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Comparative conservation genetics of giant and Neotropical otters in the Central Amazon Basin

by

Vania Carolina Fonseca da Silva

Thesis submitted for the degree of Doctor of Philosophy
Department of Biosciences
Durham University

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Abstract

Genetic diversity provides adaptive potential, which is crucial for the long-term persistence of species, allowing them to respond to disturbances and environmental changes. Quantifying genetic diversity and understanding how it emerges in natural populations are therefore important objectives towards conserving biodiversity.

Giant otters (*Pteronura brasiliensis*) and Neotropical otters (*Lontra longicaudis*) are widespread in Amazonia, but intensification of anthropogenic interference in this biome is increasingly threatening these species. Both species are under a pressing need for more local and regional scale research on their population trends, spatial patterns and genetic structure. Information on population trends and spatial patterns informs about the mechanisms driving the evolution of genetic structure. In order to contribute to expanding this knowledge, nuclear and mitochondrial DNA markers and a habitat modelling approach were employed in a comparative conservation genetics study at a regional scale in Central Amazonia.

The central goal was to assess patterns of habitat use, genetic diversity and population structure, in order to gain insight into the current levels of gene flow and connectivity among populations, and the relevant evolutionary mechanisms. Specific aims included assessing if population structure could reflect intrinsic species attributes such as sociality and behavioural ecology as well as habitat features, which can act in the promotion or limitation of gene flow.

Despite a high potential for structural connectivity and dispersal along the hydrographic network, the results indicated the existence of genetically distinct clusters of otter populations over the spatial scale considered. This type of pattern has not been detected for either species until now, and outcomes from this research provide novel information that can provide transferrable inference to the conservation and management of otters and other semi-aquatic Amazonian vertebrates.

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When I first started planning this PhD project, I heard a few things that might have discouraged me from stepping into this daunting ground. Among intimidating thoughts about the project's ambitiousness, I decided to carry on anyway. All the pages in this thesis are the final (and positive) outcome of my obstinacy, and such an endeavour would have been impossible without the support of several people and institutions. For this, I would like to first thank my supervisor, Prof. Rus Hoelzel, for being so receptive to my ideas since our first e-mail contact. He gave me the opportunity to make them happen and patiently guided me in the challenging scientific journey until the very end. My thesis committee members, Dr. John Bothwell and Dr. Philip Stephens, were also kind and helpful in all of our meetings. I appreciate their concerns and suggestions to the work along the course of the PhD. I would also like to thank my viva examiners, Prof. Anna Loy and Dr. Adrian Brennan, for the relevant comments and suggestions that helped to improve the final version of this thesis.

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Table of Contents

Abstract.....	iii
Acknowledgements	iv
List of Figures.....	ix
1. General Introduction.....	1
1.1 Human Impacts on Nature.....	2
1.2 Conservation biology and genetics.....	3
1.3 Fundamental aspects of Conservation Genetics	6
1.4 Study contexts	9
1.4.1 The study region.....	10
1.4.2 Social systems and implications on genetic structure	13
1.5 Study species.....	14
1.5.1 Neotropical otter, <i>Lontra longicaudis</i>	14
1.5.2 Giant otter, <i>Pteronura brasiliensis</i>	18
1.5.3 Social structure of giant and Neotropical otters	20
1.6 Central aims of the study	21
1.7 References	24
2. Assessment of giant and Neotropical otters' distribution patterns in central Amazonia.....	37
2.1 Introduction	38
2.2 Objectives.....	41
2.3 Methods	42
2.3.1 Study Area and Species Occurrence Datasets	42
2.3.2 Modelling	48
2.3.3 Environmental Data.....	50
2.4 Results	53
2.5 Discussion.....	66
2.5.1 Limitations of the study.....	72
2.5.2 Implications for conservation	74
2.6 Conclusion.....	76
2.7 References	78
2.8 Appendices	91
3. Comparative conservation genetics of giant and Neotropical otters	101
3.1 Introduction	102
3.2 Methods	107
3.2.1 Study area.....	107

3.2.2 Otter scat and tissue sampling	108
3.2.3 Ethics statement	111
3.2.4 Target loci selection.....	112
3.2.5 DNA extraction and library preparation	115
3.2.6 Hybridization Capture	117
3.2.7 Mitochondrial DNA Sequencing and Analyses.....	118
3.2.8 Bioinformatics pre-processing of NGS data	121
3.2.9 Population genetic analyses	122
3.3 Results	124
3.3.1 Population Genetic Structure	128
3.3.2 Genetic Diversity	136
3.4 Discussion	144
3.4.1 Giant otters	144
3.4.2 Neotropical Otters.....	150
3.4.3 Comparative genetic diversity and structure patterns	151
3.5 Conclusion	154
3.6 References.....	156
3.7 Appendices.....	162
4. Reconstructing Carnivora evolutionary relationships with a particular focus on the Lutrinae using a novel dataset of nuclear loci	259
4.1 Introduction.....	260
4.1.1 The Order Carnivora.....	260
4.1.2 Feliformia	262
4.1.3 Caniformia	263
4.1.4 Musteloidea and phylogenetic incongruences	266
4.1.5 Otter phylogeny	268
4.2 Study goals.....	271
4.3 Methods.....	272
4.3.1 Selection of loci for phylogenetic estimations.....	272
4.3.2 Phylogenetic Analyses.....	273
4.3.3 Supermatrix Tree, Calibration and Divergence Date Estimates	274
4.4 Results.....	276
4.4.1 Individual Locus Trees	276
4.4.2 Supermatrix Tree and Date Calibration	283
4.4.3 Giant and Neotropical otter Diversity.....	289
4.5 Discussion	291

4.5.1 Phylogenies and divergence times	291
4.5.2 Loci 2 and 6 Gene ontologies.....	296
4.5.3 Giant and Neotropical otter diversity and phylogenetic inferences	297
4.6 Conclusion	300
4.7 References	301
4.8 Appendices	313
5. General Discussion	331
5.1 Summary and discussion of main findings.....	332
5.2 Limitations of the study	338
5.3 Conservation implications and suggestions for future research	341
5.4 References	345

List of Figures

Figure 1.1: A male neotropical otter at Rio Urumutum, Amazonas, Brazil	15
Figure 1.2: Distributional range of <i>Lontra longicaudis</i>	16
Figure 1.3: Two wild adult individuals of giant otter in Erepecu Lake, Pará, Brazil.	18
Figure 1.4: Distributional range of <i>Pteronura brasiliensis</i>	18
Figure 1.5: A female otter and her almost adult-sized cub (in the water) observed in the River Aquidauana, Pantanal, Brazil, 2014.....	19
Figure 2.1: Satellite image showing main fieldwork study sites.....	41
Figure 2.2: Sensitivity vs. specificity (ROC curve) for giant otter and Neotropical otter.....	52
Figure 2.3: Giant otter suitability map based on the 10 percent training Cloglog threshold	55
Figure 2.4: Neotropical otter suitability map based on the 10 percent training Cloglog threshold..	56
Figure 2.5: Two zoomed areas of suitability maps showing Neotropical and giant otter suitable habitats.....	57
Figure 2.6: Binary maps of suitability generated with (maps on left) and without (maps on right) bias grids for Giant and Neotropical Otters.	58
Figure 2.7: Jackknife plots for: AUC on test data (a,b); training gain (c,d); and test gain (e,f). ...	60
Figure 2.8: Mean response curves of the effect of explanatory variables on the giant otter habitat suitability model predictions across 10 iterations	61
Figure 2.9: Mean response curves for the effect of variables on the Neotropical otter model predictions for habitat suitability across 10 iterations	62
Figure 3.1: Map of sampling locations in Central Amazonia, northern Brazil	104
Figure 3.2: Neotropical otter spraints (evidenced by yellow circles) deposited on fallen logs ..	109
Figure 3.3: Biopsy dart with a tissue sample.	110
Figure 3.4: Giant otter mitochondrial DNA sample locations from this study (in red), from Pickles et al. 2011 (in pink) and from Garcia et al. 2007 (in yellow).	115
Figure 3.6: Principal component analysis (PCA) plots generated with PCAngsd covariance matrixes. a) Giant otters; b) Neotropical otters.....	116
Figure 3.7: Admixture in giant otter populations estimated in NGSAdmix. a) Bar plot of admixture proportions, where each bar represents one individual. b) Map illustrating total admixture proportions in each location.....	124
Figure 3.8: Admixture in Neotropical otter populations estimated in NGSAdmix. a) Bar plot of admixture proportions, where each bar represents one individual. b) Map illustrating total admixture proportions in each location	125
Figure 3.9: Discriminant analysis of principal components, with Giant otter plots on the left and Neotropical otter on the right.	126
Figure 3.10: FCA plot from GENETIX, using SNPs from giant otter called genotypes.....	128
Figure 3.11: FCA plot from GENETIX, using SNPs from Neotropical otter called genotypes..	129

Figure 3.12: Bayesian tree based on partial sequences of mitochondrial control region for giant otter individuals.	131
Figure 3.13: Bayesian tree based on partial sequences of mitochondrial control region for Neotropical otter individuals.	132
Figure 3.14: Median-joining network of giant otter haplotypes considering only samples from this study.	133
Figure 3.15: Median-joining network of Neotropical otter haplotypes considering only samples from this study.	133
Figure 3.16: Giant otter haplotype network with added Genbank sequences.....	134
Figure 3.17: Neotropical otter haplotype network with added Genbank sequences	135
Figure 4.1: Locus 1 BI tree obtained in MrBayes	268
Figure 4.2: Detail from Locus 8 BI tree obtained in MrBayes, showing only the Mustelidae family	268
Figure 4.3: Detail from Locus 17 BI tree obtained in MrBayes, showing only the Mustelidae family.	269
Figure 4.4: Phylogenetic relationship of Locus 2 for Carnivora species.	271
Figure 4.5: Phylogenetic relationships of Locus 6 for Carnivora species	272
Figure 4.6: Ensembl Genome browser showing the location of Locus 2 (in red, indicated by black arrows) and the ZNF646 gene in the domestic ferret (<i>Mustela putorius furo</i>) genome assembly	273
Figure 4.7: Ensembl Genome browser showing the location of Locus 6 (in red, indicated by black arrows) overlapping with the GFRA1 gene (dashed line) in the domestic ferret (<i>Mustela putorius furo</i>) genome assembly	273
Figure 4.8: BI phylogenetic tree generated in MrBayes. Each node shows its respective posterior probability value, and Carnivora families are displayed in different colours.....	275
Figure 4.9: Maximum likelihood tree produced in RaXML for the order Carnivora.....	276
Figure 4.10: BI tree produced in MrBayes.	277
Figure 4.11: Phylogeny resulting from Bayesian analysis of the supermatrix in BEAST.	280

Chapter 1

General Introduction

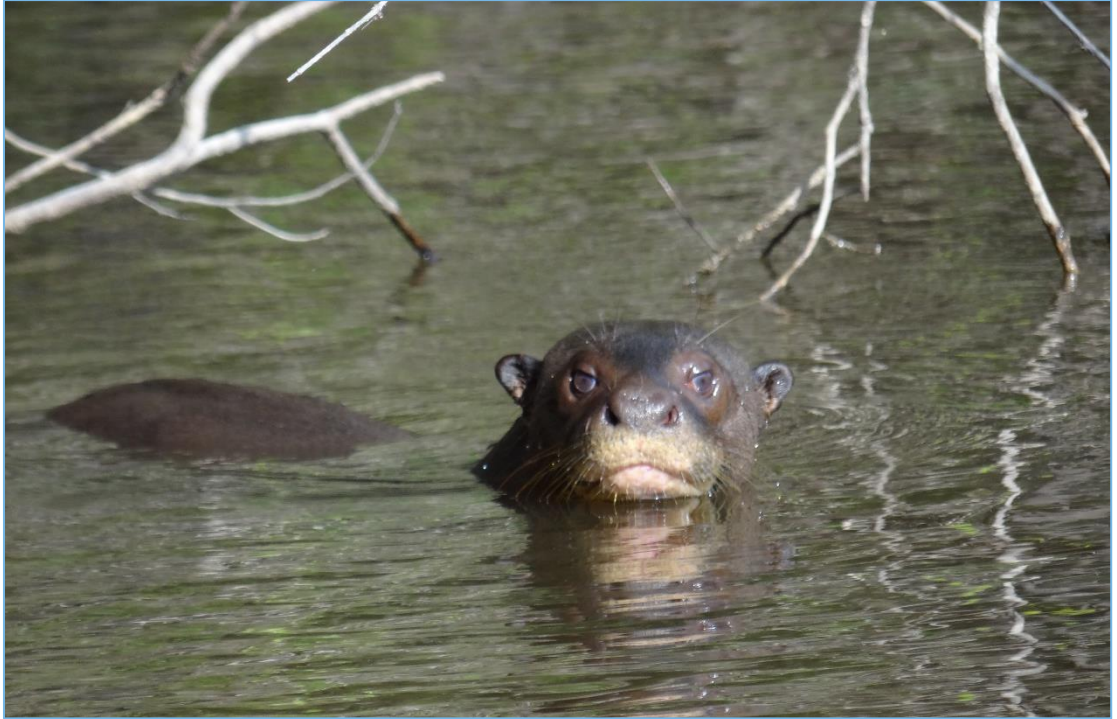


Photo: V.C. Fonseca da Silva

1.1 Human Impacts on Nature

The Earth is now facing a potential new sixth wave of mass extinctions (Barnosky et al. 2011) which, unlike the previous ones, takes place in a human-dominated world. Since the Late Pleistocene, human population increase and expansion has been a major driver of mammal species extinctions (Andermann et al. 2020). Only within the last 50 years, our global population has doubled in size – and, in parallel, we experienced a sharp growth in the world economy with a four-fold increase (adjusted to inflation) in global gross domestic product (Díaz et al. 2019, FAO 2019).

Naturally, in order to thrive, this massive population had to find means to sustain itself. Contrary to Thomas Malthus' (1798) expectations, our exponential population growth has not surpassed food production capacities. In his classic essay, Malthus did not foresee that technological advances and the expansion of globalization and international trade chains would have made it possible to immensely increase food production. But, this did not come without costs to the environment and to other species - land-use changes and its consequent habitat losses are driving most of the anthropogenic negative impacts on nature, followed by (over)exploitation of natural resources (such as logging and fishing) (Díaz et al. 2019). Livestock production is considered a major culprit of habitat loss, and developing tropical countries – where the largest amount of biodiversity is - are currently its main producers (Machovina et al. 2015). Furthermore, Lenzen et al. (2012) have shown that the overall consumption of imported goods, especially in developed countries, is linked to 30% of species threats as a consequence of international trade along complex routes.

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has recently reported startling levels of threat for the planet's

biodiversity: around 1 million species of plants and animals are threatened with extinction, which represents about 25 per cent of the assessed species (Díaz et al. 2019). Hence, a nearly 8-billion population of a single species is causing global changes at such quick rates that other species are likely not able to evolve and adapt in response (Ceballos and Ehrlich 2018). In particular, recent centuries are seeing an extensive and pervasive crisis of losses in both terrestrial and marine fauna (Dirzo et al. 2014, McCauley et al. 2015). This “Anthropocene defaunation” is expected to cause serious cascading effects in other taxa and in ecosystem interactions, functioning and services (Dirzo et al. 2014).

1.2 Conservation biology and genetics

As humanity progressively became aware of their damaging impacts on nature, although with different perspectives through time – from utilitarianism to aesthetics and finally a more comprehensive biodiversity-grounded view (see Haila 2012) – this made way to new paradigms where the need to take actions in order to preserve natural elements (be them species, or landscapes, or processes) was gradually acknowledged.

Foundations of conservation biology have been slowly consolidated since the first half of the 20th century, with the work of naturalists like Charles Elton, Victor Shelford and Aldo Leopold, among several others (Noss 1999, Meine et al. 2006). With “A Sand County Almanac”, published in 1949, Aldo Leopold paved the way for a holistic vision of nature, where man is part of the environment rather than its ruler. The publication of the Theory of Island Biogeography by MacArthur and Wilson in 1967 leveraged rapid progress and increased concerns about habitat destruction and its impacts on natural populations. In the early 1980s, conservation biology was finally formalized as a

discipline, with a mission-driven perspective to provide principles and tools for preserving biological diversity (Soulé 1995).

Despite the lately unfavourable scenarios, conservation efforts have already been proving some success over the last decades in preventing species extinctions and preserving natural habitats (Rodrigues 2006; Hoffman et al 2010). Still, to minimize the impacts of the ongoing trend of biodiversity loss and promote ecosystem functions maintenance, it is vital to continue strengthening the multiple aspects of conservation science, whose multidisciplinary nature allows scientists and policy makers to address better strategies to safeguard species and the natural environment.

As pointed out by Davis et al. (2018), biodiversity also represents the amount of unique evolutionary history in the tree of life. Among the disciplines that constitute the pillars of conservation biology, genetics had its importance recognized in the field early by Otto Frankel (1974), who highlighted the relevance of the evolutionary persistence of species relying on the genetic variation between individuals as well as between populations. In 1981, Frankel joined efforts with Michael Soulé, publishing the book *Conservation and Evolution* where the genetic principles for conservation are deeply examined and exemplified for the first time in a broad sense, bringing more attention to the then emerging field. Nowadays, conservation genetics is undoubtedly a well-established field of research; a search for the term on ISIS Web of Science returns 3,520 records of publications since 1990 – and shows an impressive increase of 23,000% in the number of papers on the topic published over the last 30 years.

One of the most famous case studies in conservation genetics, frequently evoked in textbooks, is the cheetah population bottleneck and reproductive impairment (O'Brien et al. 1983, 1985), which was recently revisited and confirmed by genomic analyses (Dobrynin et al. 2015). It became a “flagship” study to exemplify the risks of inbreeding

for threatened populations, and has contributed to raising a lot of attention to the issue since then. Regardless of the clear advance in conservation genetics research, especially since the rapid development of genomics in the last two decades, many challenges are yet to be addressed. In particular, it is crucial to define the best practices in integrating the increasing amount of molecular data to conservation management and employing successful strategies, and strengthening collaborations with non-academics (DeSalle & Amato 2004, Rodríguez-Clark et al. 2015, Britt et al. 2018).

Conservation genetics attempts to manage human influence on the evolutionary process and maintain the adaptive potential of natural populations (Latta 2008), and its greatest benefit is that it can help to identify more accurately the patterns and processes in endangered species (DeSalle & Amato 2004). The patterns observed with genetic tools can give a clearer understanding of the processes that led to, for instance, an isolated or inbred population. Though conservation is a multidisciplinary field and its decision-making processes involve not only biological but also socio-economic and political aspects, the lines of action contemplated by genetics are important - and keeping the proper conditions for the continuing evolution of natural communities should be a priority (Frankel 1974).

Future scenarios for biodiversity predicted by modelling are not very optimistic. Davis et al. (2018) have shown that in order to recover the amount of mammalian phylogenetic diversity already lost and expected to be lost in the near future due to mass extinctions, it would take millions of years, even in the best-case scenario where extinction rates drop down to a background level. These findings are alarming, since it is highly unlikely that human-driven extinction would come to a halt in the short-term. Nevertheless, saving unique evolutionary history before it is lost can aid to speed the

recovery of these diversity losses and could still have significant impacts in conservation as well as in ecosystem services (Davis et al. 2018, Veron et al. 2017).

It is relevant to mention that there is not yet a clear agreement among researchers as to which level, or kind, of diversity should be prioritised in conservation. Another recent modelling approach by Cantalapiedra et al. (2019) disagrees with Davis et al. (*op cit*) conclusions that conserving phylogenetic diversity (that is rather focused on distantly related species) would be able to better safeguard biodiversity over time, and instead proposes that more effort should be invested in rapidly speciating lineages. Either way, the debate highlights how important it is to clarify these matters and certify that genetic and evolutionary aspects are taken into account in conservation modelling and planning in face of the current global threats. As well put by Moritz (2002), academics should also attempt to simplify such complex issues, creating the means to provide more practical, “ready-to-use” information which is relevant to managers and decision-makers.

1.3 Fundamental aspects of Conservation Genetics

Many of the central questions addressed by conservation genetics are traditionally grounded in theoretical population genetics (DeSalle and Amato 2004). Although being a very broad discipline, most studies in the field can be narrowed down to one of the following main categories: i) management and reintroduction of ex-situ populations and restoration of biological communities, ii) description and identification of individuals, genetic population structure, kin and taxonomic relationships, iii) detection and prediction of the effects of habitat loss, fragmentation, and isolation, iv) detection and prediction of the effects of hybridization and introgression, and v) understanding the relationships between adaptation or fitness and the genetic characters of individuals or

populations (Allendorf & Luikart 2007). Direct applications of genetics in conservation also include wildlife forensics, aiding in the criminal investigation of illegal trade and poaching (Ogden & Linacre 2015).

Inbreeding depression and the loss of diversity in reduced populations have been a major focus of the discipline since its early development, and the significance of this factor for conservation planning has been controversial. Authors have argued that pure demography could be more relevant than genetics in management plans for small populations (e.g., Lande 1988). However, further progresses in research brought to light the importance of a non-dualistic approach where both aspects are taken into account, and it is well known now that inbreeding depression plays a role with stochastic and deterministic factors that can threaten population persistence (Frankham 2005; Mills & Soulé 2007). Decreases in genetic diversity can lead to a lower ability to cope with environmental changes through adaptive responses (Bijlsma et al. 2000), which in turn can make populations more vulnerable to extinction and also lead to an overall reduction in fitness.

Demographic aspects (population size, recruitment, inbreeding and connectivity) can be well studied using neutral genetic markers, facilitating the identification of conservation units (Hoelzel et al. 2019). Given that populations of a given species can vary in their capacity to respond adaptively, genetic data can ensure a better use of available management resources, as one can better predict the evolutionary-response potential of a set of populations (Petit et al. 1998), appropriately identifying among them the ones with more conservation interest or urgency.

Effective population size (N_e), which can be estimated using genetic data, is a key parameter for conservation of endangered species. Theoretically, it represents the size of an ideal population which experiences diversity loss through genetic drift at the same rate

as in the observed population in question. In practice, N_e can be used as an informative measure of how much a population is at risk to lose genetic variation due to drift. However, it is not very simple to estimate this parameter in natural populations; first, it is usually lower even than the actual number of breeding individuals. Evidently, real-world scenarios frequently deviate from the assumptions of the ideal population, having for example varying sex ratios and progeny numbers, non-random mating, and fluctuating population size (Allendorf & Luikart 2007; Frankham et al. 2010) which will all have an effect on N_e estimates. Plus, the effect of selection also increases such estimation difficulties, and caution is recommended when interpreting results regarding spatial and temporal scales (Wang et al. 2016). Long-term patterns of N_e can be estimated by coalescence-based approaches with genetic marker data (see Kingman 1982), and these can work well even under incomplete meeting of assumptions (Drummond et al. 2002) or changes over time and population sub-divisions (Ewing & Rodrigo 2006).

Intraspecific genetic diversity is largely maintained by the exchange of individuals among populations or subpopulations; hence, connectivity between these entities is an essential feature to the maintenance of variation and to prevent the consequent risks of population extinction due to the deleterious effects of inbreeding and genetic drift (Wright 1951, Broquet et al. 2010). This is particularly relevant in scenarios of fragmented habitats, where the maintenance of gene flow can help in overcoming the impacts of fragmentation (Frankham et al. 2010).

Following on from Wright's (1931) island model, centred on the exchange of individuals between populations or demes, the "one migrant per population per generation" was proposed as a genetic rule of thumb for the minimum number of migrants necessary per generation, in order to maintain enough gene flow to hinder the effects of drift and avoid inbreeding depression. Indeed, Vilá et al. (2002) have

documented the remarkable impact of the migration of only one individual in the increase of genetic variability and fitness in an isolated wolf population. But again, such a rule is built based on a number of assumptions which are difficult to be met in the real world, such as selective neutrality and no mutation, absence of geographical patterns to gene flow and demographic equality (Mills & Allendorf 1996). Therefore, only one migrant might not always be the ideal case, but with limited information and the need for urgent management it is generally accepted to use Mills and Allendorf's recommendation of 1 to 10 migrants. If instead more information is available, such as demographic data, more refined models can be used to estimate that number (see Wang 2004).

