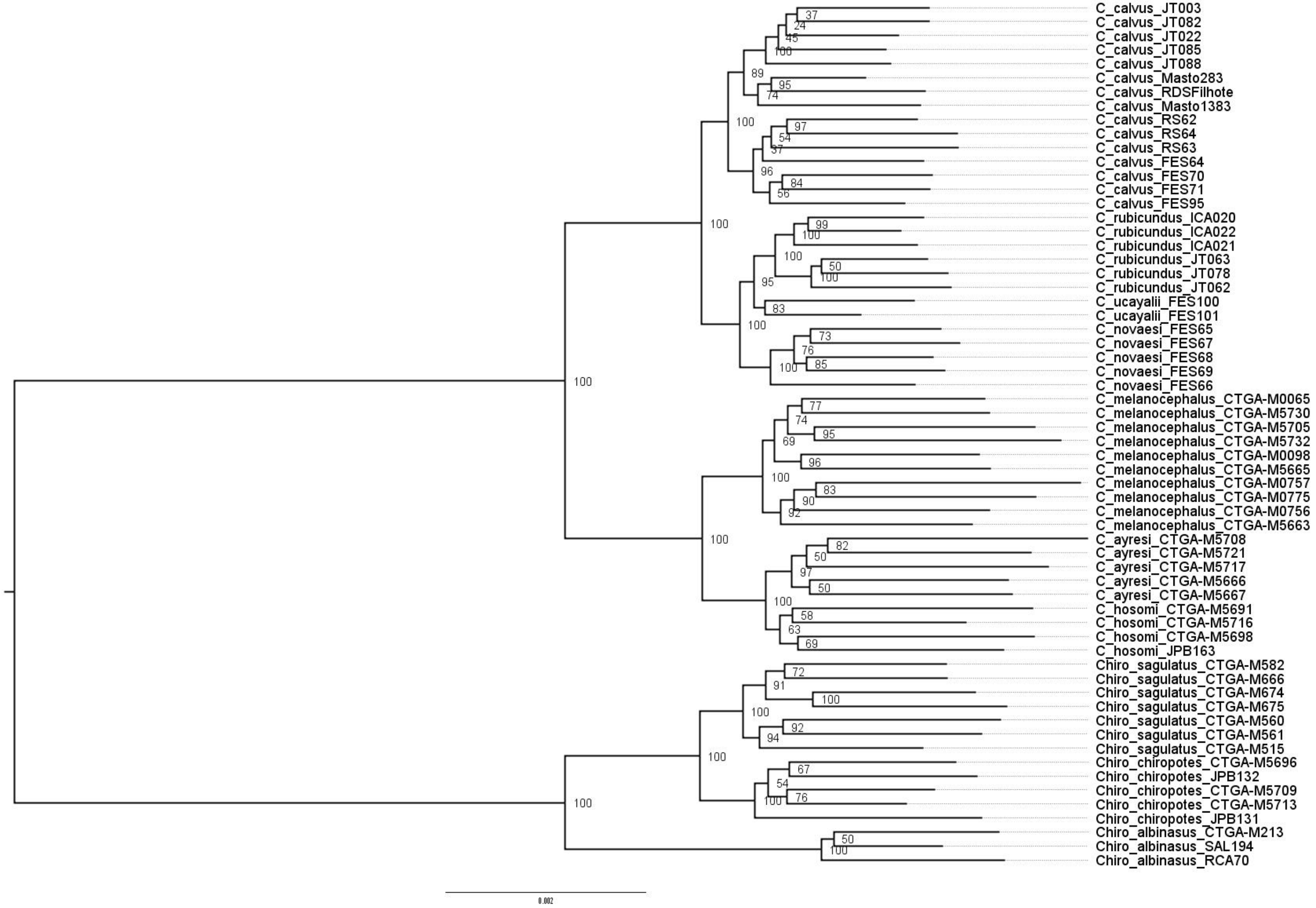
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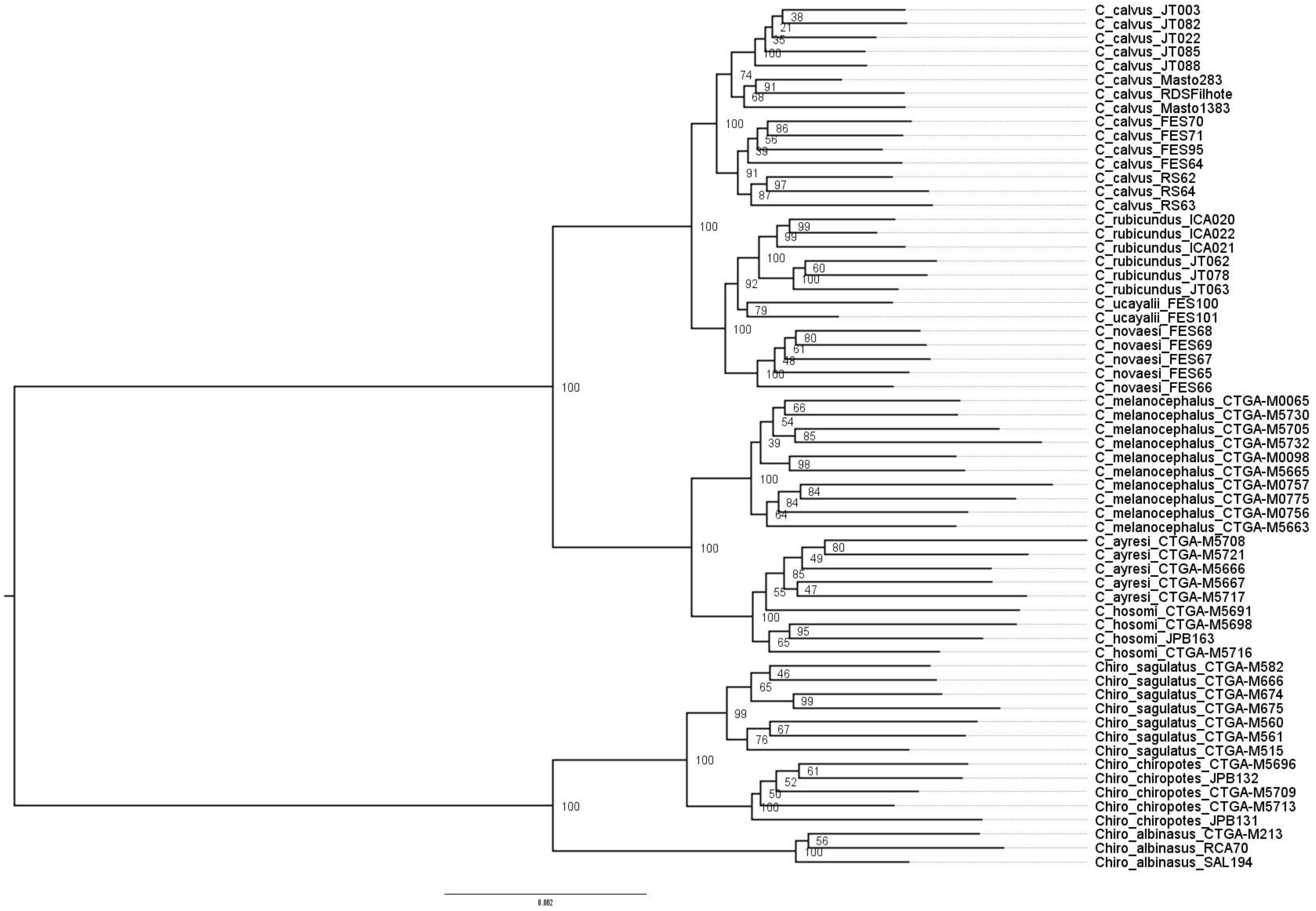