Gene flow can have a dual role in evolution: it might act either as a “creative” or “constraining” force (Slatkin, 1987); its extent and direction of occurrence can strongly influence the amount and spatial patterns of population structuring found in a species. Levels of gene flow that result in intermediate amounts of structuring allow for more genetic variation both within and between populations, giving space to a greater evolutionary potential than populations with extreme or very limited gene flow (Allendorf & Luikart 2007). This stresses the importance of assessing population genetic structure in studies with conservation-related goals.

1.4 Study contexts

In support of effective measures of conservation and management, it is important to recognize the natural processes behind patterns of connectivity and genetic structure among populations and their effective population sizes. Quantifying and understanding how genetic diversity emerges is a target that can provide subsidies for management and preventive conservation actions. In this context, the interaction of factors involving

species and environment relationships is also of utmost relevance, since predictions of a species distribution over a landscape, accounting for its heterogeneities, can provide inferences for potential genetic connectivity and better inform conservation practitioners on spatial planning and management actions.

1.4.1 *The study region*

The Amazon basin is the largest watershed in the world, covering an area of around 6 million km², and supporting the planet's largest tropical rain forest. The main rivers that form the basin are fairly wide and long, so that its own dimensions could act as a barrier limiting species dispersal and further allowing allopatric speciation - this possibility was noted early by the naturalist Alfred Russel Wallace, who postulated the "riverine barrier hypothesis" in 1852.

While several studies demonstrated the validity of Wallace's hypothesis for species of birds and primates (e.g., Peres et al. 1996, Bates et al. 2004, Boubli et al. 2015, Saldanha et al. 2019) it is still not clear to what extent rivers play a role in generating differentiation across populations and species. Several other studies could not find robust support for Wallace's hypothesis (e.g., Loughheed et al. 1999, Link et al. 2015, Santorelli et al. 2018). Gibbs et al. (2018) stated a more equilibrated conclusion in a recent study with pit vipers in the Amazon River. The authors could not find strong evidence in agreement with the river barrier hypothesis, but they did acknowledge the role of the river in impeding (not preventing) gene flow, and contributing to lineage formation.

Several other hypotheses regarding the origins of faunal diversity in the Amazon have been postulated after Wallace's. Haffer (2008) reviewed these and concluded that some of them can be relevant to different degrees for distinct taxa, or during different geological periods. However, several authors still considered hydrological features as key

historical determinant factors shaping diversity (e.g., Ayres and Clutton-Brock 1992, Hoorn et al. 1995, Marroig and Cerqueira 1997).

Even if riverine hypotheses fail recurrently to explain speciation and long-term evolutionary history across some taxa, it does not mean that these landscape features will not have any effects in contemporaneous patterns of intraspecific, between-population, differentiation. On the contrary, it has been shown that Amazonian rivers have an influence on the intraspecific genetic structure of populations that inhabit these environments, including aquatic and semi-aquatic vertebrates. This fact has been noted for instance in the pink dolphin *Inia geoffrensis*, between populations located to the north and south margins of the Solimões River, the major white-water tributary of the Amazon (Hollatz et al. 2011). Oliveira et al. (2019) also observed an influence of the Amazon River on the genetic structure of freshwater turtle *Podocnemys erythrocephala* populations in northern Brazil, and on a larger scale, Michels and Vargas-Ramírez (2018) found genetic differentiation between populations of *P. erythrocephala* in the Amazonian and Orinoco basins. Waterfalls and rapids in the rivers can also constitute potential natural barriers for aquatic and semi-aquatic Amazonian vertebrates, limiting dispersal and gene flow (Gravena et al. 2015).

Artificial or anthropogenic barriers are a concern regarding their potential to impact movements and gene flow. In the case of Amazonia these might include dams, deforested areas, and human settlements. Several large dams have been built in the basin's major rivers, such as Belo Monte (Xingu River), Balbina (Uatumã River), Santo Antônio and Jirau (Madeira River), Teles Pires; and at least three more are planned to be built within the next 10 years (BRASIL, 2018), which, if concluded, will impact many indigenous and conservation areas. Dams have already been suggested as low-quality habitats for giant otters in Amazonia (see Palmeirim et al. 2014) and could well represent

a threat for connectivity between populations of this and other species (Latrubesse et al. 2020).

Politics plays a major role in the management of Amazonia, and there has been a growing concern recently that new policies and legislation debates, triggered by the economic crisis and political instabilities in Brazil, might affect and negatively impact the rainforest ecosystem (Pereira et al. 2019). Currently, there is a strong pressure by Brazil's ruralist political lobby to reduce protected areas and indigenous lands in order to favour interests to expand large-scale farming, mining and extensive cattle ranching (Pereira et al. 2020, Rudke et al. 2020). If the current deforestation trends persist, by 2050 8 out of the 12 major watersheds in Amazonia are predicted to lose more than half of their forest cover (Soares-Filho et al. 2006).

In addition, expected changes in precipitation patterns related to climate change could seriously affect the flooding dynamics of Amazonian rivers (Zulkafli et al. 2016), leading to consequences not only for the biome itself, but also for the entire global climate (Malhi et al. 2008). Adaptive responses of animals to these changes might depend essentially on their mobility (dispersal ability) and habitat suitability and connectivity (Schloss et al. 2012). The greater intensity of droughts predicted for the Amazon River system could cause a severe reduction in connectivity for aquatic and semi-aquatic species. For instance, the annual Amazonian flood pulse has been suggested as an important factor to maintain connectivity between distant populations, enabling the existence of dispersal corridors and gene flow (e.g. Satizábal et al. 2012, Caballero et al. 2015), emphasizing the importance of knowing their current population status. In the case of mammals in particular, Schloss et al. (2012) warn that these animals may be even more vulnerable to climate change than previously thought.

1.4.2 Social systems and implications on genetic structure

The presence of geographic barriers is one obvious reason that can lead to genetic differentiation between populations; but there are several biological mechanisms that can contribute and regulate levels of gene flow leading to genetic patterns. In mammals, natural processes that generate diversity and genetic structuring may be related to mobility, dispersal ability and sociality, among other factors (Hoelzel et al. 1998, Hoelzel et al. 2007, Pilot et al. 2010). Social structures and their related dispersal patterns can have a noticeable influence on spatial genetic structures (Biek et al. 2006, Stoen et al. 2005, Croteau et al. 2010), especially in solitary species. Social behaviour can directly regulate when, how and how far dispersal events occur (Storz 1999, Macdonald and Johnson 2001). Hence, it can dictate the spatial structure of relatedness, i.e. how far kin-related individuals are established from each other and how this relates to their individual life patterns.

In the order Carnivora, there are social species living in stable groups as well as solitary species. Most of the developed studies and theories about social systems within this taxon refer to the first (Dalerum 2005, Dammhahn & Kappeler 2009), although most species (85-90%) are solitary (Sandell, 1989). This probably occurs because of the more cryptic habits of solitary species (Dammhahn & Kappeler 2009) and the consequent difficulties in studying them.

As a case in point of how the degree of sociality can play a role in shaping genetic structure, a recent study (Jacquier et al. 2020) with badgers (highly social mustelids) has shown strong genetic structuring at fine spatial scales, related to the strong philopatry within social groups. Badgers' social system is, consequently, a likely key driver of genetic structure and farther dispersal events are rare (Jacquier et al. 2020).

Lutrinae is a subfamily within the carnivore family Mustelidae that includes all 13 otter species that occur throughout the globe, except in Antarctica and Oceania. In the classic model of mustelids sociality proposed by Powell (1979), intra-sexual territoriality was defined as the standard social organization for the taxon. Yet, in the subfamily Lutrinae a wide variety of social behaviours can be found, even among closely related species with similar ecological requirements (Johnson et al. 2000, Kruuk 2006). This variation in social systems translates into inter and intraspecific differences in the degree of cooperation between individuals, group formation and the existence of single-gender groups (Kruuk 2006).

1.5 Study species

In Amazonia, two sympatric species of Lutrinae are present: the giant otter (*Pteronura brasiliensis*) and the Neotropical otter (*Lontra longicaudis*). According to IUCN, both species are in need of local and regional scale research, addressing population trends and dispersal patterns; and in general, data that can support the assessment of priority areas, better management of protected areas and corridors, and the design of new effective conservation strategies (Groenendijk et al. 2015, Rheingantz and Trinca 2015). Actions including the assessment of population genetic diversity are included as one of the main goals in the latest version of the Brazilian Action Plan for the conservation of otters (2016-2020).

1.5.1 Neotropical otter, *Lontra longicaudis*

Neotropical otters (Fig. 1.1) are medium semi-aquatic mustelids that have the typical elongated, short-legged body shape of this carnivore family, and a notably long tail. Their body length varies between 53 to 80 cm, plus the tail (36-50 cm) and they can

weigh from 5 up to 14 kg (Cheida et al. 2006). The species' distribution is wide, across Central and South America; it can be found in almost all countries from Mexico to northern Argentina (with the exception of Chile), and is present in all Brazilian biomes (Rheingantz et al. 2014; Rosas-Ribeiro et al. 2017). The map in Figure 1.2 shows the current official distribution range, although it should be noted that studies performed after the last Red List assessment in 2015 have proposed minor updates on the distribution map, especially regarding the species occurrence in north-eastern Brazil (see Rosas-Ribeiro et al. 2017). Its global IUCN conservation status has recently been changed from "data deficient" to "near threatened" (Rheingantz & Trinca 2015).

Rheingantz et al. (2017) have recently reviewed the current knowledge on the species and its conservation status throughout its geographical range, and stressed the current need to improve the comprehension on many aspects of this otter's biology, in order to support conservation and ensure its long-term survival. The authors have stated, for instance, that there should be more local and regional scale studies to provide information on demographic parameters (including dispersal patterns) and that genetic studies are necessary to evaluate diversity and connectivity among different populations, to underpin future conservation initiatives.



Figure 1.1: A male neotropical otter at Rio Urumutum, Amazonas, Brazil. (Photo: V.C. Fonseca da Silva)

Suitable habitats for this species include virtually any aquatic environments – rivers, streams, lakes, estuaries, mangroves and marshes; coastal islands are also occupied (Carvalho-Junior et al. 2012, Rheingantz et al. 2017, Rolim et al. 2019). The extensiveness of the range and variety of occupied habitats is reflected in its ecology and morphology. Rheingantz et al. (2017b), in a meta-analysis of diet studies, found a significant plasticity in the otter feeding patterns throughout its range. Diet may vary according to environmental and climatic conditions and hence the different prey communities present, evidencing their role as facultative generalist top predators. Using cranium morphometrics, Hernández-Romero et al. (2015) found significant variation in the shape and size of skulls associated with different geographic areas.

Activity patterns for this species also vary depending on the area. A camera-trapping study by Rheingantz et al. (2016) found that otters in Pantanal wetlands have a predominantly diurnal behaviour, while in the Atlantic Forest of southeastern Brazil they tend to be more crepuscular or nocturnal, avoiding daylight. In Amazonia, it is very

common to observe the species active and foraging at any time during daylight hours (personal observations), which possibly indicates a higher diurnal activity in that ecosystem as well. It is not clear, however, if such plasticity in the circadian rhythm is due to anthropogenic activities, differences in prey activity patterns or other unknown reasons.



Figure 1.2: Distributional range of *Lontra longicaudis* (Source: IUCN Red List – Rheingantz & Trinca 2015).

1.5.2 Giant otter, *Pteronura brasiliensis*

The giant otter is the largest species of the Lutrinae subfamily, reaching up to 1.8 m in length. Its morphology is remarkably adapted to the semi-aquatic lifestyle, with a distinctive strong flattened tail and large webbed feet. Another characteristic feature is the presence of creamy white throat marks and patterns that are unique to each animal, allowing for individual identification, although less frequently those marks can be very small or completely absent (Fig. 1.3). Unlike in most mustelids, there is no sexual dimorphism in this species (Rosas et al. 2009).

The species is distributed mainly in countries located in the north central portion of South America (Venezuela, Guyana, Suriname, Colombia, Ecuador, Bolivia, Brazil) (Kruuk 2006, Groenendjik et al. 2015). The current distribution is much smaller and more fragmented than the known historical range of the species (Utreras & Jorgenson 2003), due to indiscriminate hunting that took place in the 19th and early 20th centuries due to fur trade. Their numbers were drastically reduced; a historical account by Antunes et al. (2016) estimated that 386,491 individuals were harvested and exported from the Brazilian Amazonia only, between 1904 and 1969. Peru officially exported 23 980 giant otter skins between 1946 and 1973 (Smith et al. 1981). In 1973, the species has been included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora - CITES. Now, even though the species has recovered in some areas (e.g., Uscamaita & Bodmer 2009, Lima et al. 2014, Pimenta et al. 2018), it is considered as "threatened" in the IUCN Red List, and with a tendency towards population decline (Groenendjik et al. 2015).

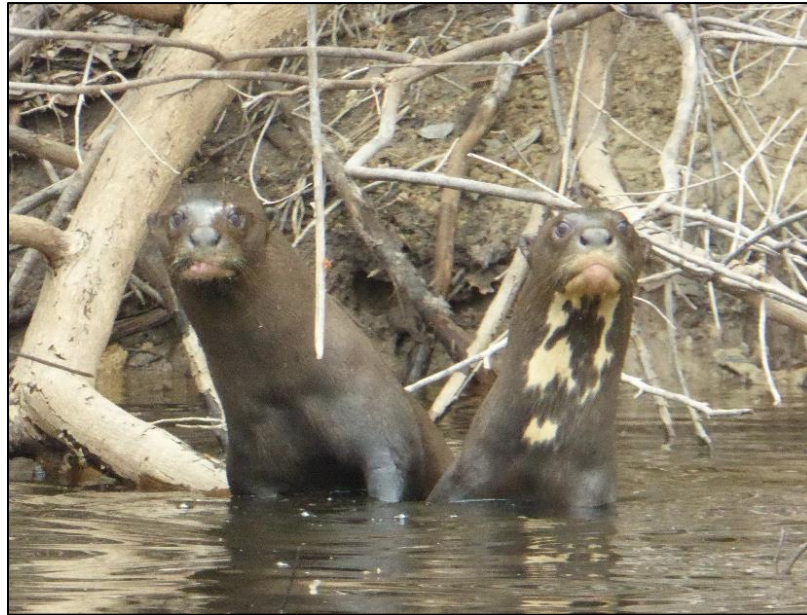


Figure 1.3: Two wild adult individuals of giant otter in Erepecu Lake, Pará, Brazil. (Photo: V.C. Fonseca da Silva)



Figure 1.4: Distributional range of *Pteronura brasiliensis* (Source: IUCN 2015. The IUCN Red List of Threatened Species. Version 2019-1).

1.5.3 Social structure of giant and Neotropical otters

Neotropical otters are considered solitary animals, although virtually no studies have focused on sociality of this species; nonetheless, field observations in different areas seem to corroborate this description (pers. obs.), and group formation has never been documented. Females can often be seen with their cubs (Fig. 1.5), but that is the only temporary social unit found for the species. Scent-marking is considered an important means of intra-species communication (Almeida & Pereira 2017). However, the vocal repertoire of the species is currently being studied in more detail, and seems to be more complex than previously thought (S. Bettoni, personal communication), which might indicate that vocal communication is also important, despite their mostly solitary habits.



Fig. 1.5: A female otter and her almost adult-sized cub (in the water) observed in the River Aquidauana, Pantanal, Brazil, 2014. (Photo: V.C. Fonseca da Silva)

Giant otters are highly social, and live in groups that can be formed by up to 16 individuals (Duplaix et al. 2015), although smaller groups from 4 to 8 individuals are more commonly found. Previously, it was believed that groups were always made of a dominant breeding pair and their offspring, but recent findings by Ribas et al (2015) showed that this is not always the case, although individuals within the group are usually related. In addition, there are the so-called transient individuals, which do not belong to a group – they might be young dispersers who left their natal group, or adults that lost their mate (Carter & Rosas 1997). Groups of giant otters are very cohesive, performing most of their daily activities together (fishing, resting, territorial marking) (Leuchtenberger & Mourão 2008, Duplaix 1980) and sharing the same den.

1.6 Central aims of the study

Anthropogenic pressures in Amazonia are continuously increasing the degree of threat to this biome and its biodiversity. This study, focused on conservation and population genetics, compared two mustelid species co-occurring in the Amazon basin – the Neotropical and the giant otter. These focal species are top-chain predators, key elements of the Amazonian aquatic ecosystem, and little is known about their genetic structure in this biome. Current threats have the potential to fragment otter populations, leading to loss of diversity and increasing the risk of local extinctions. These risks can be assessed by knowing the insularity and effective size of regional populations prior to fragmentation, and the pattern of connectivity among regions. Thus, assessing the present patterns of genetic diversity and population connectivity can provide a better understanding of the potential impacts, necessary mitigation measures and aids the

definition of regional task areas for otters and other aquatic vertebrates in order to promote conservation actions.

Therefore, the main goal of this PhD thesis was to provide baseline information on the genetic structure and predictive habitat modelling of the two species in Central Amazonia, while addressing the role of sociality and the consequent evolutionary processes leading to genetic structuring and connectivity within and between natural populations occurring in the complex river landscape of the Amazon basin. Understanding possible roles of the riverine landscape in promoting or restricting gene flow is an important component of the study, as it involved a study area including several drainages and tributaries inter-crossed by major Amazon Basin rivers. For each putative population in each species, the goal was to assess genetic structure and diversity using high-resolution markers, and the role of sociality and habitat use as possible drivers of population structure.

Additionally, I intended to test a novel set of nuclear genetic markers, which were developed for the two species in this study, validating their use in phylogenetic relationships reconstruction.

In this context, I aimed to address the following specific hypotheses and questions.

In Chapter 2, I present regional-scale species distribution models for both otters. My general hypothesis was that the modelled distribution of giant and Neotropical otters would show differences reflecting each species ecology and habitat preferences (see further discussion in Chapters 2 and 5).

Predictions from distribution models, regarding river networks connectivity, would determine expectations on each species potential dispersal routes and barriers, and

its findings would be corroborated by genetic patterns (which are assessed in Chapters 3 and 4).

With respect to landscape factors, I aimed to verify if larger rivers could act as barriers, generating differentiation between sub-basins and restricting otters' dispersal, or if populations would be structured simply as a consequence of isolation by distance (Chapter 3). Moreover, could any other environmental features promote or restrict gene flow?

Second, concerning behavioural ecology factors, I expected that the Neotropical otter, a solitary species, would show an absent or weaker genetic structure at the spatial scale examined when compared to giant otters (Chapter 3). The former are social, group-living species, with relatively short home ranges, and therefore more likely to show stronger spatial genetic structure. Moreover, concerning the likely strong impact of the fur trade on giant otter populations, a reduced genetic diversity could be expected for this species (Chapters 3 and 4).

Finally, in Chapter 4, I selected and tested a set of nuclear markers designed in this study - extracted from moderately conserved regions in the giant and Neotropical otters' genomes - to assess their potential use in phylogenetic studies within the order Carnivora.

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Chapter 2

Assessment of giant and Neotropical otters' distribution patterns in central Amazonia



Photo: V.C. Fonseca da Silva

2.1 Introduction

One of the fundamental bases for species conservation is the knowledge of their current patterns of geographic distribution and the environmental factors that likely drive such patterns. Such understanding is of high relevance in the context of global changes, as it can provide a way to project changes to biodiversity in response to future alterations (Urban et al. 2016). Modelling approaches, in particular species distribution models (SDMs), aim to quantify those species-environment relationships and predict the potential range of species or other taxa (Guisan & Thuiller 2005; Guisan et al. 2017).

The recent advances in both computing tools and availability of high-resolution environmental data has allowed the development of robust modelling approaches with strong predictive capabilities, providing researchers and managers with valuable ecological insights (Elith and Leathwick 2009). Models generated can aid, among other things, in identifying priority areas for conservation by detecting the most suitable habitats within a region, assessing the connectivity between them (Clément et al. 2014) and identifying target areas for new field surveys and studies, for cryptic species in particular (Jackson & Robertson 2011). SDMs can also be used to address intra-specific questions, such as sexual segregation (Gomez & Cassini 2014) or sub-species niche similarity (Hernández-Romero et al. 2018). Predictions obtained by modelling can thus have important genetic implications, ranking and eliciting factors that might contribute to population structuring and gene flow.

The process for obtaining SDMs is generally based on three core components: gathering data for the response variable of species occurrence and/or abundance and

explanatory environmental variables; the modelling approach, which can be based in different mathematical functions/algorithms; and model validation/assessment (Rushton et al. 2004).

SDM approaches have been applied to several otter species worldwide (Barbosa et al. 2003, Sepulveda et al. 2009, Ali et al. 2010, Jeffress et al 2011, Cianfrani et al. 2011;2013;2018, Carranza et al. 2012). The two most widespread otters in South America, the neotropical otter *Lontra longicaudis* and the giant otter *Pteronura brasiliensis*, were given contrasting different levels of attention regarding distribution and suitability models. Neotropical otters were the object of five studies involving modelling at different spatial scales (Cirelli & Sánchez-Cordero 2009, Santiago-Plata 2013, Gomez et al. 2014, Rheingantz et al. 2014, Hernández-Romero et al. 2018), while there were no published studies specifically focused on the giant otter. It was only included in the research paper by Cianfrani et al. (2018), who modelled distributions of all otter species at a global scale. Still, this work focused on global vulnerability to future scenarios of climate change, and did not provide a detailed analysis of current patterns; furthermore, it had a rather limited occurrence dataset, which was in accordance with the aims of the study, but perhaps not ideal for more in-depth and species-specific analyses.

Giant and Neotropical otters are sympatric over most of the former's range, and are known to coexist in the same rivers, showing spatial overlap. In the Brazilian Pantanal, Muanis & Oliveira (2011) found that the giant otter had a narrower spatial niche, nested within the Neotropical otter's, suggesting that the latter is a generalist species, associated to a more diverse array of features of the freshwater landscape. Overall, various findings indicate that the Neotropical otter tends to prefer wider and deeper watercourses (Muanis & Oliveira 2011, Roberts et al. 2016, Smith et al. 2020) frequently associated with the presence of deep pools (e.g., Carrillo-Rúbio & Lafón

2004, Roberts et al. 2016). The giant otter in general prefers streams and lakes with shallower waters and few suspended sediments (i.e., black or clear waters) (Duplaix et al. 2015).

Several authors have investigated factors that affect giant and Neotropical otter distribution or space use based on local-scale studies (e.g., Gori et al. 2003, Oliveira et al. 2015, Roberts et al. 2016, García et al. 2017, Smith et al. 2020). While such microhabitat-focused approaches are undoubtedly useful to define priorities for conservation-oriented habitat management, macro-scale studies are likewise relevant in the context of landscape ecology and conservation genetics, for example for identifying potential corridors to allow long-term persistence of a species in a mosaic of areas (Morato et al. 2014). Moreover, increasing accessibility to fine-resolution global scale datasets makes macro ecology studies a cost-effective tool, allowing researchers to work with species occurrence data that are already available, with no need of gathering microhabitat data, which require more field effort and can be logistically complex and expensive, especially for wide-ranging species (Rheingantz et al. 2014, Ficetola et al. 2018). Distributional studies at regional scales are equally relevant, particularly to assess connectivity between populations or sub-populations (Morato et al. 2014).

Among previous studies modelling potential distribution of Neotropical otters, three were performed at regional scales, specifically in Mexico, Costa Rica and Argentina (Cirelli & Sánchez-Cordero 2009, Santiago-Plata 2013, Gomez et al. 2014). Rheingantz et al. (2014) considered the full geographic range of the species, aiming to identify priority areas for research and update the IUCN conservation status - which, at the time of publication, was considered Data Deficient (DD). Finally, Hernández-Romero et al. (2018) modelled distribution separately for the three subspecies (*L.l. longicaudis*, *annectens* and *enudris*) over their whole presumed ranges, to assess niche

similarities. In their continental level model Rheingantz et al. (2014) found that Amazonia had most of the higher suitability areas for Neotropical otters across its whole range. Yet, no studies to date assessed or modelled distribution of either species in regional scales in the Amazonian region.

Modelling the distribution of freshwater species, including semiaquatic mammals, such as otters, which are highly associated with watercourses, holds specific challenges. Particularities of streams and rivers, such as linearity, directionality and heterogeneity, in fact, make lotic habitats fundamentally different from terrestrial or marine habitats (Domisch et al. 2015, Quaglietta et al. 2018), not to mention the rivers flood pulse (Junk et al. 1989), which in Amazonia can have an intra-annual variation of up to 10 m (Irion et al. 1997). Until recently, the scarcity of adequate freshwater-specific data was a limitation for SDM studies performed in this realm; Domisch et al. (2015b), for instance, have provided a near-global freshwater dataset of abiotic factors at 1-km resolution to lessen the issue, which can improve robustness of such studies.

2.2 Objectives

The main goal of this chapter was to assess Neotropical and giant otter potential distribution in a central area of Amazonia rainforest through a SDM approach, focused on river networks and freshwater-specific environmental variables.

Considering that the two species are reported to show somewhat different habitat preferences, SDMs are expected to reflect such patterns if the data provided is sufficient in representing their distribution. The specific objectives of this study were, therefore, to identify environmental factors influencing the potential distribution of the two otter species; compare predictions for both species; evaluate overall patterns of connectivity

between suitable areas; assess the overlap in suitable habitat for both species; and estimate the proportion of suitable habitat in protected areas. Such findings are of great relevance, providing more background information for management and further research, including conservation genetics.

2.3 Methods

2.3.1 Study Area and Species Occurrence Datasets

The study area is located in northern Brazil, in the Amazonian Rainforest, between longitudes 5° 18' N - 11° 30' S and latitudes 68° 18' – 49° 18' W. Distribution model analyses were performed in an area delimited according to minor tributary basins level 3 (Venticinque et al. 2016; see Fig. 2.1), where species presence data was available both from fieldwork (this study) and literature records. Records from both kinds of sources include a mix of direct observations of the species or their typical indirect signs of presence (scats, dens, latrines and campsites – see Groenendijk et al. 2005).

In the present study field data collection, seven main locations in the central/western portion of Brazilian Amazon were visited – these were located in the states of Amazonas, Roraima and Pará (Fig. 2.1). The sampling scheme was planned in order to take into account separation of main drainages and different sub-basin. Four sites are located on northern (left bank) tributaries of the Negro and the Amazon River, one on a southern (right bank) tributary of the Amazon and two in the interfluvium between Negro and Amazon. Criteria for the selection of sampling sites also included available infrastructure and/or logistic facilities. The climate in the whole area is wet equatorial (Af, according to Köppen classification), and water bodies are subject to an annual flood pulse leading to variations in water level between dry and wet seasons. Both the flood

pulse and the dry/wet seasons vary over the different Amazonian sub-basins. In general, otter surveys and censuses (for monitoring population trends) are recommended to be performed in the peak of the dry season (Groenendijk et al. 2005), as otters are more restricted to permanent water bodies, which facilitates the observation and individual counting of animals. But for general detection purposes, which can include direct as well as indirect records of species (such as vocalizations and recent signs of use in latrines and dens), fieldwork can be performed in any season - although of course heavy rains (which can happen at any time, even on dry season) can negatively affect the observation probability - in which case, fieldwork is usually avoided in such days.

Virúá National Park (VNP), declared a Ramsar site in 2017, was the northernmost sampling location visited in this study, at the Brazilian state of Roraima. It is dominated by white-sand forests (*campinas and campinaranas*) with interspersed lowland forests (*terra firme*), along with seasonally flooded *igapó* forests (Laranjeiras et al. 2014). The peak of the rainy season spans from May to July, while the dry season takes place from December to April (Laranjeiras et al. 2014). This site was visited in January of 2018, and the total surveyed extent was approximately 85 km, including the rivers Anaúá and Virúá and a short stretch of Branco River, a major tributary of the Negro River (Appendix 2.1). A planned hydroelectric power plant (UHE Bem Querer), which would be situated only 30km upstream from the park, potentially threatens this area; but so far, its construction has not been authorized.

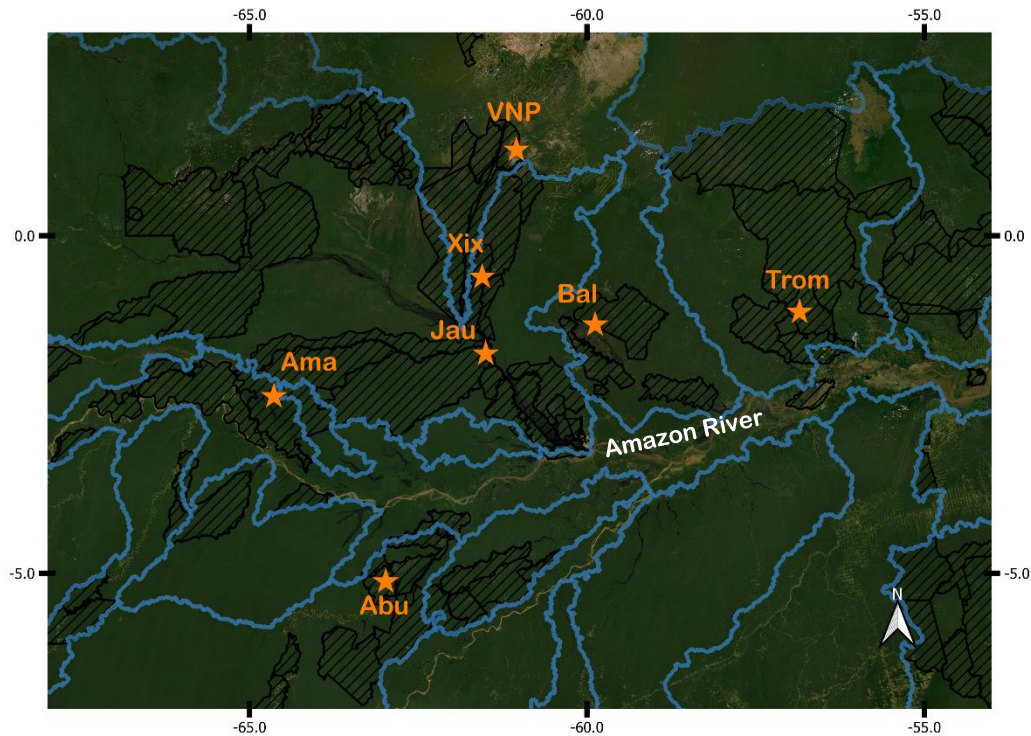


Figure 2.1: Satellite image showing main fieldwork study sites (marked with orange stars), protected areas (hashed in black) and level 3 tributary limits (outlined in blue). Source of the basemap: Esri World Imagery.

Xixuaú/Jauaperi (Xix) is an area located within the recently created Jauaperi Extractivist Reserve (Resex) at the middle course of the black water river with the same name, which is another northern tributary of Negro River. This area included the Xixuaú stream, part of Jauaperi River and several oxbow lakes, totalling an extension of about 60 km (Appendix 2.2). This area was visited twice (February 2016 and February 2018), both during the dry period - which usually occurs from October to February.

East of Xixuaú, there is the Balbina site (Bal), that is partially within the limits of Uatumã Biological Reserve (Appendix 2.3). This sampling area included the Balbina Lake, which is as reservoir created by the damming of Uatumã River in 1987; and the Pitinga River, a tributary of the former. Balbina Lake has more than 3000 islands (formed by higher lands that were submerged), and giant otters show an intense use of

these islands' shorelines for building dens and campsites (Rosas et al. 2007, Palmeirim et al. 2014). Rainfall is concentrated mostly between December and May, and the dry season is between June and November (Kemenes et al. 2011). The dam has affected the flood pulse in the area, but a seasonal variation of around 3.5m still takes place annually (Rosas et al. 2007). Balbina was surveyed twice for this study, in December 2016 (at the end of the dry season); and between February-March 2017 during the wet season.

The Jaú National Park area (Jaú hereafter) includes stretches of the black water rivers Jaú, Carabinani and Unini, southern tributaries of the lower Negro River (Appendix 2.4). The national park is one of the world's largest protected forests and, together with three other protected areas (Anavilhanas National Park, Amanã and Mamirauá Sustainable Development Reserves), forms the Central Amazon Conservation Complex, recognised as World Heritage Site by Unesco. The vegetation is well preserved, being dominated by *terra firme* forests but also including *campinaranas* and *igapó* forests. There, the rainy season occurs from December to May, with an average rainfall of 1750-2500 mm; and the dry season extends from June until September (FVA, 1998). The fieldwork in Jaú occurred in December 2017, at the beginning of the rain season. The total survey extension was approximately 100km.

Amanã (Ama) area includes the lake of the same name and its associated tributaries within the Amanã Sustainable Development Reserve, which is flanked by Negro and Japurá sub-basins. The lake is formed by black waters rich in humic acids, but has influence from a white-water system (Japurá River, connected to Amanã through its upstream tributary Joacaca); still, most of its tributaries are black water streams (personal observation). During the rainy season, at least one of Amanã Lake's tributaries, the Baré stream, is seasonally connected to the Negro River Basin (Appendix 2.5). The flood pulse in the Lake is more influenced by the pulse in the Japurá/Amazon river basins,

while its tributary streams show more variation being also highly influence by local rainfall (see Carvalho et al. 2007), although they overall conform to the same pattern. From June to October is usually dry, while from December to May the wet season occurs, with a peak in precipitation usually during May (personal observations). Fieldwork in Amanã was performed in January/February 2017 and again on November 2017.

The Abufari (Abu) site is situated on the middle Purus river basin, and is named as such for being mostly within the Abufari Biological Reserve, Amazonas state. The Purus is a major white-water tributary at the southern (right) margin of the Amazon River, and is also one of the most meandering waterways in the region, favouring the formation of numerous secondary channels and oxbow lakes. This was the only study site with predominance of white water, that is rich in suspended sediments. Precipitation in Abufari is more concentrated from November until June, and dry season ranges between June and October (Silva et al. 2010). The area was surveyed in September 2017, totalling around 160km (Appendix 2.6).

Finally, Trombetas (Trom) study site is located within the Trombetas Biological Reserve in the state of Pará and it includes the Trombetas River and the Erepecú, plus minor lakes and tributaries associated to both. Trombetas is a clear water river and a northern (left margin) tributary of the Amazon. Most rain in the area falls from January to May, and the driest period is from mid-July to December (Leão et al. 2019). The total extent surveyed in watercourses and lakes was close to 170 km during the fieldwork campaign in October 2017 (Appendix 2.7).

Concerning the modelling extent, the sub-basins selected for each species differed slightly, due to a different spatial distribution of occurrence data in literature records. The

reason for this choice is that using areas much larger than the range of occurrence points available can cause over-fitting of the models. Restricting the area analysed is known to improve model performance (Acevedo et al. 2012). Hence, the external contours were chosen parsimoniously according to the data available for each species in each tributary basin considering both field records and literature sources. Still, the spatial range of the analysis is very similar for both otters (within the same range of geographic coordinates) and most of their analysed areas are overlapped, allowing for comparisons regarding the suitability of habitats and importance of different environmental variables.

Besides the location records registered by the author for this study, additional data for Neotropical otter was obtained from: Santos et al. (2007), Rheingantz et al. (2014), Andrade et al. (2019), and data sourced from iNaturalist (2020). For giant otter, additional data was available from Siciliano et al. (2008), Tirelli (2010), Rosas-Ribeiro et al. (2012) (inferred coordinates), Colodetti (2014), Pacca et al. (2016), Pimenta (2016) (inferred coordinates), Prist et al. (2017) and Coelho et al. (personal communication).

Spatial bias caused by differences in sampling effort or data availability, which is common over large study areas, can lead to a significant environmental bias, over-representing the features present in locations where more occurrence points are available (Phillips et al. 2009, Kramer-Schadt et al. 2013). To take such sampling bias into account in the present analyses, two correction measures were taken: spatial filtering and background manipulation. Redundant presence points were eliminated in a filtering process using the `gridSample` function from R package `dismo` (Hijmans et al. 2017). After this selection, 56 (ou of 223) and 120 (out of 411) occurrence points were retained to generate SDMs for neotropical and giant otters respectively. The use of a sampling bias grid that represents the uneven sampling efforts is also recommended; in order to generate such grids for each species, the function `sp.kde` from the R package `spatialEco`

(Evans 2020) was used to perform a Gaussian 2-dimensional Kernel density estimation with the occurrence points. The results were transformed into a raster spatial layer and converted to ascii format, and this file was used in Maxent so the program could take into account this bias for drawing the random background points. To assess the effect of sampling bias grid in the analyses, models were generated with and without it for posterior comparison.

2.3.2 Modelling

The Java-based software MaxEnt (v. 3.4.1 – Phillips et al. 2017) was employed as the modelling algorithm, as it is widely used in ecological studies (e.g., Ready et al. 2010, Jackson & Robertson 2011, Morato et al. 2014, Eriksson & Dalerum 2018, Braun et al. 2019, Alfaya et al. 2019, Freeman et al. 2019) and requires presence-only data. MaxEnt estimates the potential distribution of a species by maximum entropy, generating a probability distribution over the pixels in a grid of the study area. The models were generated by bootstrapping; a random test percentage of 30% was used for Neotropical otter and 40% for giant otter (due to the larger sample size of the latter), and main settings were as following for both species: Cloglog output, auto feature selection, 5000 iterations, maximum 5000 background points, 10 replicates and convergence threshold 10^{-5} . A Jackknife approach was used to measure the contribution and importance of each variable.

Model performance was assessed by a combination of two metrics: the area under the curve (AUC) of the receiver operating characteristic (ROC) (Fielding and Bell 1997) and the True Skill Statistics (TSS) (Allouche et al. 2006). AUC is a threshold independent metric that is commonly used to evaluate SDMs (Merckx et al. 2011). When working with presence-only data, as in the present study, the maximum achievable value

of AUC is always less than 1, since the metric is dependent on the area covered by the species (Wiley et al. 2003), being exactly $1 - a/2$ (where a is the fraction of the area corresponding to the species distribution). If $AUC \leq 0.5$, it means the model generated is no different from random. TSS, on the other hand, is a threshold-dependent metric; it takes both omission and commission errors of the model into account. It is calculated as:

$$TSS = \frac{ad-bc}{(a+c)(b+d)}$$

Where: a is the number of true (test) presence pixels, b of background presence pixels, c of background absence pixels, and d of test absence pixels. Its values may range between -1 and 1, where values equal to or below zero indicate a model performance no better than random and values closer to 1 mean better performance (with 1 indicating perfect agreement) (Allouche et al. 2006). The 10th percentile training presence was used as the presence threshold for calculation as it provided the best accurate model for both species based on TSS (see Results). This threshold is less conservative, and has been used in other studies with mammals (e.g., Brito et al. 2009, Escalante et al. 2013, Morato et al. 2014). It considers the probability at which 10% of the training presence records are omitted from suitable areas.

In order to assess the effect of bias grids in model performances, maps were generated for visual comparison. In addition, averages of two metrics generated by Maxent, AUC (detailed previously) and training presence test omission (which quantifies errors of type II in the models, i.e., the rate of real occurrences inside areas predicted as unsuitable by the model), were compared using paired t-tests.

Final suitability maps were generated by first reclassifying the average model raster layers outputted by Maxent into binary maps of suitable/unsuitable habitats. The

binary maps were generated using the 10th percentile training presence thresholds for each species. This threshold was chosen because it provided a more realistic distributional area when compared to other thresholds estimated by Maxent (data not shown), considering knowledge on the ecology and natural history of the species (Norris, 2014). Suitable pixels of this map have the value of one, while unsuitable are equal to zero. The binary maps were then multiplied by the original rasters to create the final maps; this way, suitable pixels from the previous binary map will have re-scaled values of suitability. To estimate the proportion of suitable habitats within protected areas, the Zonal statistics tool in QGIS v.3.12 was used (QGIS Development Team, 2020).

2.3.3 Environmental Data

Biogeochemical, topographic, edaphic, hydrological and climatic predictors were chosen considering their ecological relevance to the species (Table 1). With the exception of Net Primary Productivity (NPP), Density of human settlements and Walsh Index, the remaining predictors were obtained from the freshwater-specific raster database by Domisch et al. (2015b), clipped to the defined study area. This database was defined along the global 1km HydroSHEDS river network (www.hydrosheds.org). In this way, distribution was modelled considering only the watercourses. The layer describing density of human settlements was created through a kernel density estimate of point locations of riverine and rural settlements, using the R package spatialEco (Evans 2020).

The NPP dataset (Running et al. 2015) was downloaded from the MODIS sensor MOD17 database (<https://www.ntsg.umd.edu/>), and the Walsh Index from the public repository Ambdata (<https://www.dpi.inpe.br/Ambdata>); both were clipped to the study area using the river network from the previously described steps.

Flow accumulation and drainage density are important hydrological attributes, included in light of the strong dependence of otters on watercourses (Kruuk 2006). The former translates for water draining to each cell in a spatial grid, and can serve as a surrogate for drainage area, while the latter describes the density of drainage length per area.

Giant otters excavate and build their own dens in riverbanks; therefore, soil attributes might play a role in the species habitat preferences. Neotropical otter occurrence has been positively related to the presence of rock formations and sandbanks in a river in the eastern Brazilian Amazonia (Andrade et al. 2019). Two edaphic variables were then included in the analyses to evaluate their potential predictive power and importance for each species (upstream averages of soil clay content and coarse fragments). Furthermore, such variables could also have effects on prey species or vegetation cover that in turn can influence otter's distribution.

The Walsh index of perhumidity (Walsh 1996) can integrate the influence of both dry and wet season precipitation patterns. Higher values of the index are usually characteristic of areas where the wet season is long and intense enough to “buffer” the effects of drier months, while values at the lower spectrum of the index are typical of drier areas with little rainfall. Since such seasonal changes are known to influence space use and habits in otter species (Utreras et al. 2005, Leuchtenberger et al. 2015, Quaglietta et al. 2018), this index was as considered a relevant predictor for the model.

Maxent requires all input predictor data to be in the same projection, spatial resolution and extent. Since two variables were obtained from different sources (NPP and Walsh index), a layer of watercourses was created with all pixel values equal to the same value (1) to be used as a template. NPP and Walsh Index layers were then multiplied by

this template using the raster calculator in QGIS v. 3.12 (QGIS Development Team, 2020), so the final resulting layers would overlap with the other ones, while keeping their original pixel values. Finally, all data was re-projected to the same coordinate system (WGS 84) and to the same extent and resolution (30-arc seconds - approximately 1 kilometer) in R, and converted to ascii format as needed for Maxent (R packages used: raster, rgdal, sf, tidyverse, rgeos and fasterize – Hijman 2020, Bivand et al. 2019, Pebesma 2018, Wickham et al. 2019, Bivand et al. 2017, Ross 2005). All environmental layers were tested for correlation using the module r.covar implemented in QGIS v.3.12 processing toolbox (QGIS Development Team, 2020) , in order to assess the need to exclude any variables showing high correlation coefficients.

Table 2.1: Environmental predictors used in the SDMs. [†]Number of upstream catchment grid cells

Variable	Type	Unity	Source
Average annual Net Primary Productivity (2000-2015)	Biogeochemical	C/m ²	Running et al. 2015
Upstream average of Coarse fragments (> 2 mm fraction)	Edaphic	%	Domisch et al. 2015b, Hengl et al. 2014
Upstream average of clay content mass fraction	Edaphic	%	Domisch et al. 2015b, Hengl et al. 2014
Tree Cover	Land cover	%	Domisch et al. 2015b, Tuanmu et al. 2014
Regularly Flooded Vegetation	Land cover	%	Domisch et al. 2015b, Tuanmu et al. 2014
Flow accumulation	Hydrological	Count [†]	Domisch et al. 2015b, Lehner et al. 2008
Drainage Density	Hydrological	N/A	Ximenes (2008), derived from SRTM (Shuttle Radar Topographic Mission) data
Average Slope	Topographic	degrees * 100	Domisch et al. 2015b, Lehner et al. 2008
Walsh Index	Climatic	N/A	Amaral et al. 2013
Kernel Density of Human Settlements	Anthropogenic	N/A	Instituto Brasileiro de Geografia e Estatística (www.ibge.gov.br)

2.4 Results

None of the environmental variables used presented significant covariance between them, so all were kept in the analyses. The resulting receiver operating characteristic (ROC) curve for both species (Fig. 2.2) shows that models can confidently forecast sites at which the species are present or not, since the curve is mainly closer to the vertical axis meaning that true positive rates are more frequent than expected by chance. The average test AUC (area under the curve) values obtained were 0.82 ± 0.036 and 0.75 ± 0.058 for giant and Neotropical otter respectively. AUC values close to 0.5 indicate that model predictions are similar to random; here, both values were > 0.7 , indicating a good predictive accuracy. The TSS average values were 0.51 ± 0.05 and 0.48 ± 0.09 for giant and Neotropical otters, which also indicates that models were accurate, performing better than random predictions.

Maps illustrating the species potential distribution were generated using the 10 percent training thresholds obtained in Maxent (which were equal to 0.48 for giant and 0.40 for Neotropical otter) (Figs. 2.3 and 2.4). The maps indicate an overall low suitability for both species on smaller (1st-3rd order) streams, but giant otter potential distribution differs from that for the Neotropical otter (Figs. 2.3, 2.4 and 2.5), as the latter has shown a more restricted range than the former. Giant otters seem more likely to occur in medium order tributaries and in lakes and their associated streams, showing more continuity of suitable areas. Neotropical otters, instead, show a rather fragmented distribution of suitable habitats, which nonetheless includes both main channels of rivers and minor tributaries as well as higher orders rivers, such as the Amazon (Figure 2.5). Notably, most of the Neotropical otter's estimated distribution is included within the giant otter's suitable range, indicating their overlap.

Visually, it can be noted that the total area of predicted distribution is substantially reduced when bias grids are not incorporated in the models, especially for giant otters (Figure 2.6). Considering the quantitative comparison between models with vs. without a bias grid, the average test AUC for both species was significantly higher without it according to t-test results; and, although average test omission rates were slightly higher in models without the bias grid, this difference was not significant across model iterations for neither species (Table 2.2).

Table 2.2: Average Test AUC and Omission for models generated with and without bias grids and t-test results.