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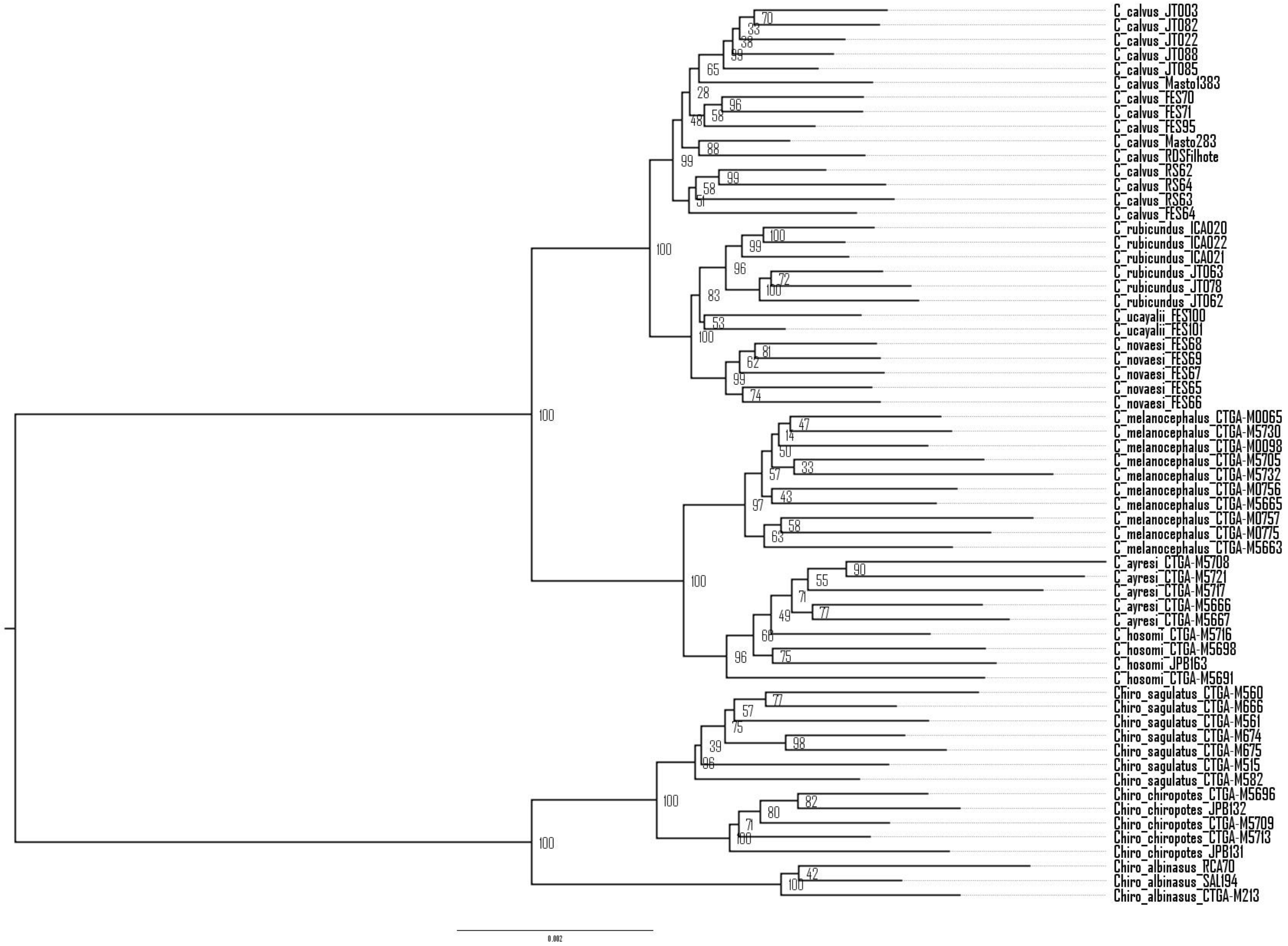
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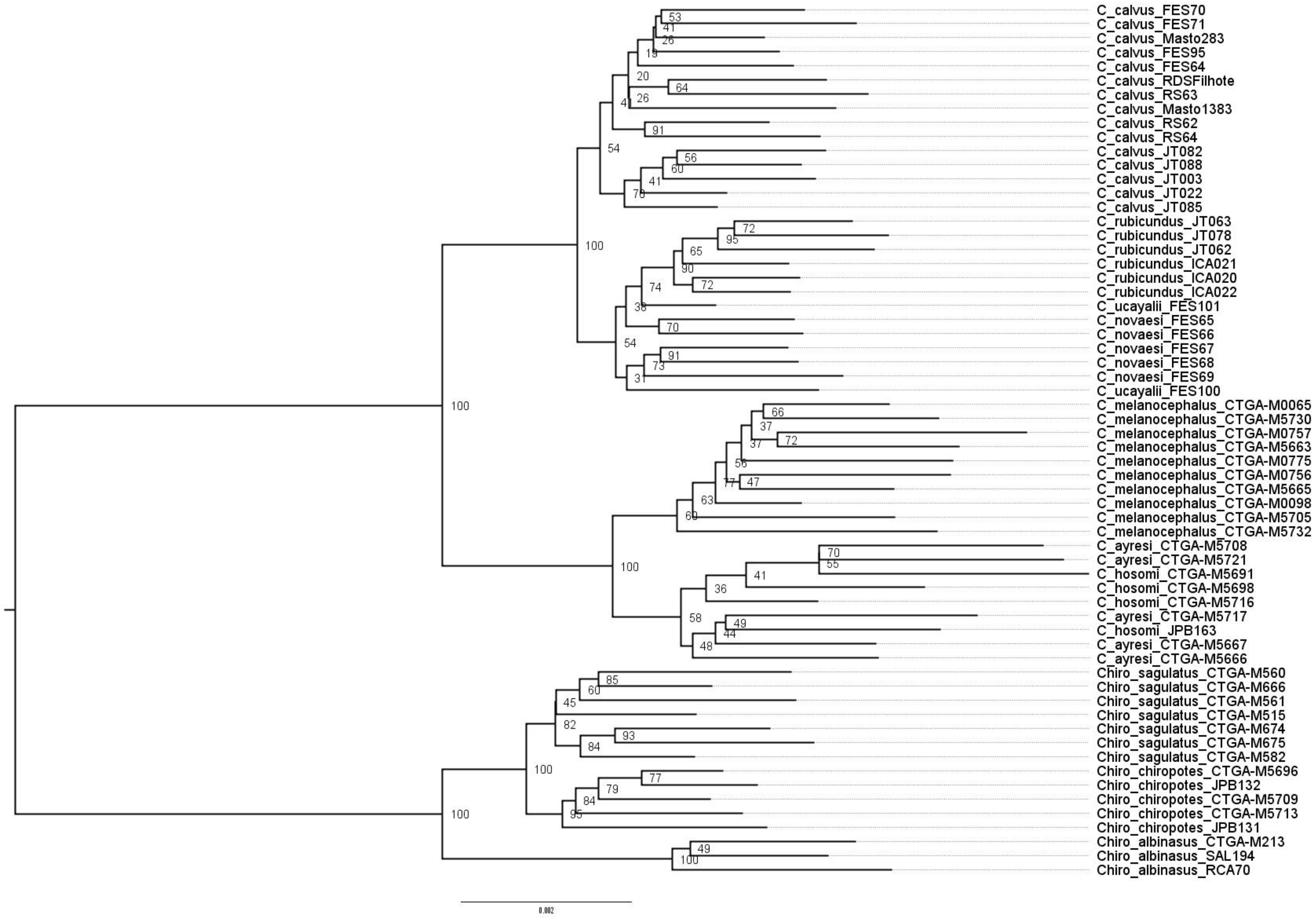
Denovo20