		<i>With Bias Grid</i>	<i>Without Bias Grid</i>	<i>t</i>	<i>p</i>
<i>Average Test AUC</i>	Giant	0.82	0.87	-4.95	0.000
	Neotropical	0.75	0.83	2.95	0.0085
<i>Average Test Omission</i>	Giant	0.17	0.16	1.11	0.283
	Neotropical	0.26	0.25	-0.39	0.69

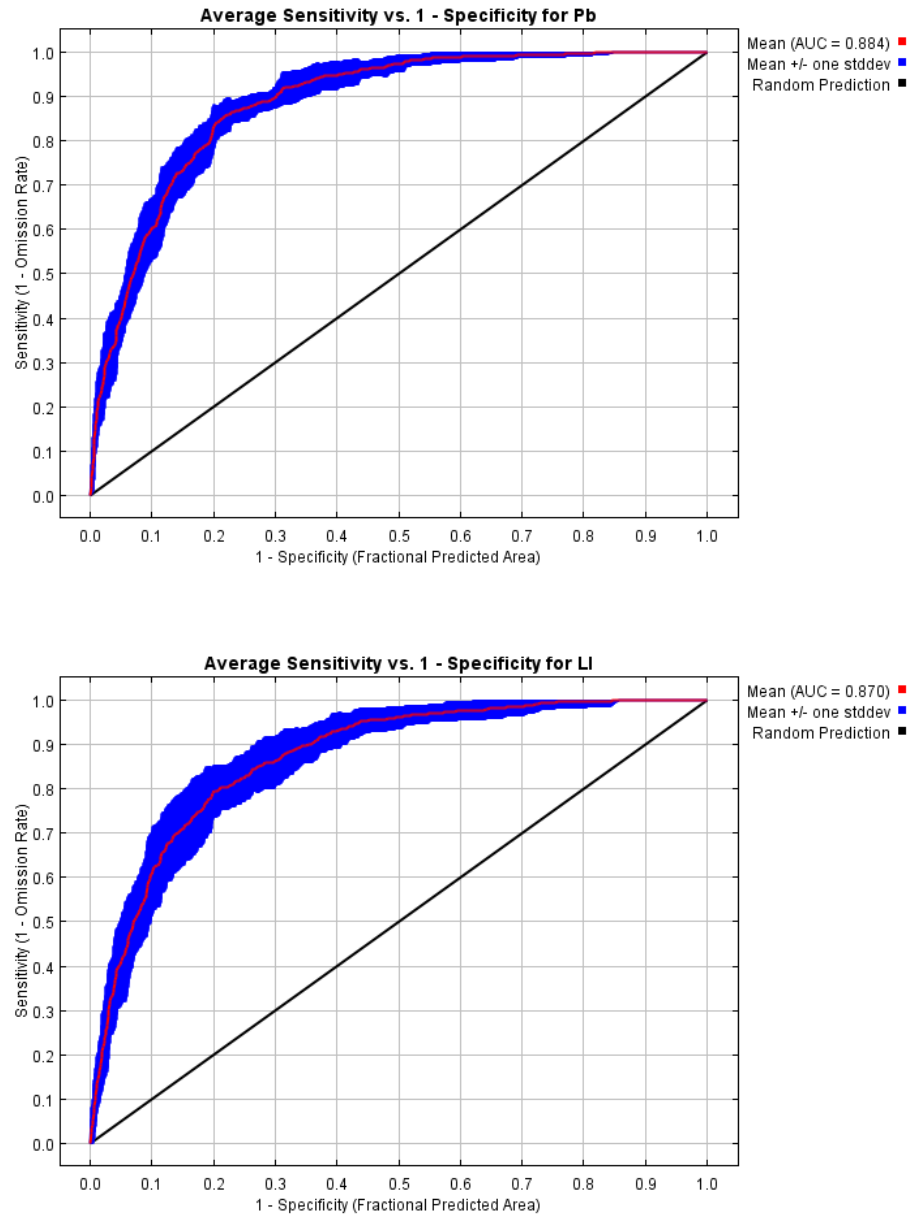


Figure 2.2: Sensitivity vs. specificity (ROC curve) for giant otter (top) and Neotropical otter (bottom).

If percent contribution is considered, flow accumulation was considerably more important for the giant otter than all other variables; on the other hand, looking at permutation importance, the difference between flow accumulation and other variables is not so striking (Tables 2.3 and 2.4). For Neotropical otter, drainage density had a higher percent of contribution, while coarse soil fragments ranked first in permutation importance; interestingly, the same variable was also distinctively up ranked for giant otter, being the third most important variable according to this metric (Tables 2.3 and 2.4).

Jackknife test results aid in identifying the variables with strongest individual effects, and the histograms (Fig. 2.7) illustrate the effects of removing variables one at a time and of using each one on its own. For the giant otter, flow accumulation stood out as being the variable with most predictive power on the distribution of both test (Fig. 2.7 a, c) and training (Fig. 2.7 b) data. If this variable was used on its own, the model could still reach an acceptable AUC value (> 0.7). Regularized training and test gain, though, would likely be lower if only flow accumulation was used, suggesting that the whole set of variables together do play a relevant role in the overall accuracy of the model. For the Neotropical otter, drainage density showed a high effect on model predictions for test and training data. But again, using only this variable as a single predictor would mean a considerable loss in gain, especially on the training dataset (Fig. 2.7 d). It is also worth noting that removing some variables could slightly increase model performance, such as NPP and Slope. NPP was indeed ranked much lower when considering its permutation importance, although its percentage of contribution was higher (Table 2.3).

Finally, response curves can give additional insight as they show how the predicted probability of presence changes as each environmental variable is varied (Phillips, 2017). Normally, it is recommended to interpret curves created using only a

single variable for each model. Figures 2.8 and 2.9 show the response curves of the most relevant predictors for each species (considering the results described above), illustrating the dependence of the models' predicted suitability on each variable and on dependencies induced by correlations between the selected variable and other variables obtained by the models generated with the whole set of variables. Responses to the main predictors in both species show an overall noteworthy variation. Giant otter modelled distribution had a similar response curve shape to Flow accumulation, Coarse soil fragments and density of human settlements: a sharp increase in the beginning of the curve giving a brief positive response for lower values of the variables, followed by a negative response. The overall trend of the response to Tree cover was positive. Neotropical otter model, in contrast, showed a positive trend in the response to the variable Density of human settlements until a certain threshold, where the response becomes neutral.

Finally, regarding the proportion of predicted distributions that is included within protected areas, figures were similar for the two species: Neotropical otters had 29.9% of their suitable habitat inside protected areas, while for giants this estimate was 25.1%.

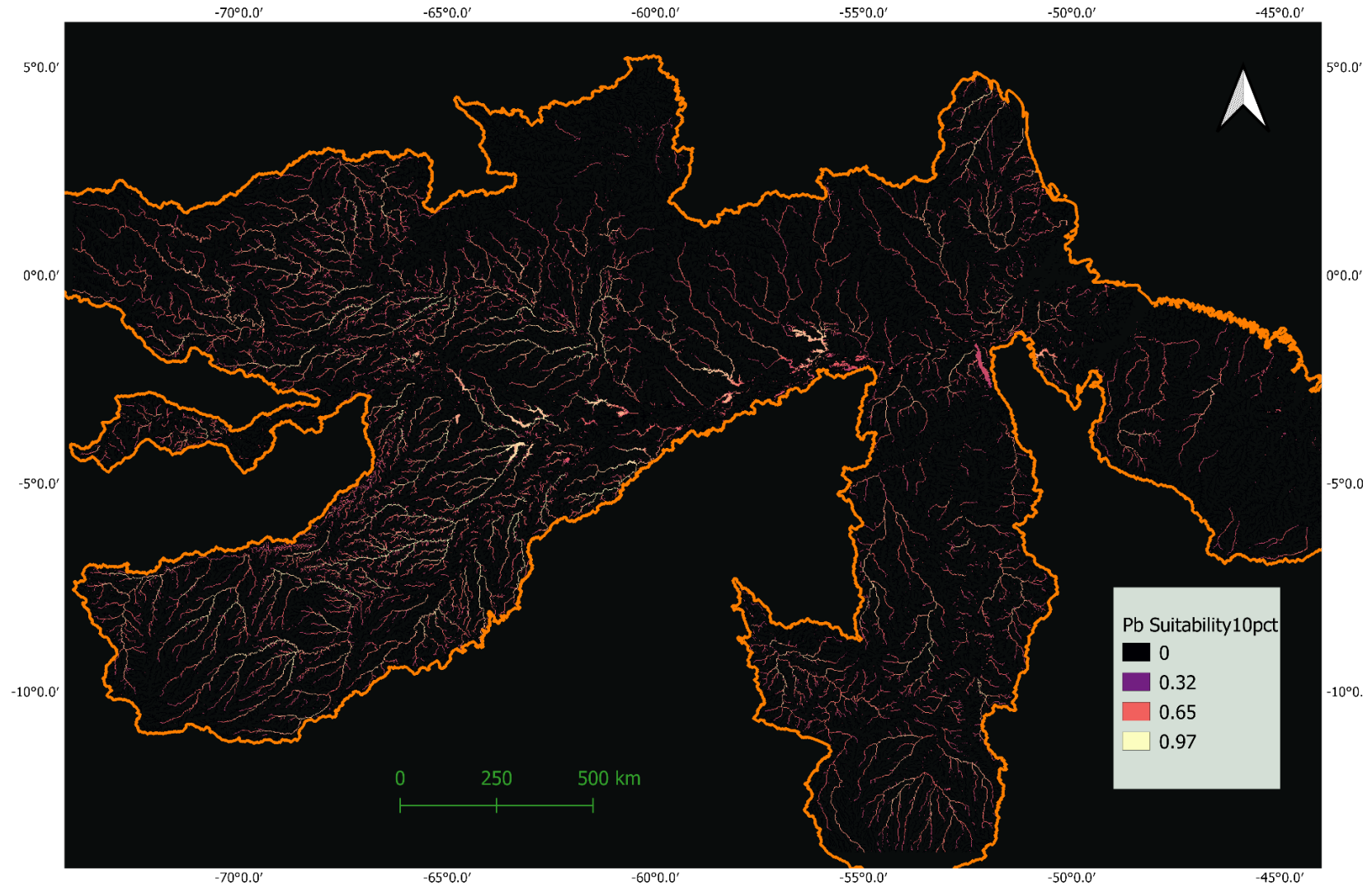


Figure 2.3: Giant otter suitability map based on the 10 percent training Cloglog threshold.

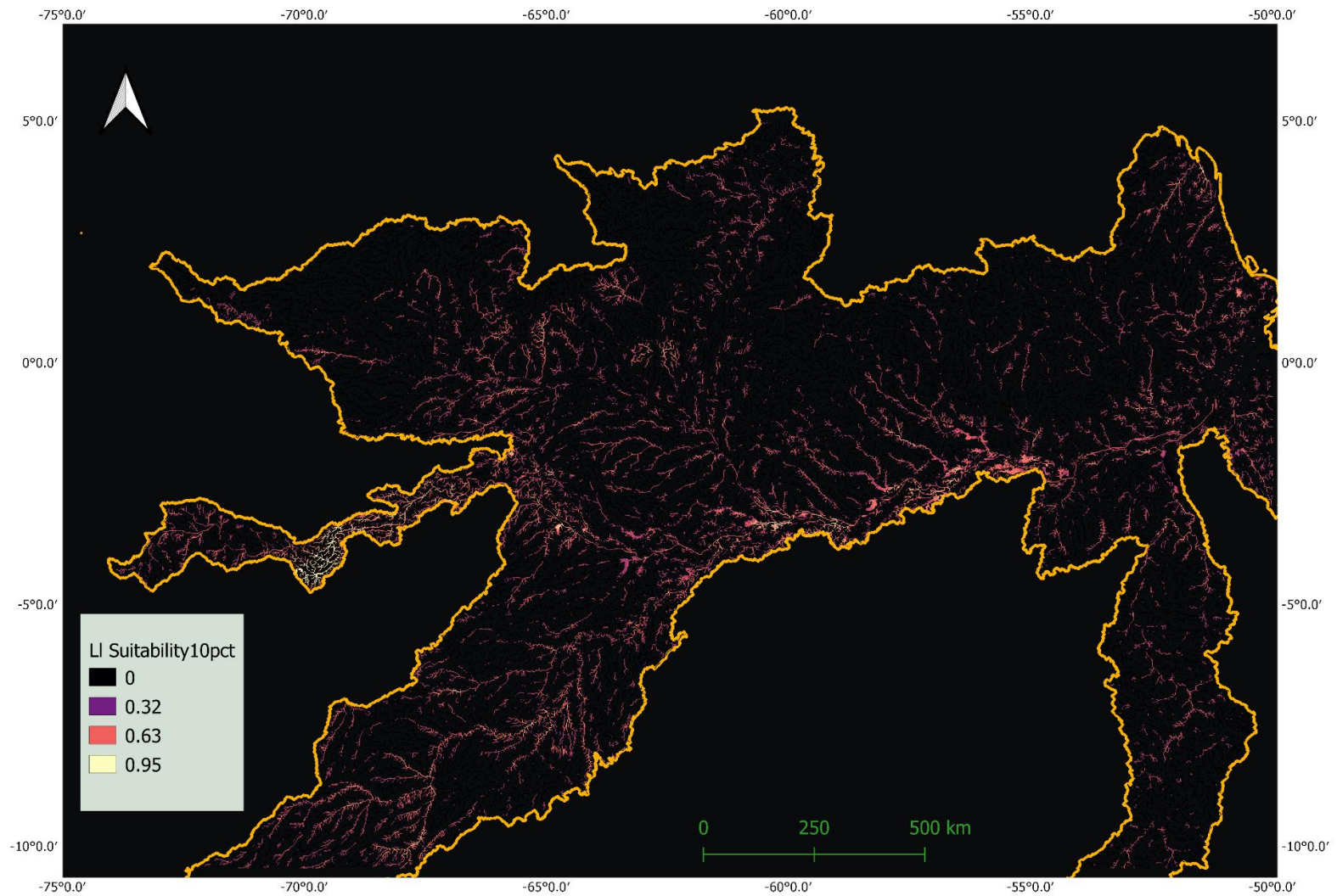


Figure 2.4: Neotropical otter suitability map based on the 10 percent training Cloglog threshold

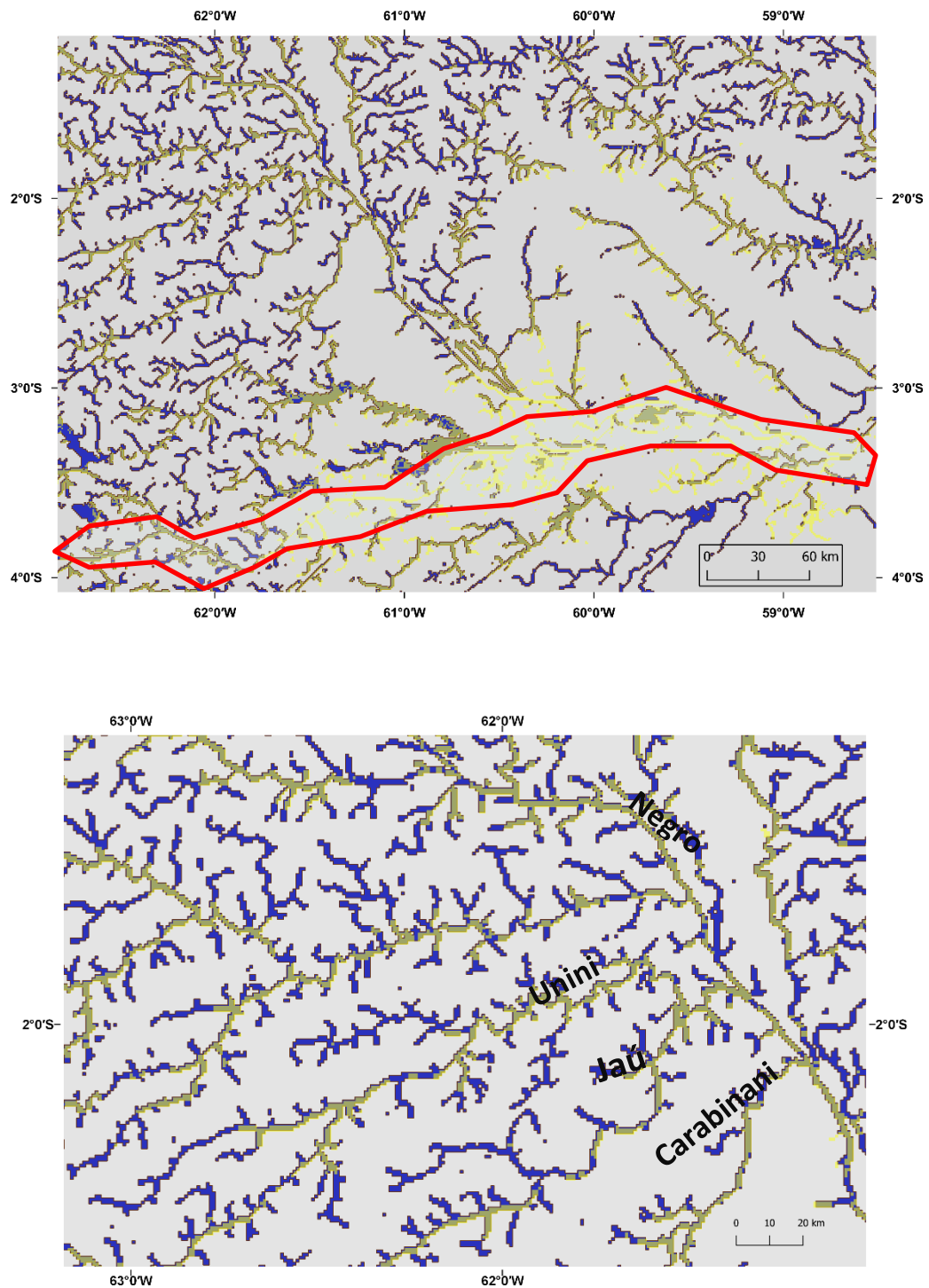


Figure 2.5: Two zoomed areas of suitability maps showing Neotropical (in yellow) and giant otter (in navy) suitable habitats. Transparency was used on Neotropical otter's symbology in order to better visualize the overlap between them. On top, an area including a stretch of the Amazon river (highlighted in red) and on the bottom, an area including the Jaú, Carabinani, Unini and part of Negro rivers.

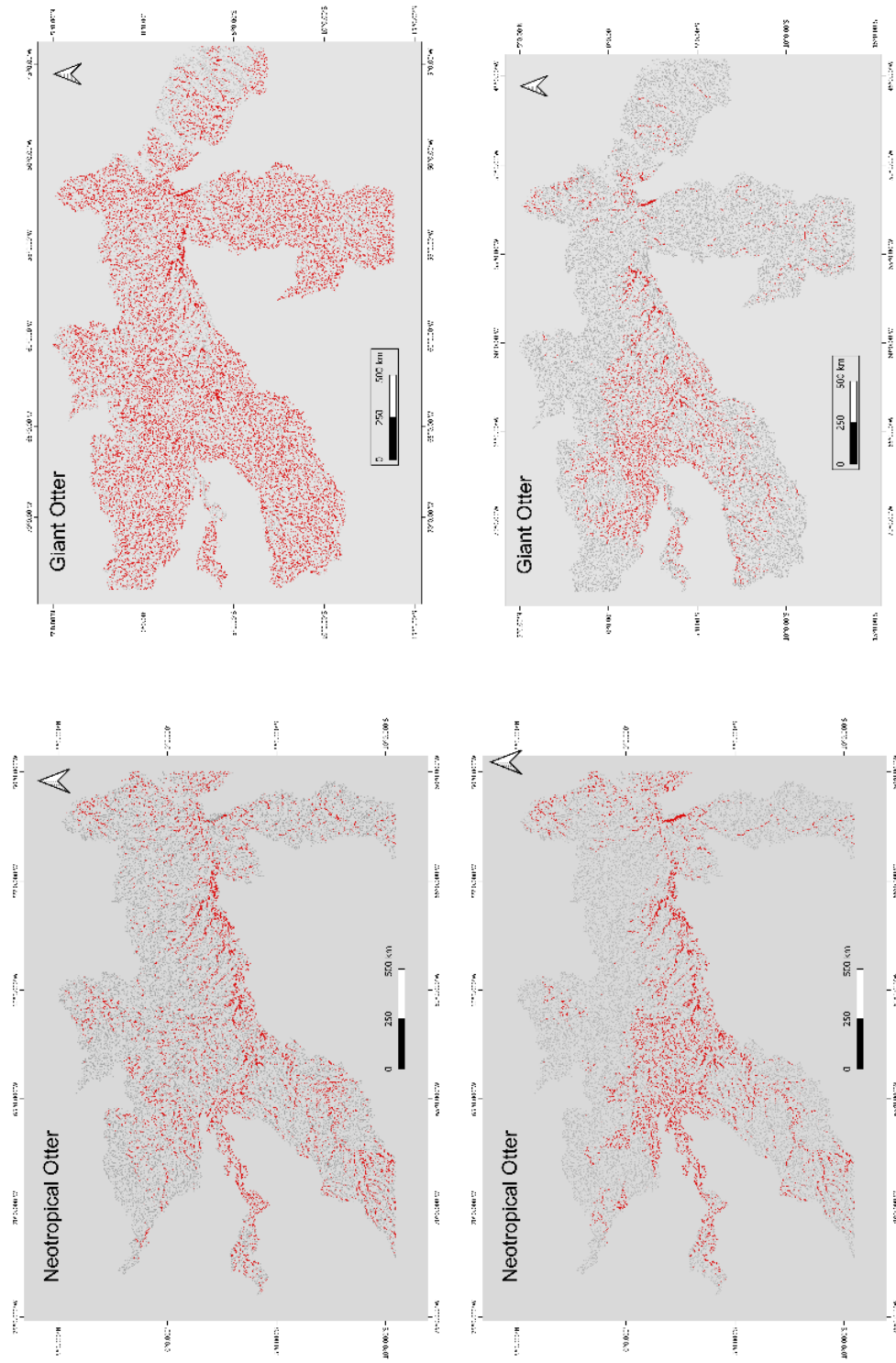


Figure 2.6: Binary maps of suitability generated with (maps on left) and without (maps on right) bias grids for Giant and Neotropical Otters. Areas in red correspond to suitable habitat.

Table 2.3: Percent of contribution and permutation for each predictor for the giant otter model.

Variable	Percent contribution	Permutation importance (%)
Flow accumulation	63.6	28.8
Settlements	6.7	18
Tree cover	5.5	9.1
Slope	5.3	4.5
Walsh Index	4.2	11.5
Coarse fragments	3.4	15.4
Drainage density	3.3	2.2
NPP	3	3.6
Regularly flooded vegetation	3	4.3
Clay content	2	2.6

Table 2.4: Percent of contribution and permutation for each predictor for the Neotropical otter model.