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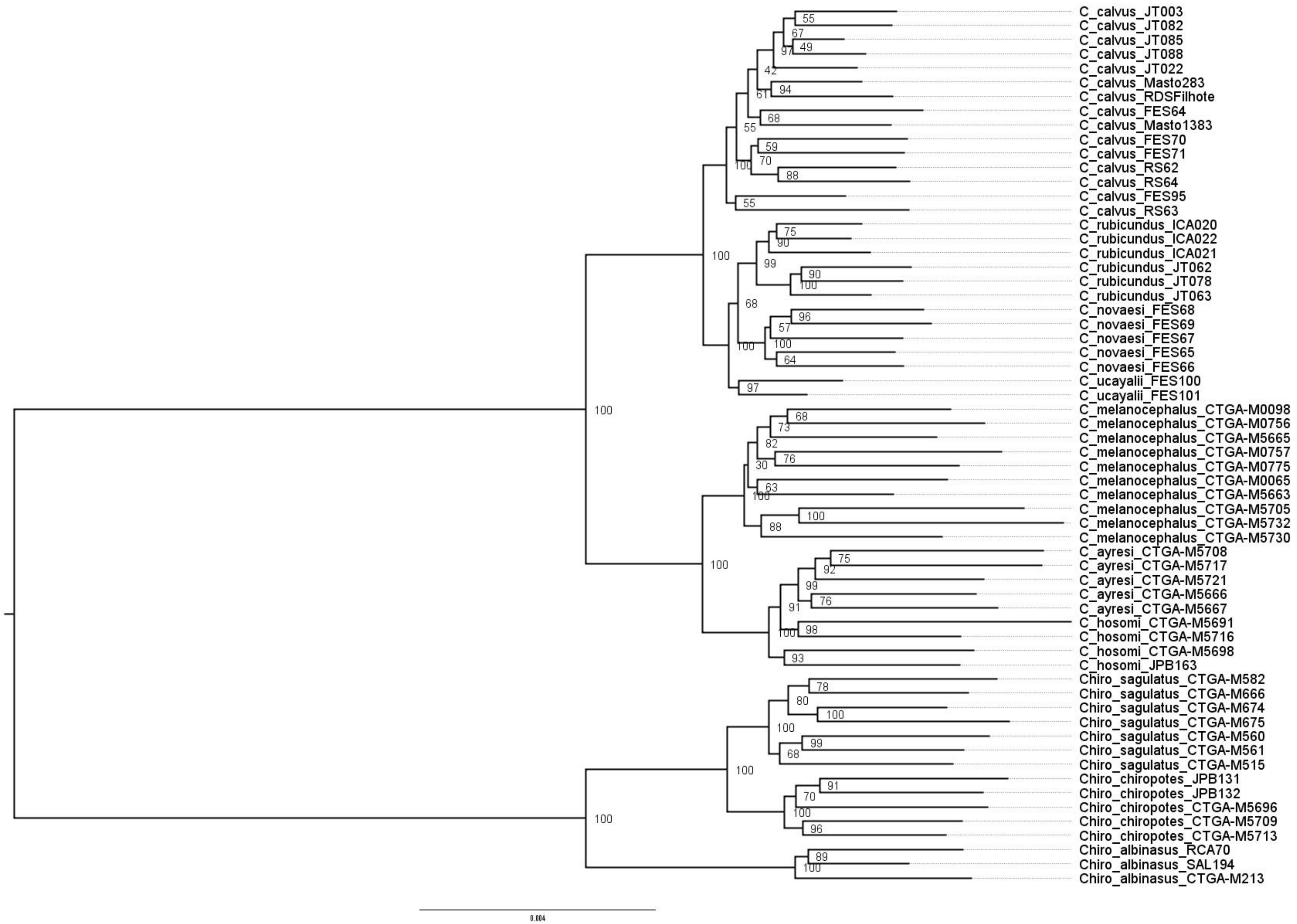
Denovo21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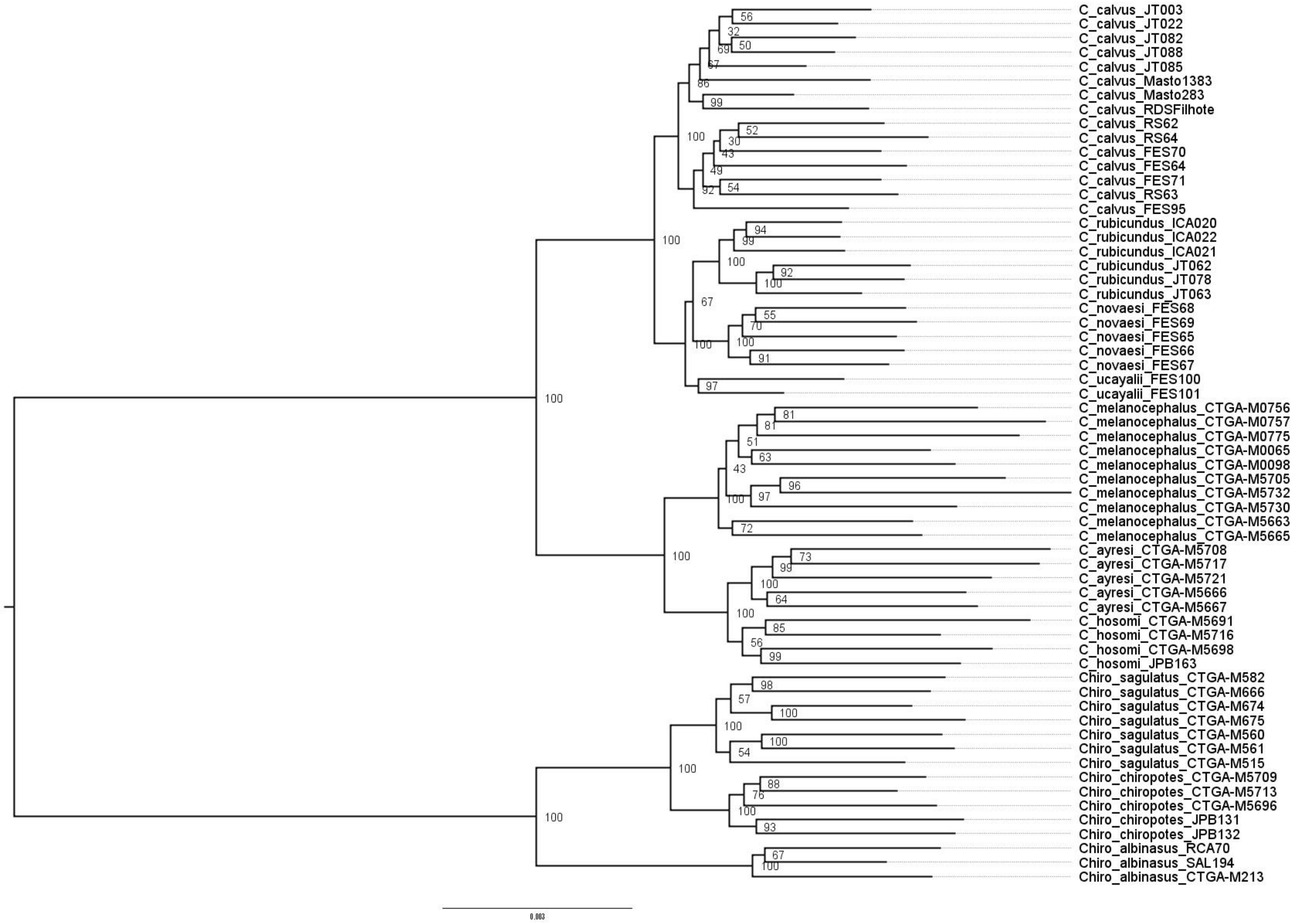
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