Variable	Percent contribution	Permutation importance (%)
Drainage density	28.5	17.7
Flow accumulation	22.7	14.5
Settlements	14.4	16.1
NPP	8.1	3
Slope	5.9	7.2
Coarse fragments	5.5	24.3
Walsh Index	4.9	6.8
Regularly flooded vegetation	3.9	2.5
Tree cover	3.5	3.9
Clay content	2.7	4

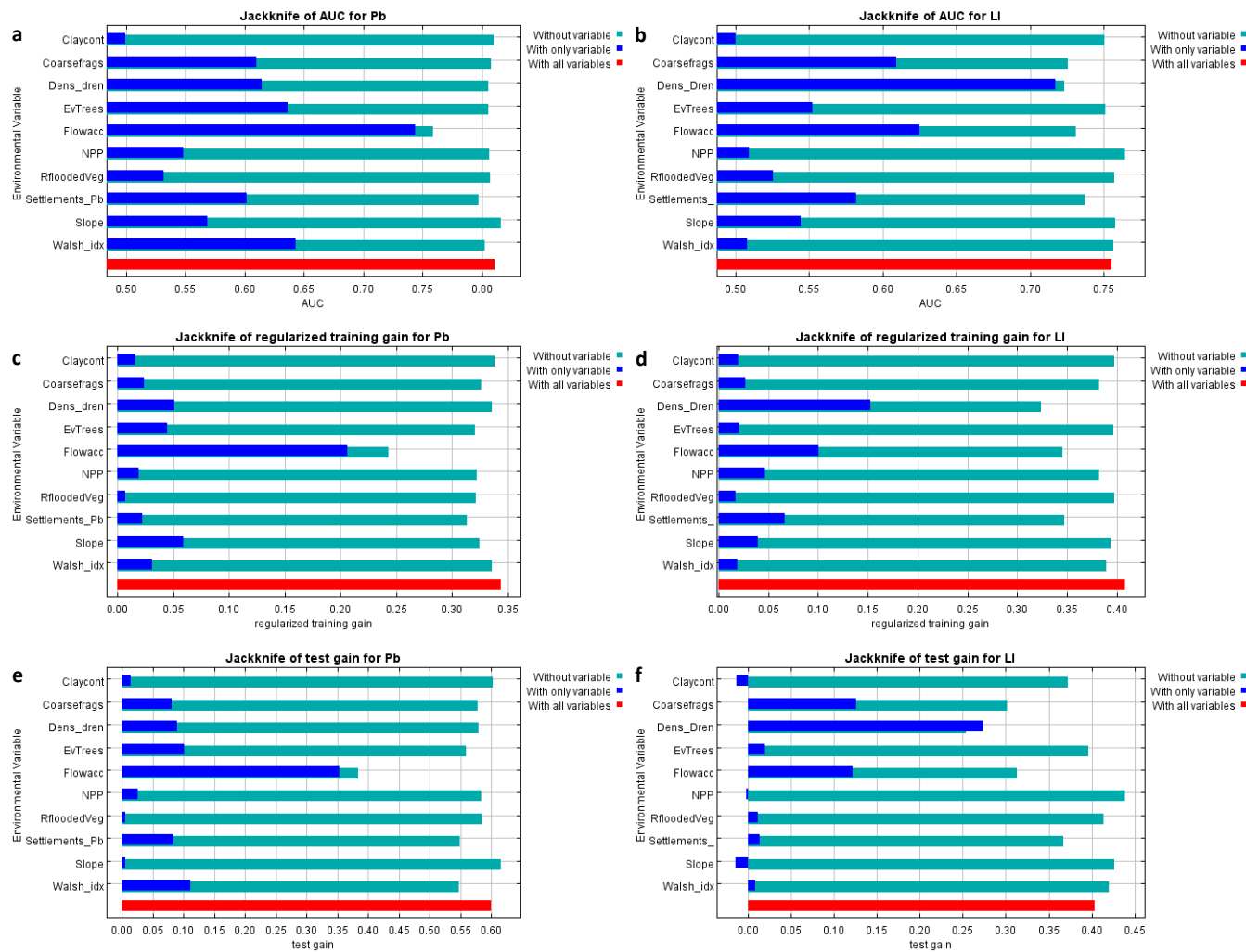


Figure 2.7: Jackknife plots for: AUC on test data (a,b); training gain (c,d); and test gain (e,f). Light blue bars show effects on the metric when the variable is removed, and darker blue bars show the effect when the variable is the only one used. Red bars correspond to AUC values of the model using all variables. Pb=giant otter and LI = Neotropical otter.

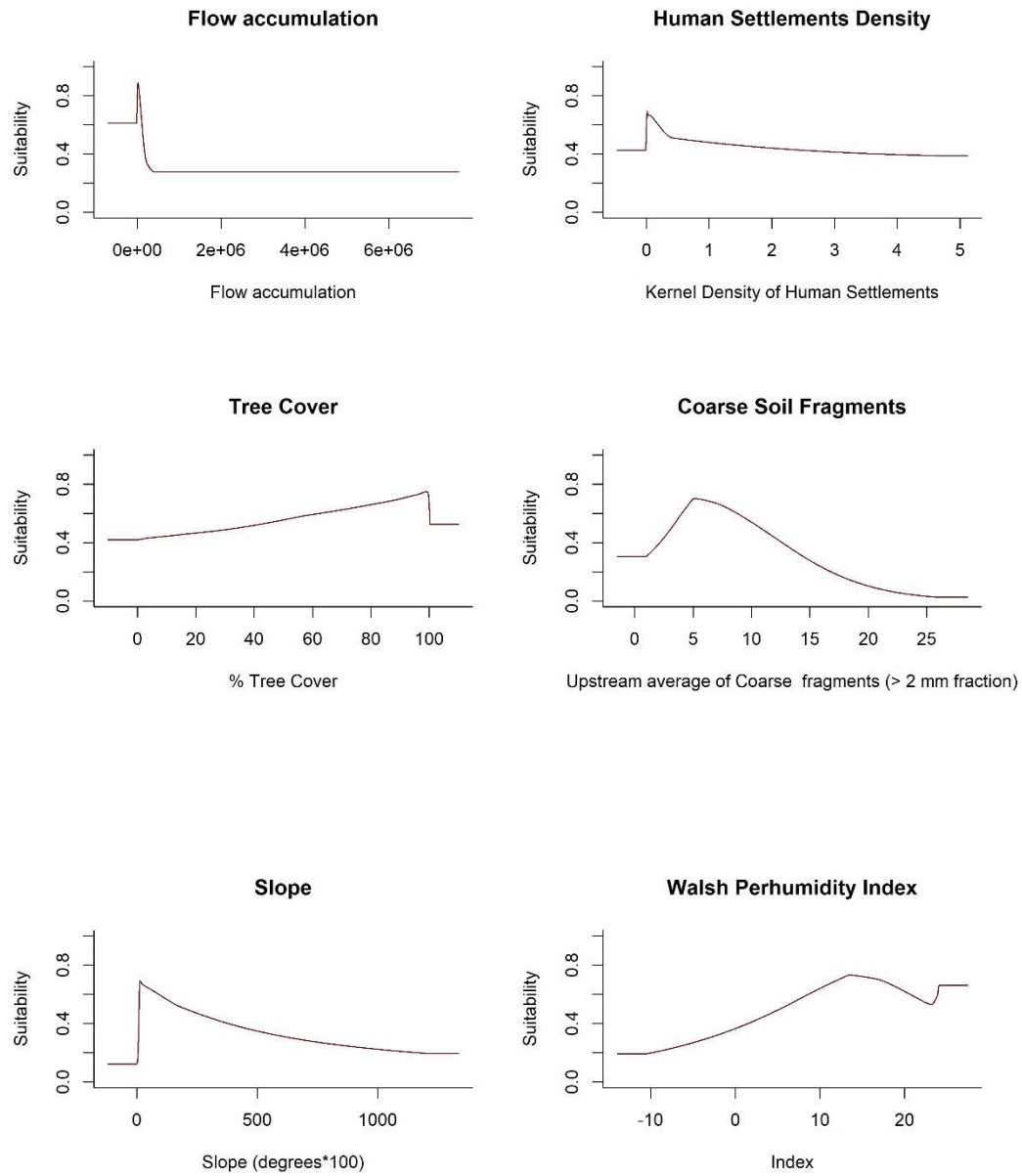


Figure 2.8: Mean response curves of the effect of explanatory variables on the giant otter habitat suitability model predictions across 10 iterations.

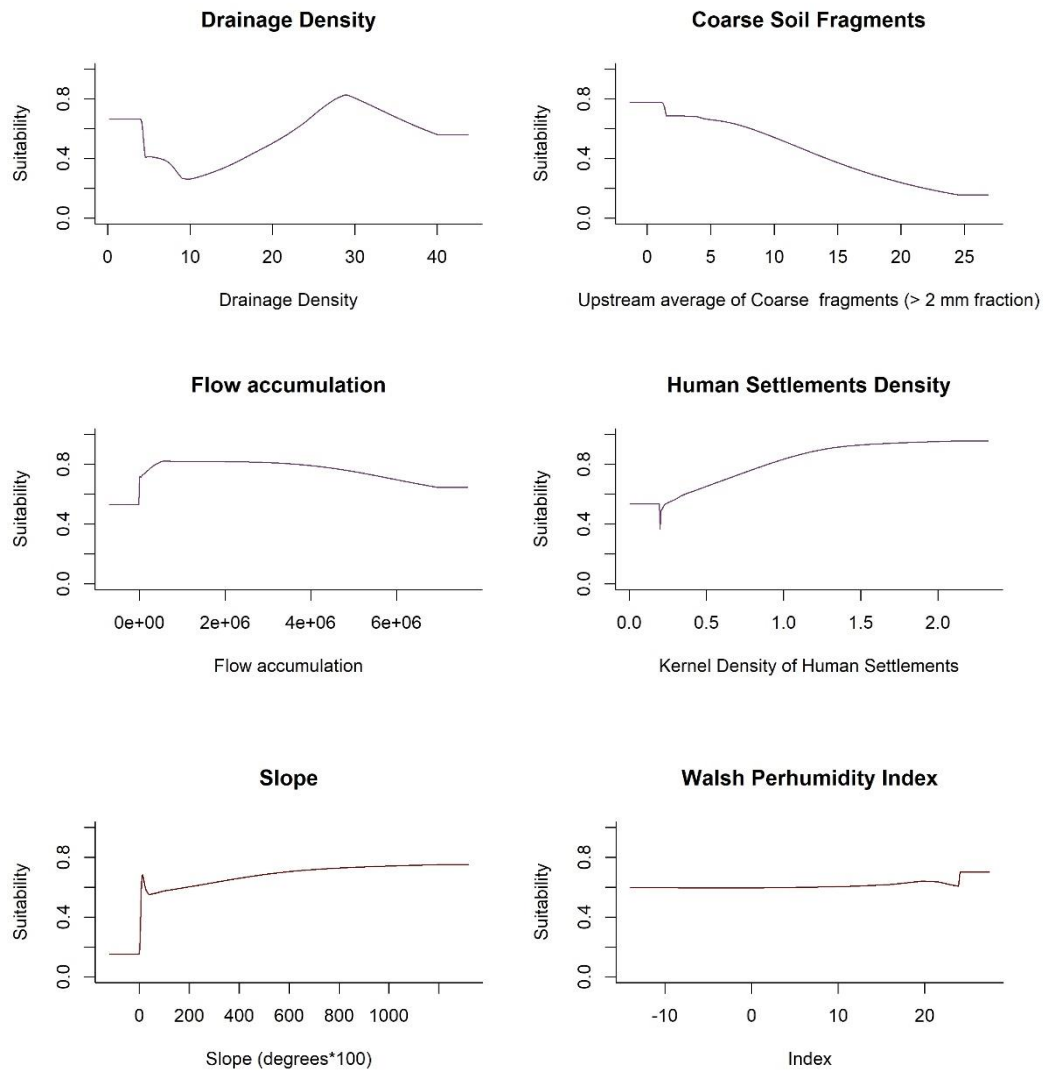


Figure 2.9: Mean response curves for the effect of variables on the Neotropical otter model predictions for habitat suitability across 10 iterations.

2.5 Discussion

In this study, potential distribution models based on habitat suitability were built for giant and Neotropical otters at a regional scale in central Amazonia, Brazil. This was an unprecedented approach of fine-scale modelling for the species, and such resolution can better aid or improve the prediction and identification of potential key management areas (Jiménez-Alfaro et al. 2012, Valerio et al. 2020).

The models generated here could accurately predict species potential distribution in the study area, as indicated by AUC and TSS values. Differences observed in SDMs generated with and without the incorporation of a bias grid highlight the importance of such approach. When occurrence data is biased and clustered in certain areas, it might cause spatial autocorrelation and erroneous identification of suitable habitats (Cordeiro et al. 2016). By default, Maxent draws random background locations from the whole spatial range, and applying a bias grid makes the algorithm down-weight areas with a higher clustering of presence points. In this study, not applying a bias grid has greatly reduced the extent of suitable areas in SDMs excluding several main river basins, and suitable areas were in fact concentrated around the higher densities of occurrences. AUC values, on the other hand, were higher when not accounting for bias; the same was reported in other studies (e.g., Syfert et al. 2013, Fourcade et al. 2014). Despite such apparent reductions in model performance, Kramer-Schadt et al. (2013) point out the importance of account for sampling bias by both spatial filtering and the use of bias layers. More importantly, considering the general knowledge we have on the species currently, the potential distribution maps generated by the non-bias approach are unrealistic, even though there was no significant difference in the omission rates between both approaches. This emphasizes the importance of considering expert opinion and species

characteristics when evaluating model results, as in Norris (2014). An external validation of the models, using independent data, would hence be useful to clarify the differences found and estimate omission rates more confidently.

The overall estimated distributions were spread over most of the area within the defined limits for each species, indicating that central Brazilian Amazonia does provide a large adequate environment for the two species of otters. Indeed, the Amazon Basin is thought of as the best opportunity for conservation of Neotropical otters, due to the diverse mosaic of protected areas and indigenous territories (Rheingantz et al. 2018). Amazonia is where most large and stable populations of giant otters are concentrated as well (Carter & Rosas 1997, Kruuk 2006, Leuchtenberger et al. 2018), with some still in recovery, expansion or reoccupation after local extinctions caused by last century's fur trade (Recharte & Bodmer 2009, Lima et al. 2014, Pimenta et al. 2018).

The maps produced were in line with initial hypothesis concerning the diverse habitat preferences of the two species. Their suitability maps presented different patterns at a finer scale, which are in agreement with the general patterns described in the literature: giant otters are more likely to occupy narrower streams, lakes and their associated habitats (e.g., Pimenta et al. 2018) whereas Neotropical otters tend to select wider and deeper water bodies (e.g. Muanis & Oliveira 2011).

The maps show, indeed, that most creeks deemed suitable for giant otters were not incorporated in the Neotropical otter distribution model. The present results have, although, one main contrasting point when compared to Muanis & Oliveira's (2011) findings: these authors concluded that, in the Brazilian Pantanal, Neotropical otters were more generalist in relation to habitat features, and the ecological space used by giant otters was smaller and included in Neotropical otters'. Here, in contrast, the SDMs

suggest an opposite trend for Amazonia. But animals can, indeed, show major differences in habitat selection over distinct areas, as shown by Crosby et al. (2019) in a study with boreal songbirds.

It is a consensus among giant otter researchers that these animals show seasonal differences in their ranging behaviour. According to Duplaix (1980), in Suriname giant otters move seasonally (during rainy months) to smaller streams. In Amanã, the same happens: when streams flood and most banks are submerged, giant otters are mainly found at *terra-firme* creeks and surrounding flooded areas (which are very shallow or nearly dry during dry season) (personal observations). These creeks are located in more elevated areas of the forest, where giant otters can find higher banks for setting their dens. Utreras et al. (2005) estimated giant otter wet season home ranges to be between 4 and 13 times greater than that of dry season in the Ecuadorian Amazon, and Leuchtenberger et al. (2013) obtained similar findings in the Brazilian Pantanal.

It is not clear what interplay of factors drive these seasonal movements, as they could also be related to food availability, since most fish also concentrate in the flooded forest during the high-water periods (Goulding 1993, Carvalho et al. 2007). Still, considering the distinguished response of giant otters to flood pulse variations, it is possible that this species has a stronger land-dependence when compared to Neotropical otters. Although there is virtually no information concerning Neotropical otter space use in the Amazon, occasional observations reported in the literature may indicate a more flexible behaviour, as they can use the top of submerged trees as shelters during the flood (Santos et al. 2007) and are also able to climb tall trees (Silva & Quintela 2010). So perhaps, during the flood season, Neotropical otters could seek additional opportunities of refuge in the canopy of submerged trees, reducing thus their need to expand or shift

home ranges like giant otters do. That would be a possible explanation for the more restricted predicted distribution of the former.

The species also responded differently to the environmental predictors used in the modelling approach, which was likewise expected if one considers their dissimilar habitat selection patterns reported in the literature, cited above. The stronger predictors in terms of AUC contribution for the two otters were both hydrological variables, flow accumulation (for giant) and drainage density (for Neotropical), in line with their semi-aquatic life-styles. Pimenta et al. (2018) compared the influence of environmental features in giant otter habitat selection at local and landscape scales, and their findings stressed the importance of the presence of small and connected water bodies for the species.

A diverse response of the two species was observed to flow accumulation (the amount of drained water to each map pixel), though. For the same range of accumulation values, giant otters had lower suitability, while Neotropical otters had an almost constant response of high suitability. This result could be explained by Neotropical otter's reported preference for deeper rivers and/or courses with abundant pools (Carrillo-Rúbio & Lafón 2004, Muanis & Oliveira 2011); and also, by the fact that the whole main course of the Amazon River (which has the highest values of flow accumulation of the whole basin) was predicted as suitable habitat for Neotropical otters - but not for giant otters. The Amazon is a white-water river, with a high level of sediments in suspension and little transparency. Giant otters, conversely, prefer black and clear water rivers with higher transparency, owing to their visually oriented foraging strategies (Duplaix 1980, Duplaix et al. 2015). This does not mean they do not occur in areas with predominance of white-water, but their space use may be differentiated in those habitats. In Peru, for instance, there is a well-studied giant otter population in Manú, a white-water river;

however, the core of otter group territories is not the river itself, but black water oxbow lakes where they spend most of the time, while the river is mainly used as a linking route (Groenendijk et al. 2014). The same probably happens in one of the areas surveyed in this study, the Abufari Biological Reserve, located in the middle course of the Purus River, which is also white-water. All giant otter occurrences registered in this area were in oxbow lakes and their associated streams, not in the main river.

Giant otter's suitability response to tree cover and settlement density further corroborates described habitat preferences of this species for undisturbed water bodies with high-quality vegetation cover (Duplaix 1980, Duplaix et al. 2015). In previous studies, human activity has been found to significantly decrease the chances of sighting giant otter groups and signs, suggesting that anthropogenic disturbances indeed can play a role in affecting giant otter occurrence (Oliveira et al. 2015). Taken together, these findings are in agreement with the discrete negative trend observed in the response of giant otter suitability to human settlements. This is especially relevant considering the low proportion (25%) of giant otter suitable habitat that is within protected areas (where settlements are reduced or totally absent, depending on the official category of each natural reserve)

In contrast, Neotropical otter suitability had an overall positive association with human settlements, contrary to findings by Gomez et al. (2014) and Rheingantz et al. (2014), who observed a decrease in habitat suitability values with increasing human density. Nonetheless, Rheingantz et al. 2014 acknowledge the fact that, even in human-dense areas, suitability values were high for the species. It is also worth noting that the study area limits in Gomez et al. (2014) were already within a populated region, which included the suburbs of Buenos Aires city in Argentina. Likewise, Rheingantz et al. (2014) studied the whole distribution range of the species, which include areas of high

human density, such as the southeast of Brazil (where the São Paulo-Rio de Janeiro megalopolis is). The present study area, on the other hand, has the lowest demographic densities in Brazil (an average of 3.7 inhabitants/km² - <https://cidades.ibge.gov.br/>). In a study area within the present SDM limits, Andrade et al. (2019) detected that, at the microhabitat scale, Neotropical otter presence was positively associated with the presence of fishing gear and boats, suggesting that fish trapped in gears may attract otters. Personal observations of the species in areas concomitant with the presence of sport anglers and intense boat traffic in the ecotone of Pantanal and Cerrado biomes (Central Brazil) also suggest that this species is less likely to be affected by this kind of human disturbance. More studies on anthropogenic influence in different biomes where Neotropical otters occur are needed, in order to better clarify this important topic.

Regarding climatic factors, Neotropical otters had a neutral response to the only climate-related variable used in the modelling approach, Walsh's perhumidity index. Giant otter suitability, in turn, was mostly positive correlated to this index. Lower values of perhumidity reflect more intense dry seasons, suggesting that giant otters could be more sensitive to seasonal variations in rainfall and water level than Neotropical otters. This is in accordance with the findings of Cianfrani et al. (2018), who measured otter species intrinsic sensitivity to climate change based on their niche specialization and marginality. They documented a high level of specialization for the giant otter, an indication of the species sensitivity, whereas the neotropical otter had the lowest niche marginality of all species of otters (i.e., there is little difference between the available environment and the species' ideal conditions) and also the lowest specialization, being likely less vulnerable to climate variations.

2.5.1 Limitations of the study

A common limitation of this and other SDM studies with these species, especially regarding conclusions related to climatic preferences, is a potential seasonal bias in data collection. Most of the occurrence points registered in the scope of the current study were obtained during the Amazonian dry season, with the exception of two out of the seven study sites, that were also visited during the rainy season. Some records for the remaining areas were also obtained at the period where water levels were rising, but none during the peak of the flood season. On the other hand, locations reported by Pacca et al. (2016), for example, were registered during the flood season, since rivers in their study area are only navigable during this time.

As described above, giant otters may expand or change territories during the wet season in Amazonian. It is therefore important to have a dataset including presence points registered in diverse seasons. For the present study, there is incomplete information about the season of each occurrence point used from extra (literature) sources; but additional analyses trials (data not shown) revealed that models comprising all data and dry-season only data led to similar results. Furthermore, since most aspects of the models generated were corroborated by previous knowledge about the species, it is unlikely that they were affected by this kind of bias. Further cautions were taken, e.g., the model was parsimoniously fitted within reasonable geographic limits, and a bias grid was used. There was no evident clustering of suitability around presence points, and AUC values were moderate, suggesting that models were not over fitted (Vaughan & Ormerod 2005).

Amazonia and its vastness bring logistical challenges to researchers that can also lead to accessibility-related bias. For example, indigenous lands have more restricted access and require different permits than other protected areas, so it is uncommon to find studies in those areas. In fact, only one giant otter study in Brazil was done in such context (Pimenta et al. 2018). Long distances, which can only be travelled by boat, can make displacements to remote areas extremely expensive, time-consuming and impracticable. And indeed, there is a lack of occurrence data for both species at more remote areas of the Amazon. A possible way forward would be the implementation of small-scale citizen science projects, in cooperation with local NGOs and university campi present in more remote municipalities – following the example of Melo et al. (2019). Interiorized survey efforts set forth by locals, regionally coordinated and with standardized methods, would be of great value for a greater knowledge on the species occurrence and associated factors.

External validation of the model (i.e., when extra/new occurrence data, not used in the original analyses, is contrasted with the predicted model to verify its predictive power) was not possible. For this, an increased field effort would be necessary, together with more funding to reach more remote and previously unsampled areas. Due to time and resource constraints, such additional approach would be unfeasible in the scope of his study. There were, however, a few field findings considered relevant for discussion on the matter. During the field sampling for this study, there were no detections of direct or indirect signs of Neotropical otters in 3 out of 7 study sites visited: Viruá National Park and the Biological Reserves of Trombetas and Abufari (see Fig. 2.1). Looking closely at those areas in the suitability maps (Appendix 2.8-2.10), the areas comprising Trombetas and Abufari Reserves did not show a particularly high proportion of unsuitable areas; although, compared to the giant otter map, there seems to be a higher

amount of suitability for Abufari. The Viruá National Park area, on the other hand, was indeed predicted to be a mostly unsuitable area for Neotropical otters. Furthermore, anecdotal information obtained from local residents in Trombetas and Abufari during fieldwork indicates that Neotropical otters might be indeed rare or absent in those areas.

2.5.2 Implications for conservation

Neotropical otter suitable habitat in Central Amazonia was more fragmented than that of giant otter according to the models, with reduced connectivity between patches of suitable habitat. It is important to investigate those patterns more deeply, since a scenario of low connectivity can be harmful to the maintenance of genetic variation as it hampers gene flow between populations (Frankham 2005, Wan et al. 2018). The more isolated a population is, the more it is under risks of genetic diversity loss by combined effects of inbreeding and genetic drift and thus more vulnerable to deleterious effects such as reduction in fitness and increased extinction risks (Keller & Waller 2002). With partial isolation, variation among populations can be augmented: higher levels of gene flow may increase the overall adaptive potential of a species, *i.e.*, its capacity to respond to environmental changes (Swindell & Bouzal 2006, Hoelzel et al. 2019).

A study in Western Amazonia has reported high haplotypic diversity for Neotropical otter populations using three mtDNA genes (*COI-II* and *Cyt-b*, 1024 base pairs) (Ruiz-García et al. 2018), suggesting either sufficient levels of spatial connectivity or recent isolation and incomplete lineage sorting. Trinca et al. (2013) have found significant genetic structure for the species across South America using a 1471bp sequence of mtDNA (Control region, *ATP8*, *ATP6* and *ND5* gene regions), identifying one phylogroup in Amazonia. Although diversity within this phylogroup was high, the

sample size was small and with some spatial bias. Therefore, it is necessary to increase genetic sampling efforts across the Amazonian basin, as potentially more demographic groups could be found (Trinca et al. 2012). It is also important to assess diversity using other types of genetic markers, especially from nuclear DNA, which allows admixture analyses that can identify population clusters (such analyses are not possible with mtDNA markers). In this way, population connectivity issues would be better clarified for the species.

With respect to giant otters, although the predicted distribution is more continuous along watercourses, inter-river basins connectivity might not be so high; so, as for the Neotropical otter, increased efforts to monitor population status should be put into practice, while two key points ought to be kept in mind. First, giant otters might be avoiding important potential dispersing routes due to human disturbance or natural habitat characteristics (for instance, the main courses of Amazon or Purus Rivers). If the former indeed has a substantial impact on giant otter dispersal, it will be crucial to designate a more stringent strategy of mosaic conservation, considering not only protected areas but also the possible connections between them, which might have a higher degree of anthropogenic influence.

Second, intrinsic behavioural ecology characteristics of the species have to be considered as well. In the Brazilian Amazonia, giant otter linear home range sizes reported range between 4.5 and 10 km, which is rather small compared to other similar sized carnivores. Dispersal distances reported in Manu National Park (Peru) are on average 57.2 km (30 km for females and 65.4 for males) (Groenendijk et al. 2014). Despite being highly-mobile animals, it is likely that either giant otters' social system or local densities of family groups somehow reduces their need or potential to establish

larger territories or disperse longer distances, in a way similar to reported findings in Eurasian otters (Quaglietta et al. 2013).

Moreover, there is a high mortality rate associated to the dispersal phase of giant otters, especially for males (Groenendijk et al. 2014, 2017). High mortality during dispersal is actually not uncommon in carnivores, including other mustelids and Lutrinae (Waser, 1996; Persson et al. 2003; Quaglietta et al. 2013 – observing that the latter, though, refers mostly to roadkilled dispersing Eurasian otters). But, if dispersal is already being limited by other factors, and if this mortality affects mainly males - which are the longer distance dispersers – this reinforces the need for assessing optimal conditions to maintain connectivity between populations and hence a proper level of gene flow.

2.6 Conclusion

In this chapter, I addressed potential distribution of Neotropical and giant otters over Central Amazonia, through a maximum entropy method implemented in the program Maxent. This was the first attempt in modelling Amazonian otters' distribution at a regional scale and focusing on watercourses. The current approach allowed the identification of environmental factors that might affect inter-population connectivity in the studied species, and the maps generated can serve as a baseline for testing hypothesis regarding comparisons of predicted connectivity patterns and effective connectivity, which can be revealed and inferred by genetic structure patterns (addressed in the following chapter). Overall patterns of the two species reflect the current consensus among researchers that Amazonia is indeed an important refuge for otter populations, since the predicted distribution observed was widespread across the study area.

Taking all findings into consideration, it is possible to rank some relevant points concerning each species. Neotropical otter management strategies should, for instance, focus on obtaining more baseline information which is lacking for the species, in order to allow more robust inferences on habitat requirements and seasonal patterns. Current knowledge on Neotropical otters would benefit especially from more studies on the species' spatial patterns, providing more evidence to understand better what might lead to the patchy aspect of their predicted distribution. Nevertheless, the model was useful to support some field impressions that there could be areas in Amazonia where Neotropical otters are rare or even absent, despite not showing any striking structural differences from areas where they are abundant. More subtle aspects of the species behavioural ecology might lead to different perspectives on factors influencing its distribution and connectivity.

Despite the larger predicted distribution of giant otters, it is important to assess the functional or effective connectivity between populations of the species, especially among different drainages. Some potentially key dispersing routes (such as the Amazon River) were identified as unsuitable for the species, and if this reflects in their functional connectivity, it could lead to reduced gene flow among populations.

The SDMs estimated therefore provided useful insights for further studies in this region. Such modelling approaches potentially constitute a useful resource for conservation and landscape genetics studies, as they allow us to better foresee populations at risk of isolation and assess degrees of habitat connectivity.

2.7 References

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2.8 Appendices

Appendix 2.1. Satellite image of the Viruá National Park study site. The orange lines correspond to surveyed water bodies.

Appendix 2.2. Satellite image of the Xixuaú (Jauaperi River) study site. The orange lines correspond to surveyed water bodies.

Appendix 2.3. Satellite image of the Balbina study site. The orange lines correspond to surveyed water bodies.

Appendix 2.4. Satellite image of the Jaú National Park study site. The orange lines correspond to surveyed water bodies.

Appendix 2.5. Satellite image of the Amanã study site. The orange lines correspond to surveyed water bodies.

Appendix 2.6. Satellite image of the Abufari (Purus River) study site. The orange lines correspond to surveyed water bodies.

Appendix 2.7. Satellite image of the Trombetas study site. The orange lines correspond to surveyed water bodies.

Appendix 2.8. Detail of Neotropical otter's suitability map highlighting the VNP area. Waterbodies in red correspond to suitable areas, while grey corresponds to unsuitable. The shaded area corresponds to park limits.

Appendix 2.9. Detail of Neotropical otter's suitability map highlighting the Trombetas area. Waterbodies in red correspond to suitable areas, while grey corresponds to unsuitable.

Appendix 2.10. Detail of Neotropical otter's suitability map highlighting the Abufari area. Waterbodies in red correspond to suitable areas, while grey corresponds to unsuitable.

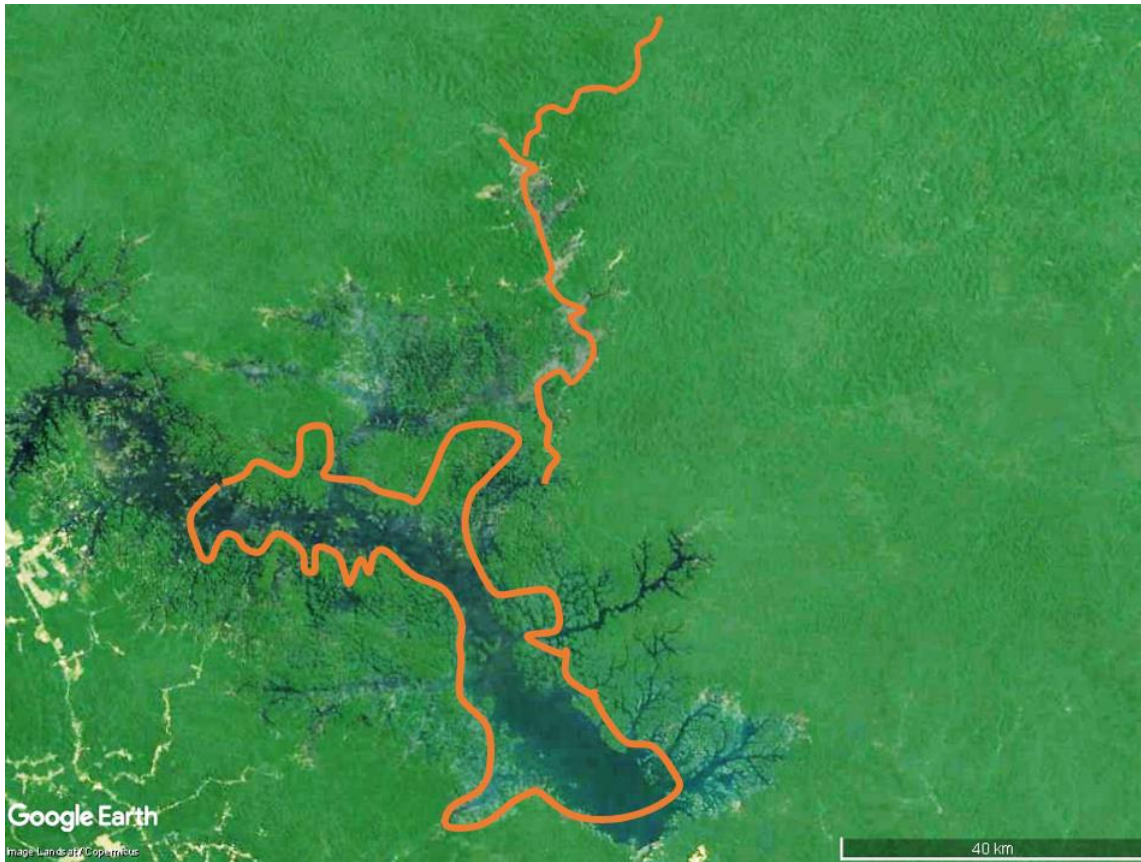
Appendix 2.1



Appendix 2.2



Appendix 2.3



Appendix 2.4



Appendix 2.5



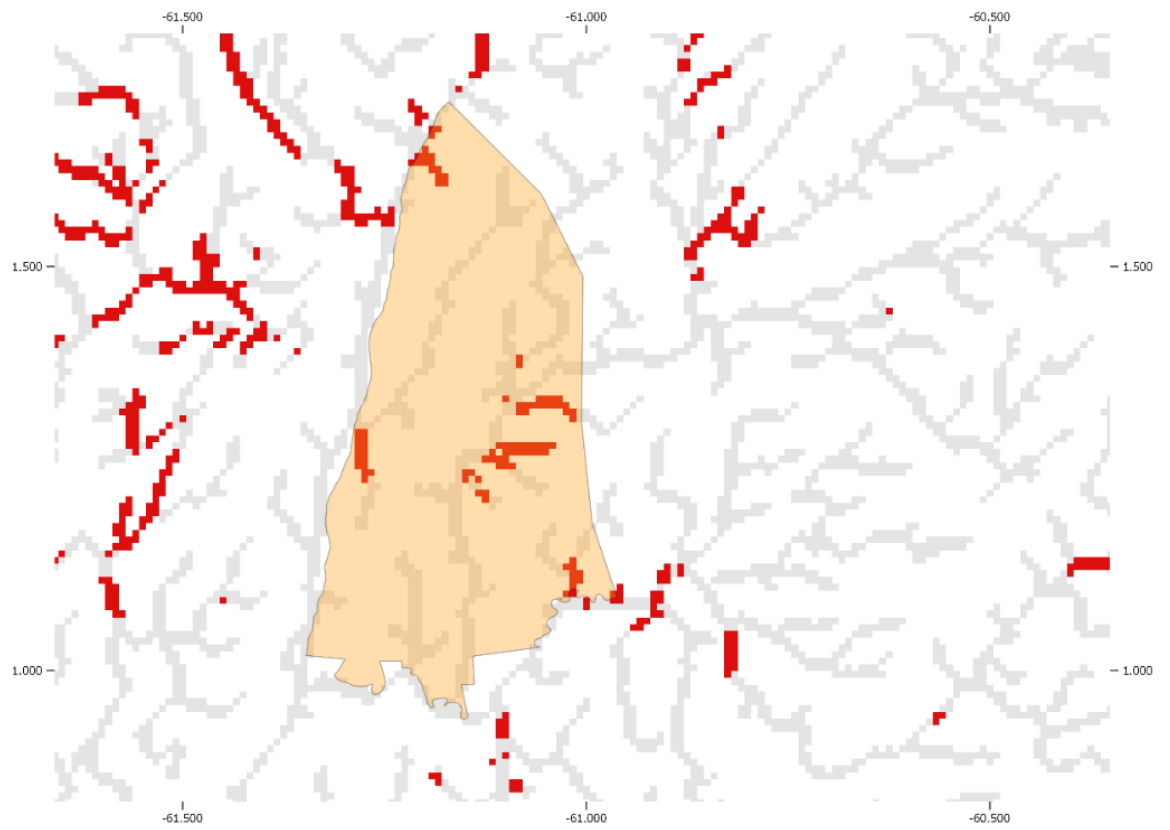
Appendix 2.6



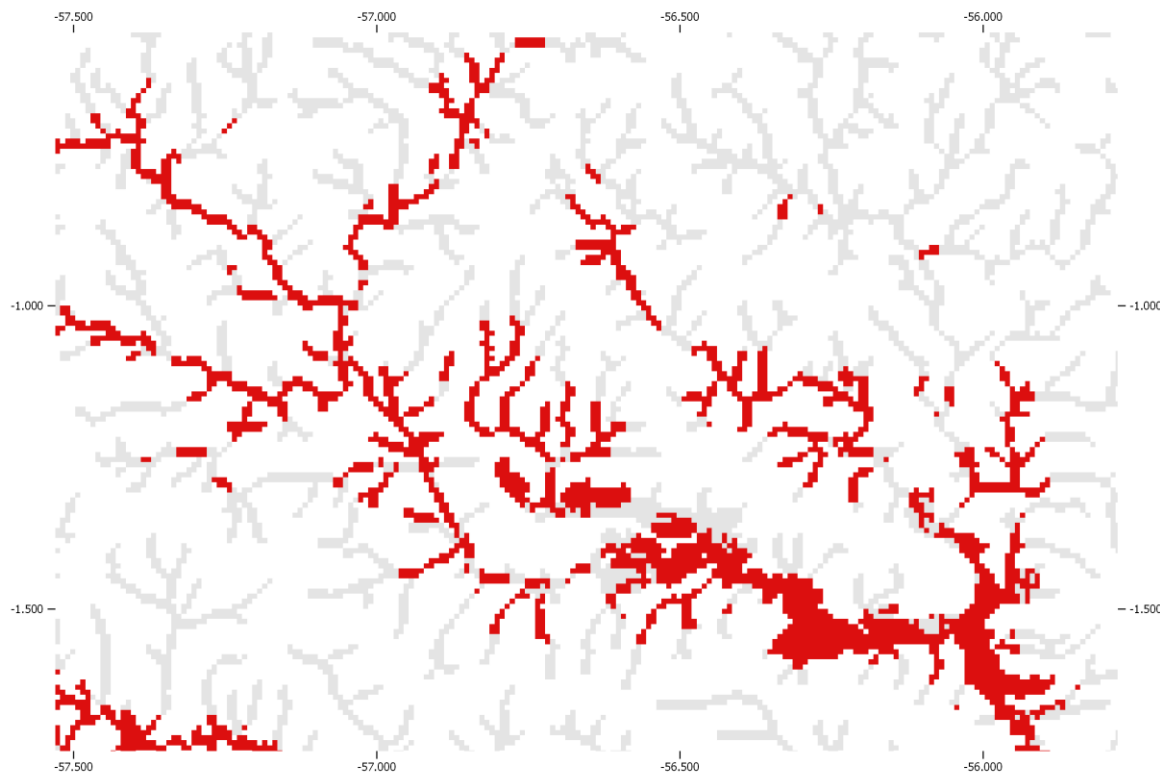
Appendix 2.7



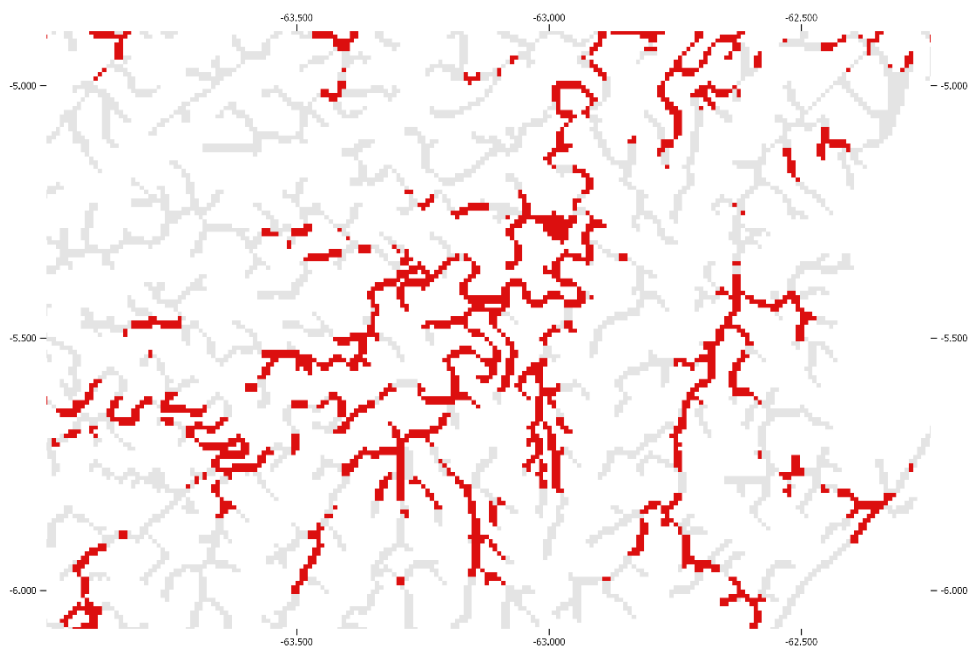
Appendix 2.8



Appendix 2.9



Appendix 2.10



Chapter 3

Comparative conservation genetics of giant and Neotropical otters



Photo: V.C. Fonseca da Silva

3.1 Introduction

The two species of otters in the Amazon region, *Lontra longicaudis* (Neotropical otter) and *Pteronura brasiliensis* (giant otter), have a history of human exploitation for supplying the wild animal hide and pelt international trade in the 20th century (Doughty & Myers 1971, Smith 1981, Antunes et al. 2016, Pimenta et al. 2018). Populations of giant otter have been particularly impacted by the hunting pressure, being driven to multiple local extinctions and having overall population numbers greatly reduced (Pimenta et al. 2018, Duplaix et al. 2015). In 1972, the species was included in the IUCN's top-10 list of the world's most threatened mammals (Duplaix et al. 2015). By the end of the 60s and beginning of 70s, some countries have started legally protecting otters, and after 1975 the global demand for otter skins has virtually ceased with the strict ban in the global trade, as both species were included in Appendix I of the CITES agreement.

The trade ban is, nevertheless, still recent - around 5 generations for otters - and the severe impact caused by hunting on giant otters is still noticeable. Although a gradual recovery of the species is being detected through the repopulation of areas where previously there were local extinctions (Recharte Uscamaita & Bodmer 2009, Lima et al. 2014, Pimenta et al. 2018), the total number of individuals in the wild is still considered low, and subpopulations are mainly small and fragmented (Groenendijk et al. 2015). As new anthropogenic threats have emerged over the last decades, giant otters remain listed as Endangered by the IUCN (Groenendijk et al. 2015). Neotropical otters, despite their higher resilience that likely lessened the impacts of the former commercial hunting (Pimenta et al. 2018), are classified as Near-threatened (Rheingantz & Trinca 2015). This is due to the potential impact of a number of anthropogenic threats and the species' declining trends in several countries (Rheingantz & Trinca 2015) as well as the

uncertainties regarding subspecies classification (Hernández-Romero et al. 2015, 2018) and evidence for small effective population sizes in some populations (Latorre-Cárdenas et al. 2020_a).

Among priority research actions, both species are in need for studies on population sizes and trends (Groenendijk et al. 2015, Rheingantz & Trinca 2015), as such kind of data is lacking, with no confident estimates of numbers over their distribution ranges. Populations in the Amazonian region in particular are even less studied – as it is more difficult to carry out *in situ* research in this biome, due to its remoteness and vastness. In addition, Neotropical otters present a further challenge with its elusive, more timid behavior - as opposed to giant otters which are more conspicuous, curious and vocal, therefore more likely to be sighted (Almeida & Pereira 2017, Pimenta et al. 2018). Visually distinguishing Neotropical otter individuals in the field is also practically impossible, while giant otters can be recognized by their throat markings. A long-term study at a local scale (Manu National Park, Peru) was in fact able to provide the only robust data on giant otter demography, based entirely on individual identification by throat patterns over 16 years (Groenendijk et al. 2014).

Through the last decade, next-generation sequencing technologies (NGS) have become more accessible and less costly, allowing researchers to increasingly use this powerful resource in molecular ecology studies with non-model species (Futschik & Schlötterer 2010, Ekblom & Galindo 2010, Zavodna et al. 2013, Narum et al. 2014, De Wit et al. 2015). The parallel sequencing of multiple pooled samples provides a cost-effective way to identify a large number of neutral molecular markers, such as single-nucleotide polymorphisms (SNPs) (Futschik & Schlötterer 2010, De Wit et al. 2015). SNPs can be used to genotype individuals and address several aspects of population genetics and historical demography patterns; therefore, they have been increasingly used

in recent molecular ecology studies (Seddon et al. 2005, Tokarska et al. 2009, Seeb et al. 2011, Ogden et al. 2012, Herrero-Medrano et al. 2013, Hess et al. 2015, Kleinman-Ruiz et al. 2017).

SNPs can have several advantages over data provided by microsatellites (older, but still largely used, single locus genotyping markers) for instance. Such advantages include, for example, the ability of examining both neutral variation and regions under selection (Helyar et al. 2011). Unlike microsatellites, SNP mutations do not show a highly variable pattern (since they are normally biallelic - i.e., only two nucleotides segregate at that position), and instead follow simpler mutation models (Morin et al. 2004). SNPs can also be even more stable in degraded or ancient samples, as the target DNA sequence can be quite short as 50-70bp, which facilitates studies based on non-invasive and museum sampling (Morin et al. 2004, Morin & McCarthy 2007). Assessing fine-scale genetic structure is particularly challenging in wide-ranging and/or highly mobile species, and SNPs have been considered as useful markers for such cases due to their high information content (considering a large number of concurrent SNP markers) (Viengkone et al. 2015).

Sequence capture, also known as target enrichment, is an approach where specific loci or genomic regions are selected, “captured” from the DNA samples, and then sequenced. By targeting a reduced number of pre-determined regions, this method can be more time and cost-effective compared to other high-throughput methods (Mamanova et al. 2010) and can provide enhanced quality data with accurate SNP calling (Jones & Good 2016).

Initially, sequence capture was used in majority for biomedical applications (Hodges et al. 2007, Gaudin & Desnues 2018), but molecular ecology and evolutionary

studies can also take many benefits from using such an approach, and it is slowly becoming more common in the literature of these fields. An obvious advantage of capture for conservation and evolution research is that it facilitates the sequencing of DNA from non-invasive samples with high exogenous DNA content and/or very low copy and rare DNA. Some studies already have indeed successfully used sequence capture with faecal (e.g., Perry et al. 2010, White et al. 2019), historical museum samples (Knyshov et al. 2019a, b) and environmental DNA (Seeber et al. 2019). Considering such, this method was chosen as it would increase chances of isolating otter DNA from scats (the main sample type used in this study) and allow the use of high-throughput sequencing technology. Moreover, it would not be possible to apply another reduced-representation sequencing method, such as RADSeq. RADSeq is now widely-used in molecular and evolutionary ecology (Davey & Blaxter 2010, Andrews et al. 2016), but it is impractical to apply on faecal material – it requires pure species DNA, and whole DNA extracts from scats usually contain high concentrations of prey and bacterial DNA (Hernandez-Rodriguez et al. 2018). In addition, the technique is not as effective when working with degraded samples (Graham et al. 2015), which is most often the case for non-invasively collected otter scats (e.g., Lerone et al. 2014).

Previous genetic studies with giant and Neotropical otters have mainly used traditional Sanger sequencing technologies, genotyping individuals by microsatellites or using mitochondrial DNA markers (e.g., Pickles et al. 2011-2012, Trinca et al. 2007, Trigila et al. 2016) – see Table 3.1 for a summary on main genetic papers published on each species within the Amazonian realm. None of the studies so far have applied NGS and higher-resolution molecular markers to address population genetics of these species. Moreover, studies performed at finer spatial scales (e.g., regional level) are lacking, and apart from large scale patterns of differentiation, for instance, among major hydrographic

basins - such as the Amazon and Orinoco for giant otters (Ruíz-Garcia et al. 2018) – nothing is known regarding population genetic structure at lower spatial scales for the hydrographic networks in Amazonia, such as between sub-basins of Amazon River’s tributaries.