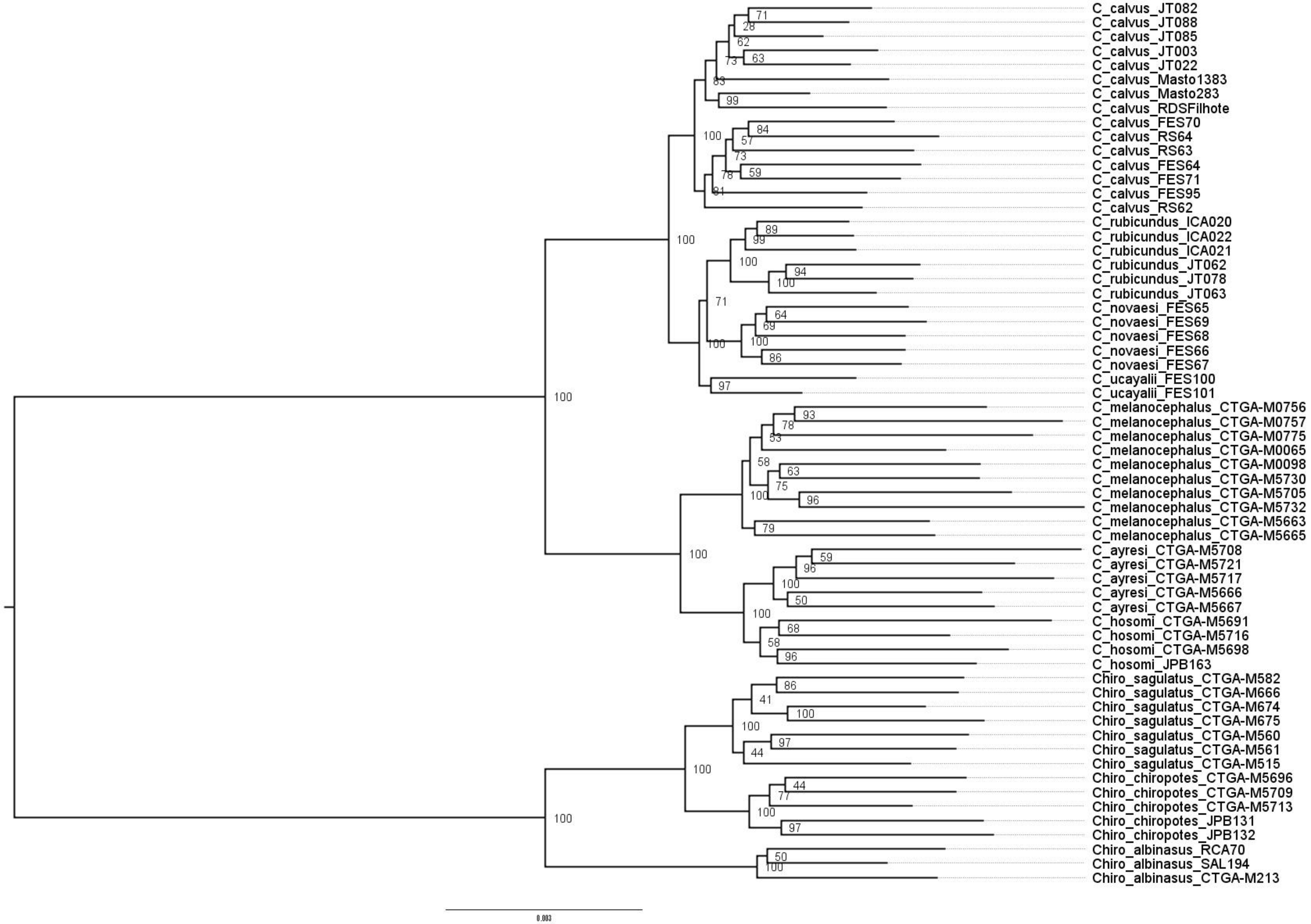
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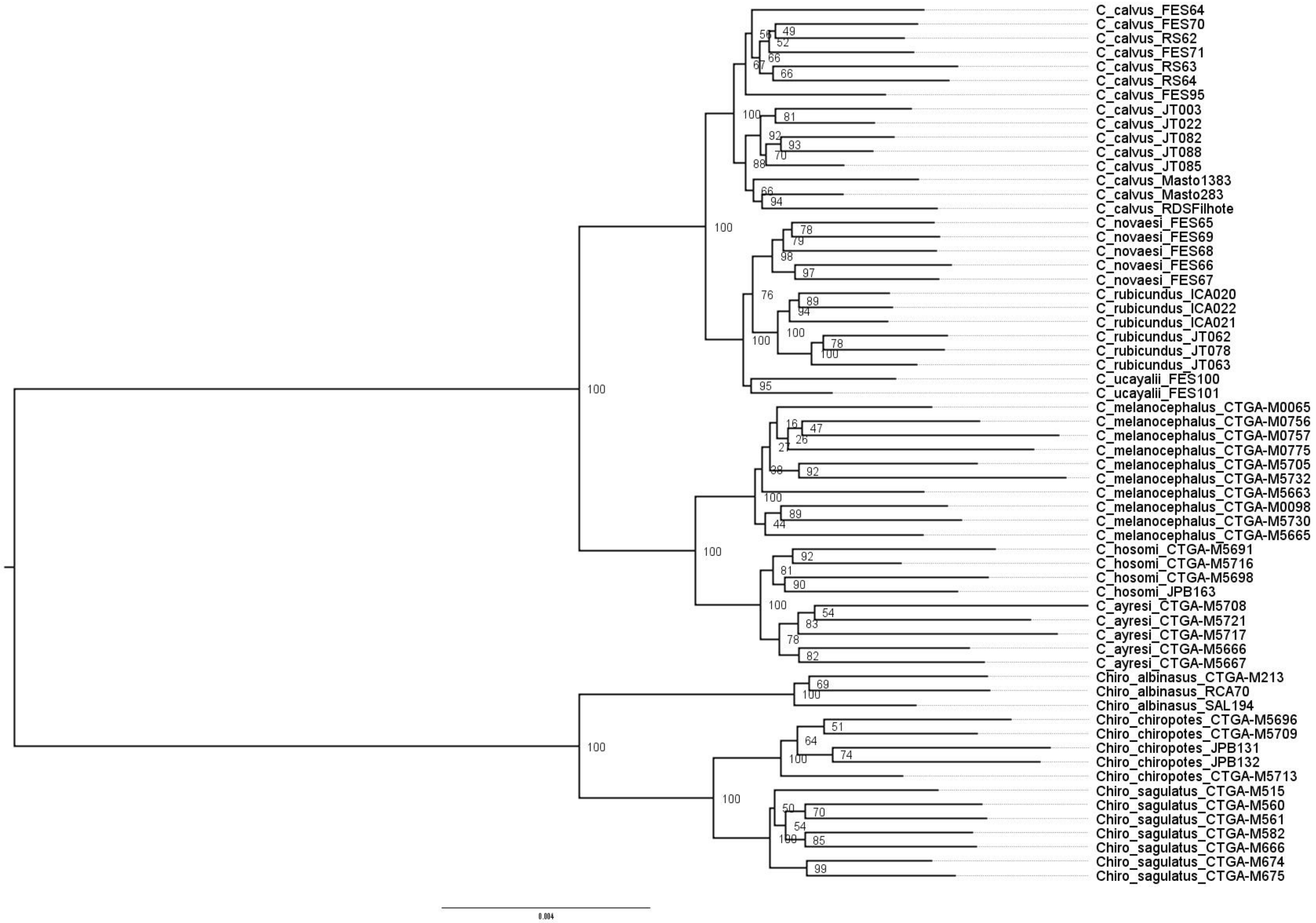