Table 3.1: Summary of genetic studies undertaken with giant and Neotropical otters including samples from Amazonia (Pb=giant otter, Ll=Neotropical otter). CR= Control region, Cyt-b=cytochrome b, COI/II= Cytochrome c oxidase subunit I/II, ND5= NADH-ubiquinone oxidoreductase chain 5 protein gene

Study	Species	Sample Size	Markers used	Geographical range
Garcia et al. 2007	Pb	30 (22 from Amazonia)	CR, Cyt-b, COI (1444 bp)	Brazil - but Amazonian samples had a spatial range similar to this study; see Fig. 3.4
Pickles et al. 2011	Pb	70	CR, Cyt-b (1295 bp)	8 countries, 4 drainage basins (including Amazonia, Orinoco and Pantanal)
Pickles et al. 2012	Pb	59	13 microsats	5 countries, most concentrated on northern/northwestern S. America
Caballero et al. 2015	Pb	109	CR (258 bp)	Continental (with a focus on the Colombian Orinoco)
Ruiz-Garcia et al. 2018	Pb + Ll	33 / 47	Cyt-b, COI, COII (1024 bp)	4 countries; more concentrated on western and north western S. America (Bolivia, Peru, Colombia)
Trinca et al. 2012	Ll	51 (15 from Amazonia)	CR, <i>ATP6</i> , <i>ATP8</i> , <i>ND5</i> (1471 bp)	Continental – but the Amazonian sample range was more concentrated in central/eastern Brazilian Amazon basin

Knowing and understanding the processes underlying genetic diversity patterns and effective population size in natural populations is necessary for effective conservation planning, because they can reveal main risks and the potential for mitigation. As previously described in Chapter 1, the two species of otters show distinct degrees of sociality. They provide, therefore, a good case-study to test hypotheses on the influence of sociality on population structure in freshwater animals. Assessing their current patterns of genetic diversity and population structuring can further provide a better understanding of threats and their impacts, necessary mitigation measures, with a potential to aid conservation strategies for otters and other aquatic vertebrates.

The major goal in this chapter was to investigate population genetic structure and diversity of giant and Neotropical otters in central Amazonia rainforest, using nuclear DNA markers obtained by Next-Generation Sequencing, mainly from non-invasively collected samples (scats). Specifically, the aims of the study were: 1) to estimate intra and inter-population genetic variability; 2) assess admixture and spatial genetic structuring for the putative populations; 3) assess if the higher degree of sociality in giant otters reduces connectivity (promoting more differentiation among local populations) and diversity; 4) assess the possible role of hydrography in shaping genetic structure patterns.

3.2 Methods

3.2.1 Study area

Samples were obtained from six main areas in Brazilian Amazonia (Figure 3.1), on the watersheds of Amazonas and Negro Rivers. Geographical coordinates are approximately between longitudes 0°20' - 4°40'S and latitudes 65°08' - 58°04' W. In addition, for giant otters, extra samples were provided from collaborators working in the Rupununi River, Guyana, close to the Brazilian border (approximate coordinates -59.3°S, 3.7°W), and one Neotropical otter sample was provided from the Ati-Paraná (location “Aua”), a river located at the drainage divide between the Amazon and Japurá Rivers (-66°S, -2°W). For more details on study area characteristics, see Chapter 2. In Table 3.2, distances between sampling sites (measured as linear distances along the river network) are provided.

Table 3.2: Linear distances along rivers (in km) between the study sites.

	Amanã	Abufari	Balbina	Jaú	Trombetas	Xixuaú
Amanã	-					
Abufari	538	-				
Balbina	5690	1290	-			
Jaú	1340	820	309	-		
Trombetas	834	1150	475	414	-	
Xixuaú	834	980	233	160	1050	-

3.2.2 Otter scat and tissue sampling

Rivers were surveyed on a small boat with outboard motor (5 or 15hp) searching for giant otter groups and fresh mucus or scats from both species. Searches were also undertaken by foot along river or lake banks when boat access was not possible. The overall strategy for finding faecal samples was similar for both species, although for giant otter, a few particularities had to be considered. Ideally, giant otter scats should be very fresh (i.e., no more than a few hours old) - the strong odour emanating from latrines attracts insects and other animals that can not only consume all the mucous material, but also increase contamination. Due to the typical trampling of excrements by giant otter groups, it is not always possible to identify individual scats. If they were mixed and could not be recognized as distinct scats, they were not sampled. The best situation for sampling was when the group could actually be observed defecating and, after they left

the site, to go straight away to collect the material. A good opportunity for such events was in the early morning, when groups usually use the latrine after leaving the den.

Neotropical otters in Amazonia frequently defecate on fallen logs by the river banks (Fig. 3.2), sometimes on cavities and hollows on the banks, less frequently on sandy beaches. Binoculars are very useful when rivers are wide since, unlike the case of giant otters, Neotropical otter faeces do not have a strong scent that can be noted from a distance, so one has to count only on sight to find samples. Scats were sampled in the same way as described above for giant otters, but in this case, older (dry) samples were also taken occasionally, although preferably fresher samples were aimed.



Figure 3.2: Neotropical otter spraints (evidenced by yellow circles) deposited on fallen logs.

Faecal samples of both species were collected using disposable plastic spoons and put inside sterile 15- or 50-mL Falcon tubes. In general, it was attempted to collect the whole scat or most of it, sometimes dividing it into multiple tubes and always filling only half of each tube with the sample. When present, mucus and/or anal jellies were aspirated with a syringe and then transferred to one or more microcentrifuge (1.5 mL) tubes. All samples were preserved with 20% DMSO saturated with NaCl at room temperature in the field and transported in a cooler box to avoid heat. They were refrigerated as soon as possible after the end of fieldwork and stored at -20°C until DNA extraction.

Biopsy darts (Fig. 3.3) were used in the beginning of the study to collect skin samples from giant otters (Pneu-darts fired from a CO₂ projector; see Ribas, 2012). Protocols were approved under Brazilian law, under permit from the government biodiversity institute ICMBio. Strategies for dart sampling were chosen according to each situation, based on characteristics of each particular area (e.g., abundance of oxbow lakes or smaller tributaries, bank height, behaviour of the animals). But as a standard, the following strategy was used: searching for recently active dens and latrines and erecting a hide when the group is away, remaining camouflaged and silent, usually on the top of the bank. In this way, darting can be undertaken with minimal disturbance, and also facilitates individual recognition of animals by their throat marks. A priority was given to target the dominant individuals within a group, as they are likely less or unrelated (see Ribas et al. 2015); cubs were not shot due to risks of injury involved. Digital photographs/videos were taken from individuals sampled to aid individual recognition and avoid re-sampling, using handheld and Go-Pro® cameras installed close to the den/latrine whenever possible. Darts could also be shot from the boat, depending mainly on the behaviour of animals but also on the kind of motor used and water level conditions. Biopsy samples obtained were also preserved in sterile tubes containing a solution of 20% DMSO saturated with NaCl.



Figure 3.3: Biopsy dart with a tissue sample.

3.2.3 *Ethics statement*

Biopsy darting and fecal sampling, as well as the access to federal conservation areas, were authorized by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) under permit number 49273-1.

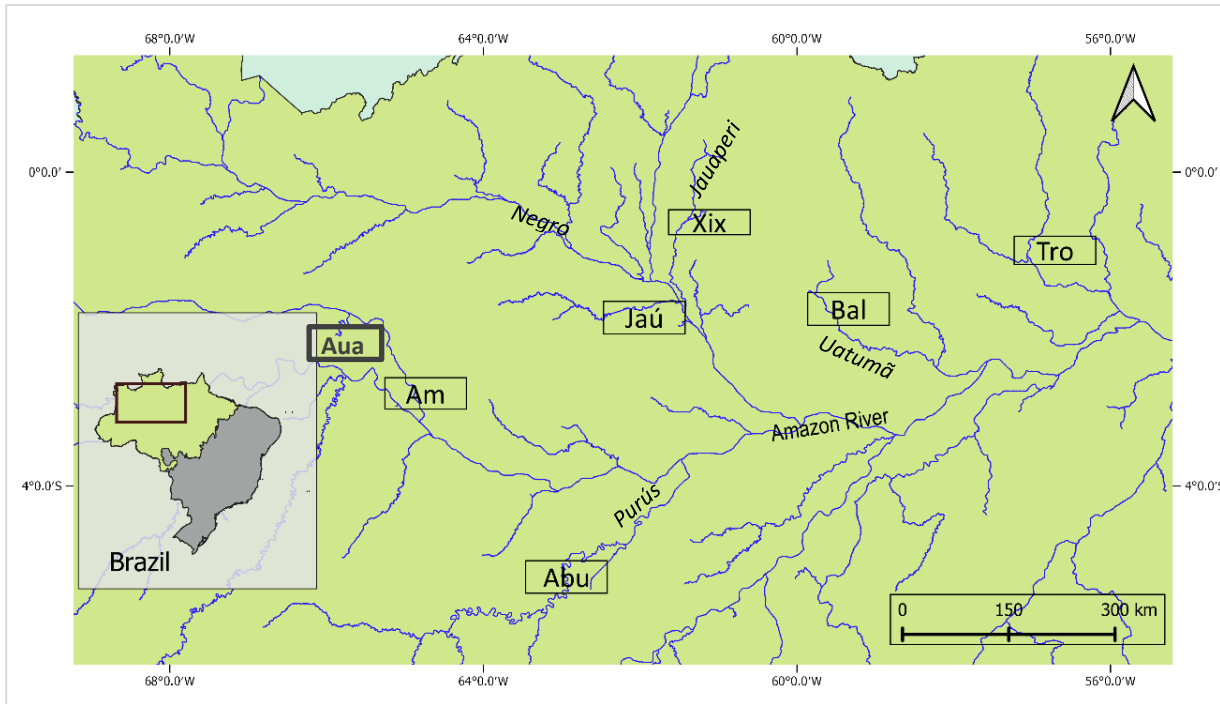


Figure 3.1: Map of sampling locations in Central Amazonia, northern Brazil. Abu=Abufari Biological Reserve; Am=Amanã Sustainable Development Reserve; Jaú=Jaú National Park; Xix=Xixuaú/Jauaperi River; Bal=Balbina Lake and Uatumã Biological Reserve; Tro= Trombetas Biological Reserve; Aua = Ati-Paraná.

3.2.4 Target loci selection

Target sequences were designed by *in silico* approaches, using the domestic ferret (*Mustela putorius furo*) as the closest relative reference annotated genome (GenBank accession no. GCA_000215625.1); and as queries, the giant otter (GenBank accession no. GCA_004024605.1) and a draft of the Neotropical otter genome (provided by collaborators - Eizirik et al.). Two approaches were followed: one aiming at neutral/anonymous regions and other aimed at genes. For the first approach, where the focus was in putative neutral regions of the genome - less likely to be under selection - two different sub-strategies were used: i) a pipeline to find anonymous loci and ii) using whole genome-alignment tools.

Anonymous loci (ALs) are a potential source for neutrality and can provide good markers for population genetics (Perez et al 2016). The python package Alfie (Costa et al. 2016) was used for finding ALs, as it is able to find ideally single-copy, neutral, and independent loci. The ferret genome was used as reference and giant otter as query in the program workflow. Locus size was set to 1kb and the distance between loci to 200kb, in order to obtain genealogically independent loci. Since there was a huge output number of ALs, a smaller subset of randomly picked sequences from the output file was used in the end.

The second approach to obtain sequences unlikely to be under selection was to align the giant otter genome against intergenic regions from the ferret genome. The alignment was performed using the module nucmer inside the MUMmer package (Kurtz et al. 2004). The output was converted to a maf format file, using the delta2maf function in Mugsy (Angiuoli et al. 2011), that could then be used as an input in the MafFilter program (Dutheil et al. 2014) with the function WindowSplit. This step split the aligned sequences into windows of 1kb, while calculating diversity metrics for each of the windows generated. The top 300 most divergent sequences (based on values of Watterson's θ) were selected. A new fasta file was then retrieved from the window alignments, using the function getfasta in Bedtools (Quinlan and Hall 2010), which contained the target sequences from giant otter genome for this first approach.

For the gene-aimed approach, the workflow suggested by Welch et al. (2014) using the SeqSelector pipeline was followed, again using the annotated ferret genome as a reference. First, potentially relevant genes were selected using information from the literature (Housley et al. 2006, 2008) and searching for gene ontology terms on Ensembl (<http://www.ensembl.org/biomart/>). The ontology terms (considering the category “biological process”) were chosen based on their possible relevance for a carnivore

mammal: lactation (GO:0007595), olfactory receptor binding (GO:0031849), sensory perception of smell (GO:0007608) and protein digestion (GO:0044256). Gene sequences were searched using the scripts SeqFinderExons (for exon sequences only) and SeqFinderPartial (where the length of returned sequences can be chosen – here, 1kb was used). Finally, ParseBLAST script was used for searching in the un-annotated giant otter genome to retrieve the sequences that corresponded to the ferret sequences.

Since fecal samples were used in this study, some further tests were performed to check if the candidate sequences would match with other organisms, i.e., potential otter's prey. They were tested against the genomes of three fish species (as fish are the main prey of both otter species in the study areas – pers. Obs.) and one rodent, as they might occasionally prey on small mammals. BLAST+ (Camacho et al. 2009) was used for that purpose, with the dc-megablast task and default algorithm settings. It was confirmed that none of the sequences had hits against the fish genomes tested (*Tilapia Oreochromis niloticus*, guppy *Poecilia reticulata*, and *Astyanax mexicanus*). When testing against the rodent (*Mus musculus*), by contrast, several sequences (mainly from exons) showed hits and were thus eliminated.

After obtaining all candidate bait sequences with the described approaches in the giant otter genome, they were mapped against the draft Neotropical otter genome in order to ensure that they would be suitable for both species. This step was done by collaborators in Brazil, who were currently working on the assembly of the Neotropical otter genome. In the end, the two final sets of candidate sequences (from giant and Neotropical otters) were compared through BLAST+, so the best ones could be selected based on their divergence. A value of 3% difference in the percent of identity was used as cut-off to eliminate the most similar sequences. If they were identical or very similar, it means they could be very conserved, and therefore would not be good sources for

population genetic markers such as SNPs. The result was a set of 451 candidate sequences (Appendix 3.1) for each species, which were sent to Arbor Biosciences™ for producing a myBaits® custom target enrichment kit. After further filtering and screening from the manufacturers, the kit ended up with 19,558 80nt baits (at 3x tilling density) from 98.3% of the submitted target loci.

It is important to account for the fact that there was no a priori information on possible variable loci (i.e., that would contain SNPs). Therefore, it was necessary to target a large number of loci through the target capture approach – even though this could lead to a reduced number of reads per locus captured in each sample (due to poor DNA quality and quantity), that would probably also vary among individuals.

3.2.5 DNA extraction and library preparation

Total DNA was extracted from 182 giant otter and 189 Neotropical otter samples (Table 3.3). A standard phenol/chloroform protocol was used (Hoelzel 1998). Libraries were prepared using the single-tube method developed by Carøe et al. (2017) with the further improvements described in Mak et al. (2017). The only difference from the original protocols was that in the present study, instead of using dual-indexed adapters, a single-index system was used together with 8-bp barcoded P5 (3') adapters.

Table 3.3: Number of collected samples per area for each species.

	Giant Otter	Neotropical Otter
Balbina	34	77
Trombetas	31	0
Xixuau	25	12
Abufari	14	0
Jaú	25	76
Amanã	40	24
Guyana	10	0

Indexing PCR was done by amplifying 23 µL of adapter-ligated libraries in a 50µL reaction with 0.5µL Phusion Hot Start II Polymerase (Thermo Fisher), 10µL 5X Phusion HF Buffer, 1 µL 10mM DNTPs, 1µL 10 µM P5 adapter universal primer, 1 µL 10 µM P7 adapter indexing primer and 13.5 µL of Nuclease-free water. Cycling conditions were: denaturation at 98°C for 45''; *N* cycles of 98°C for 20'', 60°C for 30'' and 72°C for 30''; and a final extension at 72°C for 5', holding at 4°C upon ending. The number of cycles necessary was estimated beforehand by qPCR for each library, following the library preparation protocol. After indexing, PCR products were purified using SPRI-beads (SpeedBeads™, GE HealthCare), eluted in 25-30 µL of TET buffer and quantified by a Qubit fluorometer (Invitrogen) using a high sensitivity kit. A few libraries were selected to be screened on a 2200 TapeStation (Agilent) with a High Sensitivity reagent kit, so average size of library fragments (as well as their concentrations) could be estimated by comparison with the control DNA ladder range. Indexed libraries were stored at -20°C until target capture was performed.

3.2.6 Hybridization Capture

The recommendations for enriching degraded DNA libraries in the myBaits™ v.4 manufacturer protocol were followed, with total hybridization time >36 hours at a constant temperature of 60°C. Since the libraries were not pooled and hybridization was performed in each one individually, bait solutions were diluted to accommodate a large number of reactions per kit. In a pilot trial, a dilution of 1:8 was used, but since it yielded very low concentrations of DNA even after PCR, for the following experiments a dilution of 1:7 was used. For the final amplification, bead-bound enriched libraries were incubated at 95°C for 5 minutes and then pelleted on a magnetic plate to collect the supernatant. Then, 15 µL were taken for the final PCR with 0.5µL Phusion Hot Start II Polymerase (Thermo Fisher), 10µL 5X Phusion HF Buffer, 1 µL 10mM DNTPs, 2.5µL of each adapter primer and 13.5 µL of Nuclease-free water. Cycling conditions were: 98°C for 2'; 8-14 cycles of 98°C for 20'', 60°C for 30'' and 72°C for 30''; and a final extension at 72°C for 5', holding at 8°C upon ending. The number of cycles used had to be adjusted. Ideally, one should use as few cycles as possible and use the same number for all samples (e.g., 12-14), but with fewer than 16 cycles we obtained rather low final concentrations, so it was decided to use between 17-18 cycles for most of the samples. Final reaction clean-up was done with SPRI-beads.

Finally, quality controls were performed to check for appropriate size and quantity of material. Quantitative real-time PCR (qPCR) was used to quantify each final library using the KAPA SYBR® FAST kit and Illumina DNA standards (KAPA Biosystems) with manufacturer's protocol recommendations. Final libraries were normalized to a concentration of 2nM and mixed in equimolar pools. The material was

submitted to the DBS Genomics facility at Durham University and sequenced in a 125-bp paired-end run in the Illumina HiSeq 2500 platform.

3.2.7 Mitochondrial DNA Sequencing and Analyses

In order to gain additional insight into diversity and structure between populations, a portion of 516 bp of the mitochondrial control region (CR) (including the 5' hypervariable region and excluding the Carnivora heteroplasmic region, described In Hoelzel et al. 1994) was amplified from 21 Neotropical otters and 25 giant otters (see Results), using the primers MTLPRO2 and CCR-DR1 designed by Tchaicka et al. (2007). As the DNA was frequently degraded and fragmented, leading to difficulties in DNA amplification, an option was made to use also one of the internal primer pairs for the CR (Trinca et al. 2007) to amplify a shorter (220bp) fragment at the 5' end of the same region.

PCR reactions were carried out in 20 μ L, containing 1 μ L of diluted DNA, 0.2 μ M of each primer pair, 15 μ g BSA, 200 μ M dNTPs, 2 μ L of 10X Standard *Taq* Reaction Buffer and 0.5 units of *Taq* DNA polymerase (New England Biolabs Inc.) and nuclease-free water to complete the total volume. The following program was used in a thermocycler: initial denaturation at 94°C for 1'; 10 cycles of touchdown at 94°C for 45'', 55–45°C for 45'' and 72°C for 1.5'; and 35 cycles of 94°C for 45'', 50°C for 45'', 72°C for 1.5' and a final extension step at 72 °C for 5'. PCR products were checked in a 1.5% agarose gel stained with ethidium bromide, and cleaned up with ExoSAP- IT® (Affymetrix). Sequencing was done in the DBS genomics facility at Durham University, in an Applied Biosystems 3730 automated sequencer. Sequences were inspected, manually edited, and aligned using the MUSCLE algorithm implemented in Seaview 5.0 (Gouy & Gascuel 2010).

The phylogenetic relationships between samples based on mtDNA were inferred with a Bayesian approach in MrBayes v.3 (Huelsenbeck and Ronquist 2001), considering the GTR+G nucleotide substitution model, over 1 million generations. Optimal evolutionary models were assessed in SMS (Lefort et al. 2017) based on the Akaike information criterion. The southern river otter, *Lontra provocax*, was included as an out-group (Accession number DQ368686). Haplotypes were identified in DNAsp v. 6 (Rozas et al. 2017) and networks were calculated using the Median-joining algorithm implemented in Network 4.5.1.0 (<http://www.fluxus-engineering.com>).

To increase the scope of the analysis and allow for a broader phylogeographic comparison, analyses were also conducted including sequences retrieved from Genbank. For giant otters, 26 sequences were added from the studies of Garcia et al. (2007 - accession numbers: EF488532.1-561.1) and Pickles et al. (2011 – accession numbers JN252257-58 and JN252261), resulting in a dataset of 51 sequences (25 from this study and 26 from the literature – see Fig. 3.4 and Table 3.4). For the Neotropical otters, extra Genbank sequences from Amazonia were found in the study by Trinca et al. 2012 (accession numbers JQ038804–JQ038869). Two additional separate analyses were conducted for this species: one including all samples and analysing only the shorter (220bp) fragment; and a second analysis including only samples that amplified the whole fragment (N=12), allowing for a better comparison with the full sequences available in Genbank. The first included, therefore, 32 sequences (22 from this study and 10 from Trinca et al. 2012) and the second had a total set of 22 sequences (12 from this study and 10 from Trinca et al. 2012 – Fig. 3.5 and Table 3.5).

In order to assess a possible differentiation between populations separated by major rivers, a broader categorical division was also considered, taking into account well-known Amazonian areas of vertebrate endemism (AoE), which are defined by limits

of main rivers (see Silva et al. 2005, Ribas et al. 2012). Thus, individuals from locations north of the Amazon River and east of Negro River (see Fig. 3.1) were grouped together as pertaining to the “Guyana” AoE; and individuals from other areas of endemism to the west of Negro/south Amazon were considered as a single group (hereafter called Southern group) (see Fig. 3.1 and Appendix 3.2). To test this differentiation, pairwise FST was computed in Arlequin v. 3.5.2.2 (Excoffier & Lischer 2010), and its significance was tested by 10,000 permutations. Arlequin was also used to compute neutrality tests of Tajima’s D and Fu’s F.

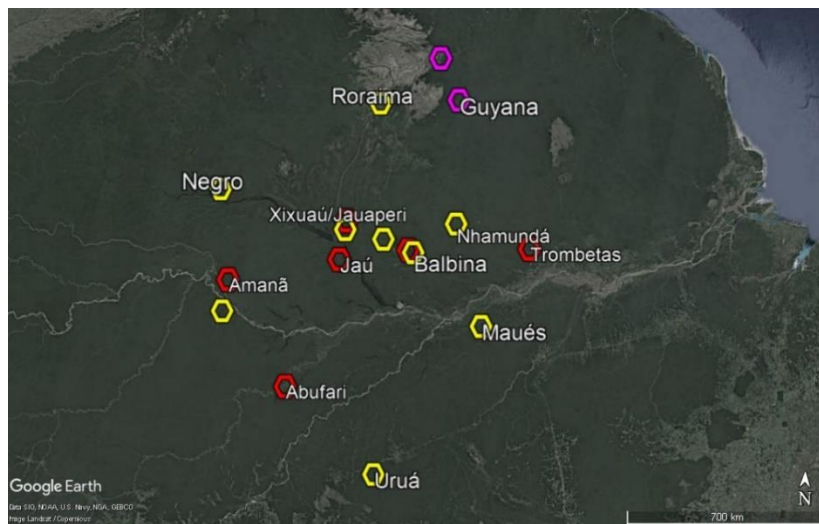


Figure 3.4: Giant otter mitochondrial DNA sample locations from this study (in red), from Pickles et al. 2011 (in pink) and from Garcia et al. 2007 (in yellow).



Figure 3.5: Neotropical otter mitochondrial DNA sample locations from this study (yellow stars) and from Trinca et al. 2012 (orange stars).