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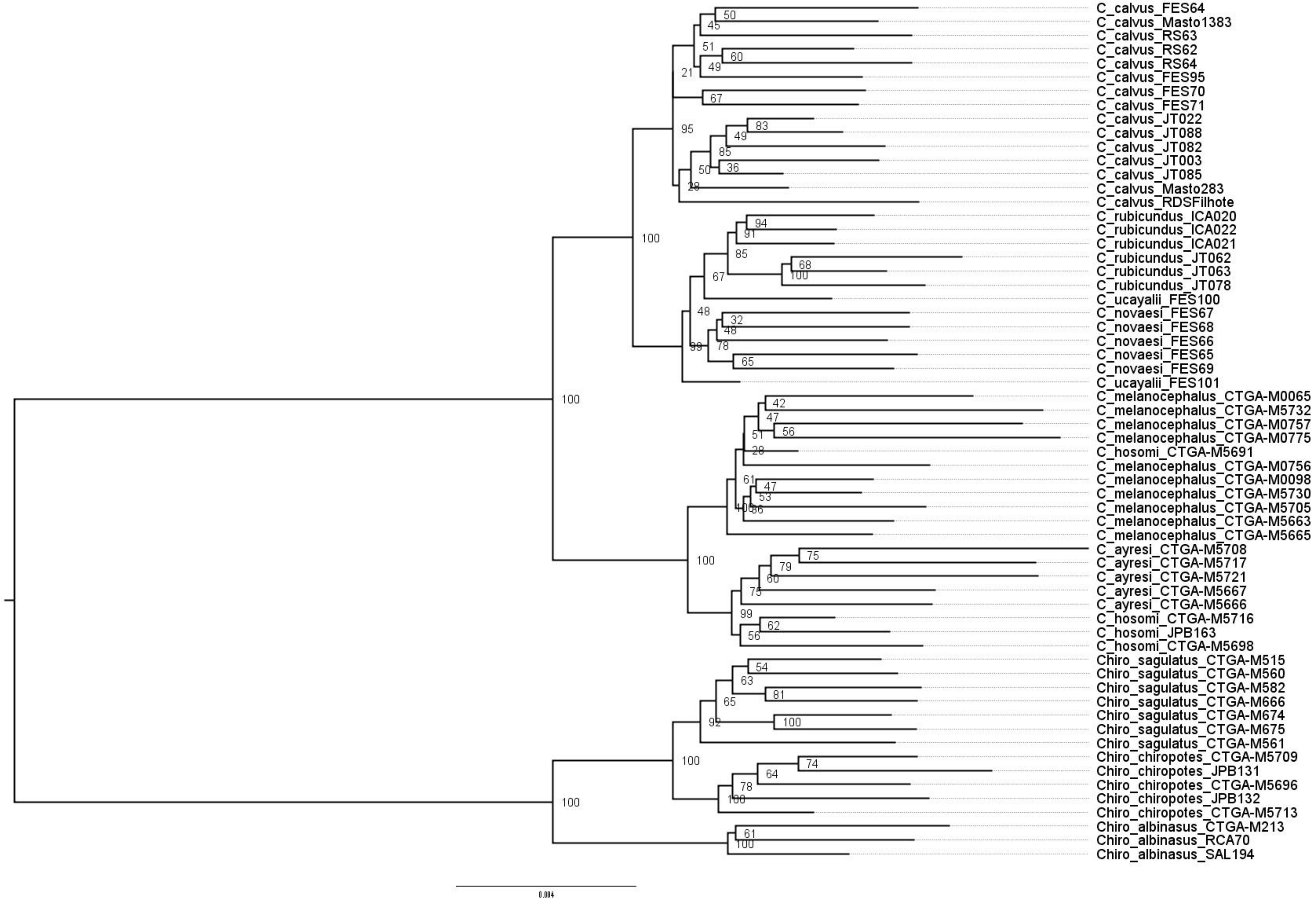
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C_calvus_Masto283
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