3.2.8 Bioinformatics pre-processing of NGS data

Raw sequencing data was converted to Fastq format and demultiplexed according to their P7 index using the bcl2fastq software by Illumina. A further demultiplex step was necessary, in order to split individual samples according to their in-read P5 barcodes. For this, we used the process_shortreads script from Stacks v.2.4 (Catchen et al. 2013). A quality check of the reads was done with FastQC software (Andrews 2010). Then, reads were quality-trimmed (keeping only reads with a minimum length of 35 bases and quality score > 20) and their adapter sequences removed, using the programs Trimmomatic v.0.39 (Bolger et al. 2014) and Cutadapt v.3.3 (Martin, 2011).

Paired reads were aligned to the giant otter reference genome using bwa mem algorithm (Li 2013). Resulting alignment files were converted to bam format, sorted, indexed, and had their reads from target regions extracted with Samtools (v.1.9; Li et al. 2009).

3.2.9 Population genetic analyses

Since most of the samples used in this study were scats that were exposed to high humidity, heat and sunlight, they presented low-quality, degraded DNA; and as expected in such cases (see Yao et al. 2020), their sequencing results had low overall depth, while only a minority of samples, mostly the ones derived from tissue, had a better sequencing depth. With such disparity, particular attention should be given to the choice of methods for finding variant sites necessary for downstream population analyses. When a limited number of reads map to a region, there is an increased chance that all of them are from the same chromosome, therefore not accurately representing the genotype of a diploid individual; this introduces uncertainty and bias in genotype and variant calling (Nielsen et al. 2011).

An alternative to genotype calling is the use of probabilistic or “genotype-free” methods (Warmuth & Ellegren 2018) that call genotype likelihoods (GLs) based, for instance, on sequence reads quality scores and allele frequency priors (Li et al. 2009, Li 2011). Here, both GL and “hard” genotype call methods were used, with resulting data being applied in different analyses. SNPs identified from genotype calls were also preferred in particular for estimates relying on allele frequencies such as F_{ST} , as in this case allele frequencies can be assessed directly from the data (rather than estimated).

The GL-based approach for SNP discovery was performed in ANGSD v. 0.93 (Korneliussen et al. 2014) following the pipeline by Yao et al. (2020), computing GLs under the SAMtools model (option `-GL 1` in ANGSD). Only samples with more than 100,000 mapped reads were included; furthermore, bases with quality scores below 20 and reads with mapping quality lower than 30 were filtered out. Major and minor alleles were inferred from GLs (`-doMajorMinor 1`), and their frequencies were estimated (-

doMaf 2). For SNP sites identification, a p-value of $1e-5$ was set to keep only polymorphic sites (sites with p-values below that threshold were discarded).

Genotypes were called using a conventional workflow with SAMtools mpileup (Li et al. 2009) and VCFtools (Danecek et al. 2011) to determine the SNPs, again filtering out sites with quality score below 20, reads with mapping quality lower than 30 and coverage depth below 3.

The following analyses were performed with SNPs obtained with ANGSD (GL approach): admixture and principal component analyses, carried out using NGSAdmix to estimate ancestry proportions (Skotte et al. 2013) and PCAngsd (Meisner & Albrechtsen 2018). NGSAdmix analyses were performed for a range of K values (2-8) with 10 replicates each. Then, optimal K values for each species were inferred by Evanno's Δk method (Evanno et al. 2005) implemented in CLUMPAK (Kopelman et al. 2015). In addition, folded site frequency spectrums (SFS) were computed for each population containing a minimum of eight individuals with realSFS (Nielsen et al. 2012). Then, Watterson's theta and Tajima's D were computed using the estimated SFSs, with the function thetaStats in realSFS (Nielsen et al. 2012).

Using the SNPs from called genotypes, the following further analyses were carried out. A Discriminant analysis of principal components (DAPC – Jombart et al. 2010) was computed in the R package adegenet (Jombart & Ahmed 2011) to investigate population structure. DAPC is a multivariate analysis, able to infer the number of population clusters by sequential K-means and model selection. The results obtained with this method were compared with the ones obtained by PCAngsd. After inferring the number of population clusters, re-assignment of the individuals according to the prior knowledge of sampling locations was performed to assess how well they can be

discriminated among groups. It is important, though, to estimate the optimum number of principal components (PCs) to be used in order to avoid over-fitting of the data. This was achieved with the function `optim.a.score` in `adegenet`, which returns the optimum number of PCs to be used for each dataset (18 PCs - Neotropical; 20 PCs -Giant). A factorial correspondence analysis (FCA) was performed in `GENETIX v.4.05` (Belkhir et al., 2000) to provide a further comparative ordination analysis. This is an exploratory method that reduces high-dimensional data sets into a few independent factors, revealing principal factorial axes; this way, results can be graphically represented in an orthogonal system where observations and variables are displayed on a reduced number of factors (Tekaia et al. 2016).

`Arlequin` (v. 3.5.2.2; Excoffier & Lischer 2010) was used to calculate heterozygosity (a measure of genetic variability) and estimate deviations from Hardy-Weinberg equilibrium expectations. `Arlequin` was also used to calculate summary statistics such as F_{ST} (the fixation index, a comparative proportion of the genetic variation across different populations) on putative population samples when the sample size was at least $N=7$. Individuals with more than 50% of missing data were excluded from F_{ST} estimations. Significance of F_{ST} was tested by permuting individuals between the populations, according to the program's default settings.

3.3 Results

Out of all 371 samples, 256 sequencing libraries passed quality controls for being sequenced, but sequencing results of 66% of the samples were discarded due to poor quality data and/or low number of reads with few mapping to the reference (a general minimum threshold between 500-700,000 reads was observed), which did not allow for

SNP calling with either approaches (GL or conventional). Of the remaining 87 samples with functional data, 55 were from giant; and 32 from Neotropical otters (see Table 3.4). Regarding mtDNA, there were attempts with 207 giant otter and 168 Neotropical otter samples, with success rates of only 12% (21 samples) and 13% (25 samples) respectively (Table 2). Further PCR effort was planned to increase this sample size, but due to time constraints worsened by the Covid-19 pandemic, it was not possible to perform additional lab work. Tables 3.4 and 3.5 summarize the sample sets used in mtDNA analyses (including samples from the Genbank dataset).

Table 3.4: Number of sequenced samples with usable data per species and geographical location. NGS=Next generation sequencing (SNP markers); mtDNA=mitochondrial DNA sequencing

Location	Giant Otter		Neotropical Otter	
	NGS	mtDNA	NGS	mtDNA
Abufari	8	2	-	-
Amanã	9	3	7	7
Ati-Paraná	-	-	1	1
Balbina	8	11	15	9
Guyana	5	-	-	-
Jaú	10	4	9	4
Trombetas	9	-	-	-
Xixuaú	6	5	-	-

Table 3.5: Neotropical otter samples included in the mtDNA analyses. Sample IDs in bold were also sequenced by NGS.

Sample ID	Geographic region	Source
25	Amanã	This study
26	Amanã	This study
LL107Uru	Amanã	This study
LL102Ub	Amanã	This study
LL103Ju	Amanã	This study
LL103Ub	Amanã	This study
LL105	Amanã	This study
27	Ati-Parana	This study
LL94b	Balbina	This study
LL93	Balbina	This study
LL64b	Balbina	This study
LL85	Balbina	This study
LL77	Balbina	This study
LL83	Balbina	This study
LL61b	Balbina	This study
LL70muc	Balbina	This study
LL62	Balbina	This study
JL41	Jaú	This study
JL15	Jaú	This study
JL29d	Jaú	This study
JL34	Jaú	This study
bLlo53	Jaú*	Trinca et al. 2012
bLlo54	Roraima state (Brazil)	Trinca et al. 2012
bLlo68	Kagka River (Peru)	Trinca et al. 2012
bLlo70	Careiro	Trinca et al. 2012
bLlo71	Jaú*	Trinca et al. 2012
bLlo72	Careiro	Trinca et al. 2012
bLlo74	Roraima state (Brazil)	Trinca et al. 2012
bLlo66	Cayenne region (French Guiana)	Trinca et al. 2013
bLlo22	Cayenne region (French Guiana)	Trinca et al. 2014
bLlo25	Cayenne region (French Guiana)	Trinca et al. 2015

Table 3.6: Giant otter samples included in the mtDNA analyses. Sample IDs in bold were also sequenced by NGS.

Sample ID	Geographic region	Source
La3B	Abufari	This study
La4	Abufari	This study
n4	Amanã	This study
Ubz2	Amanã	This study
n5	Amanã	This study
JP106Y	Jaú	This study
JP109Z	Jaú	This study
JP109FF	Jaú	This study
JP107c	Jaú	This study
n9	Xixuaú (Jauaperi River)	This study
n10	Xixuaú (Jauaperi River)	This study
n11	Xixuaú (Jauaperi River)	This study
n12	Xixuaú (Jauaperi River)	This study
n13	Xixuaú (Jauaperi River)	This study
n6	Balbina	This study
n15	Balbina	This study
n21	Balbina	This study
n24	Balbina	This study
Pb27A	Balbina	This study
Pb10F	Balbina	This study
Pb13c	Balbina	This study
Pb14	Balbina	This study
Pb26c	Balbina	This study
Pb24c	Balbina	This study
Pb10b	Balbina	This study
Expedition 2009 1.06	River Rupununi (Guyana)	Pickles et al. 2011
Expedition 2009 1.02	River Rewa (Guyana)	Pickles et al. 2011
Expedition 2009 1.03	River Rewa (Guyana)	Pickles et al. 2011
Pb05	Roraima, Brazil	Garcia et al. 2007
Pb06	Roraima, Brazil	Garcia et al. 2007
Pb11	Roraima, Brazil	Garcia et al. 2007
Pb07	Jauaperi River	Garcia et al. 2007
Pb19	Jauaperi River	Garcia et al. 2007
Pb10	Nhamundá River, Brazil	Garcia et al. 2007
Pb50	Negro River, Brazil	Garcia et al. 2007
Pb56	Amazonas State, Brazil	Garcia et al. 2007
Pb53	Abonari River, Amazonas State	Garcia et al. 2007
Pb01	Negro River, Amazonas State	Garcia et al. 2007
Pb02	Negro River, Amazonas State	Garcia et al. 2007
Pb13	Negro River, Amazonas State	Garcia et al. 2007
Pb16	Negro River, Amazonas State	Garcia et al. 2007

3.3.1 Population Genetic Structure

A total of 1,280 and 469 SNPs were identified by GLs in ANGSD for Neotropical and giant otters, respectively. Genotype calls performed with Samtools resulted in a smaller number of SNPs discovered: 135 for giant and 169 for Neotropical otters.

The pairwise F_{ST} estimated between geographic locations with ≥ 7 individuals for giant otters are shown in Table 3.7, although none of them were significant. For Neotropical otters, only Jaú and Balbina could be compared, with $F_{ST} = 0.0046$; but again, this value wasn't statistically significant.

Table 3.7: Pairwise F_{ST} values between giant otter populations based on SNPs loci.

	BalXix	Trom	Ama	Jau
BalXix	0			
Trom	0.0149	0		
Ama	-0.0342	-0.0702	0	
Jau	0.0641	-0.0363	-0.0367	0

PCAs performed for both species with the GL dataset (Fig. 3.6) indicate some degree of structuring, slightly more pronounced in giant than in Neotropical otters. In the former (Fig. 3.6a), it is possible to identify three distinguishable groups for giant otters, one containing all individuals from Abufari, the second containing most individuals from Balbina and Xixuau and the third with most individuals from Trombetas, while individuals from other locations do not seem to cluster together. Balbina and Xixuau are neighbouring locations, while Abufari and Trombetas are more distant in relation to all others (Fig. 3.1). For Neotropicals (Fig. 3.6b), only the individuals from Balbina are more clearly separated from the other two populations (Amanã and Jaú).

The admixture results for giant otters (Fig. 3.7) are consistent with PCA results. The optimal K value estimated was 3; Trombetas and Abufari form their own distinct clusters, and Balbina and Xixuaú integrate a third cluster. The remaining groups (Amanã, Jaú and Guyana) show a higher degree of admixture. For Neotropical otters (Fig. 3.8), admixture results also support the pattern observed in the PCA. There were two main clusters, one formed by individuals from Balbina and the other by Jaú and Amanã with shared ancestry coefficients.

When location identity of individuals was included as a factor (Fig. 3.9 - top), DAPC was reasonably able to discriminate geographical populations. On the other hand, without a priori assignment of population groups (Fig. 3.9 - bottom), the clusters found by DAPC did not reflect the same previous patterns detected with PCAngsd and NGSAdmix for either species. According to DAPC assignments, giant otters show more admixed individuals between the populations Balbina, Amanã and Xixuaú.

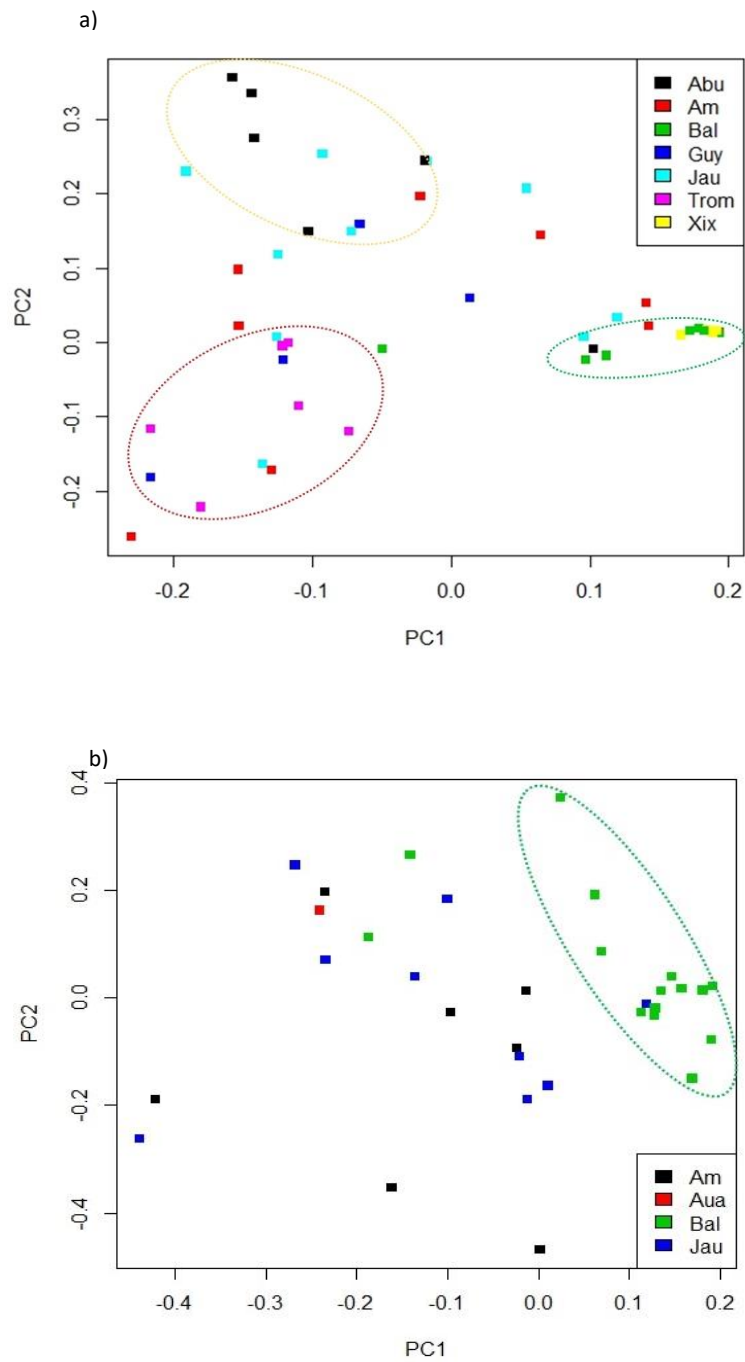


Figure 3.6: Principal component analysis (PCA) plots generated with PCAngsd covariance matrixes. a) Giant otters (PC1=66.5% of the variation, PC2=16.7%); b) Neotropical otters (PC1=33%, PC2=4.5%).

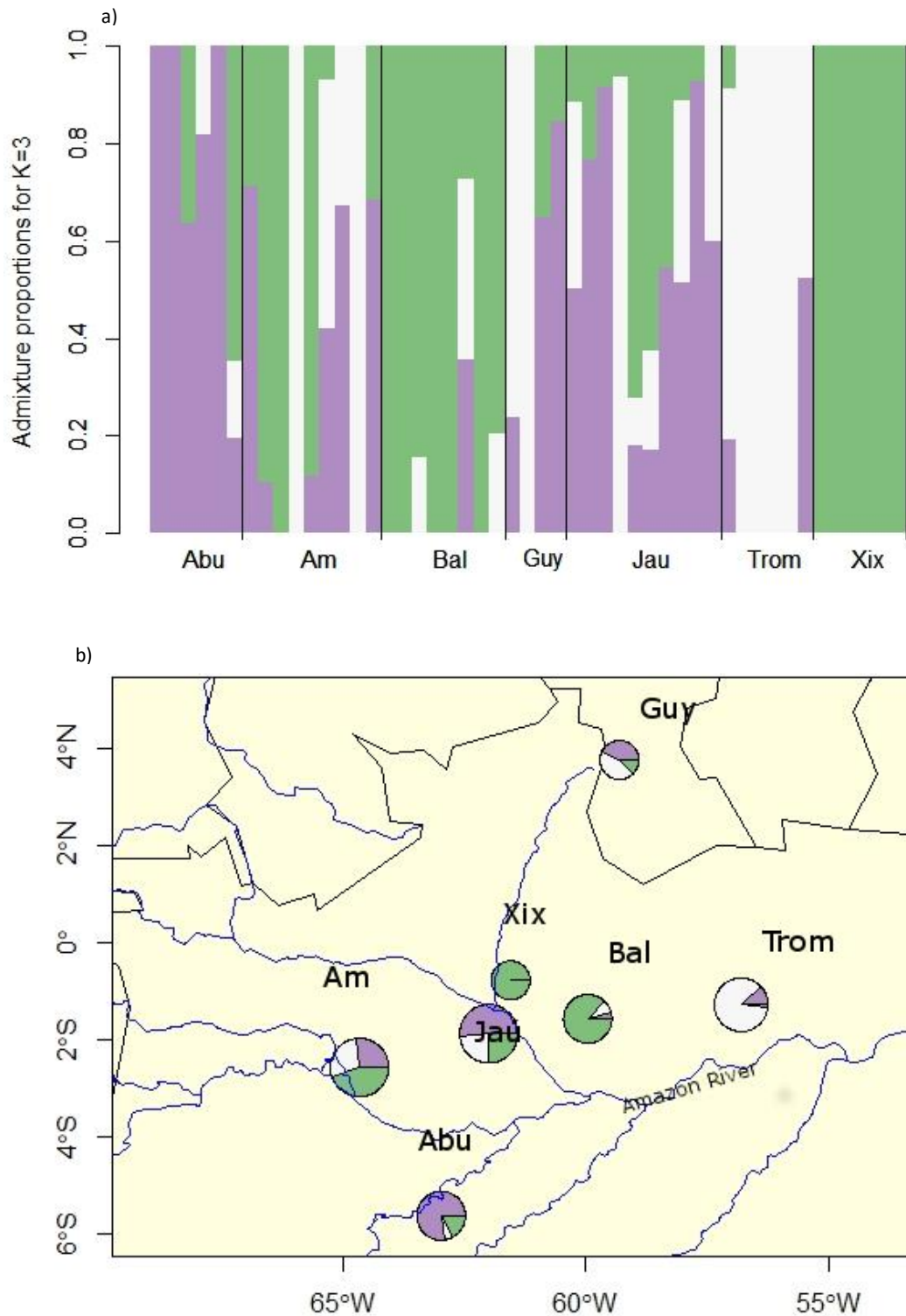


Figure 3.7: Admixture in giant otter populations estimated in NGSAdmix. a) Bar plot of admixture proportions, where each bar represents one individual. b) Map illustrating total admixture proportions in each location. Size of the pie charts is proportional to the sample size in each population. (Only main rivers are shown)

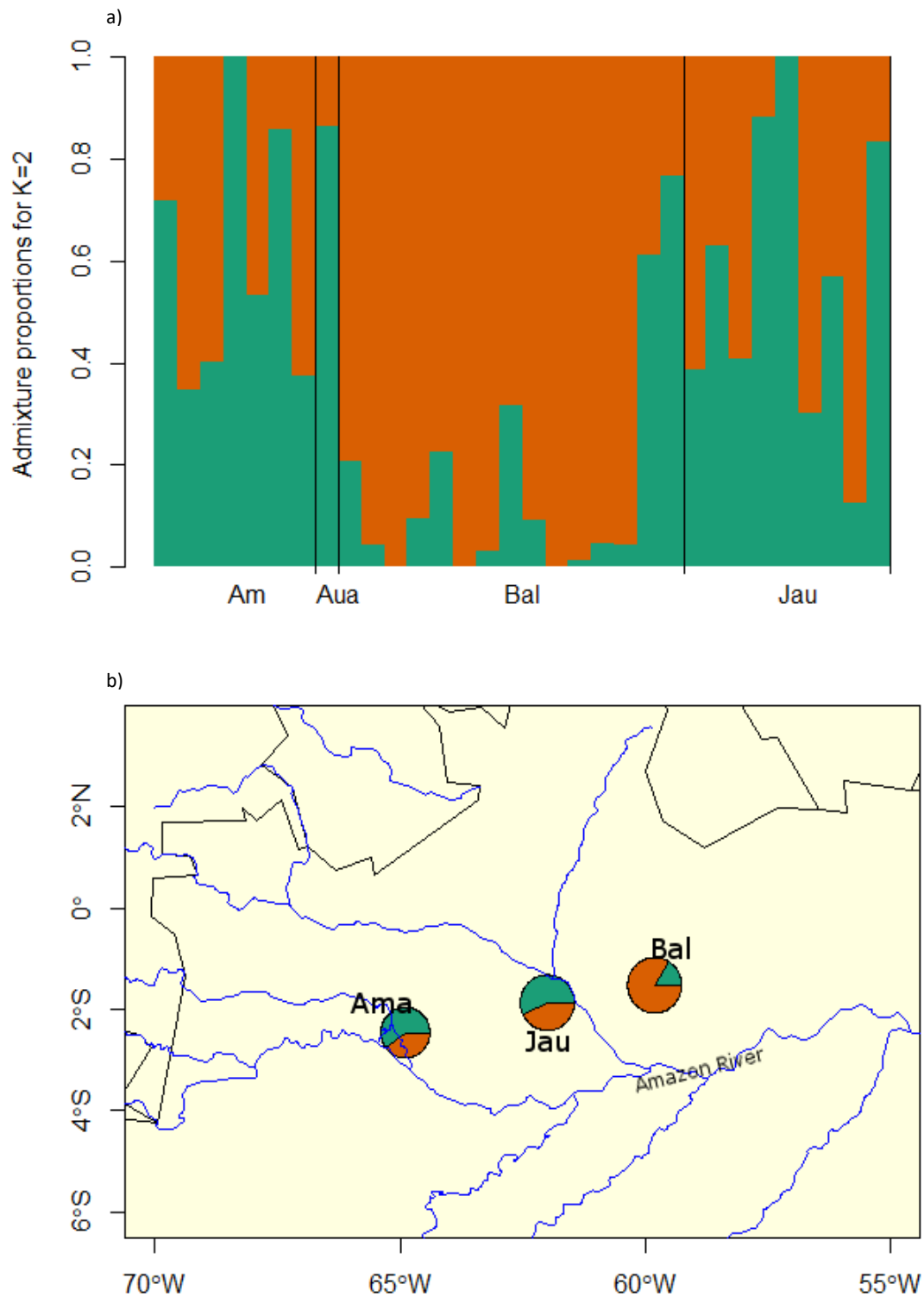


Figure 3.8: Admixture in Neotropical otter populations estimated in NGSAdmix. a) Bar plot of admixture proportions, where each bar represents one individual. b) Map illustrating total admixture proportions in each location (excluding Aua, which was represented by only one individual). Size of the pie charts is proportional to the sample size in each population. (Only main rivers are shown)

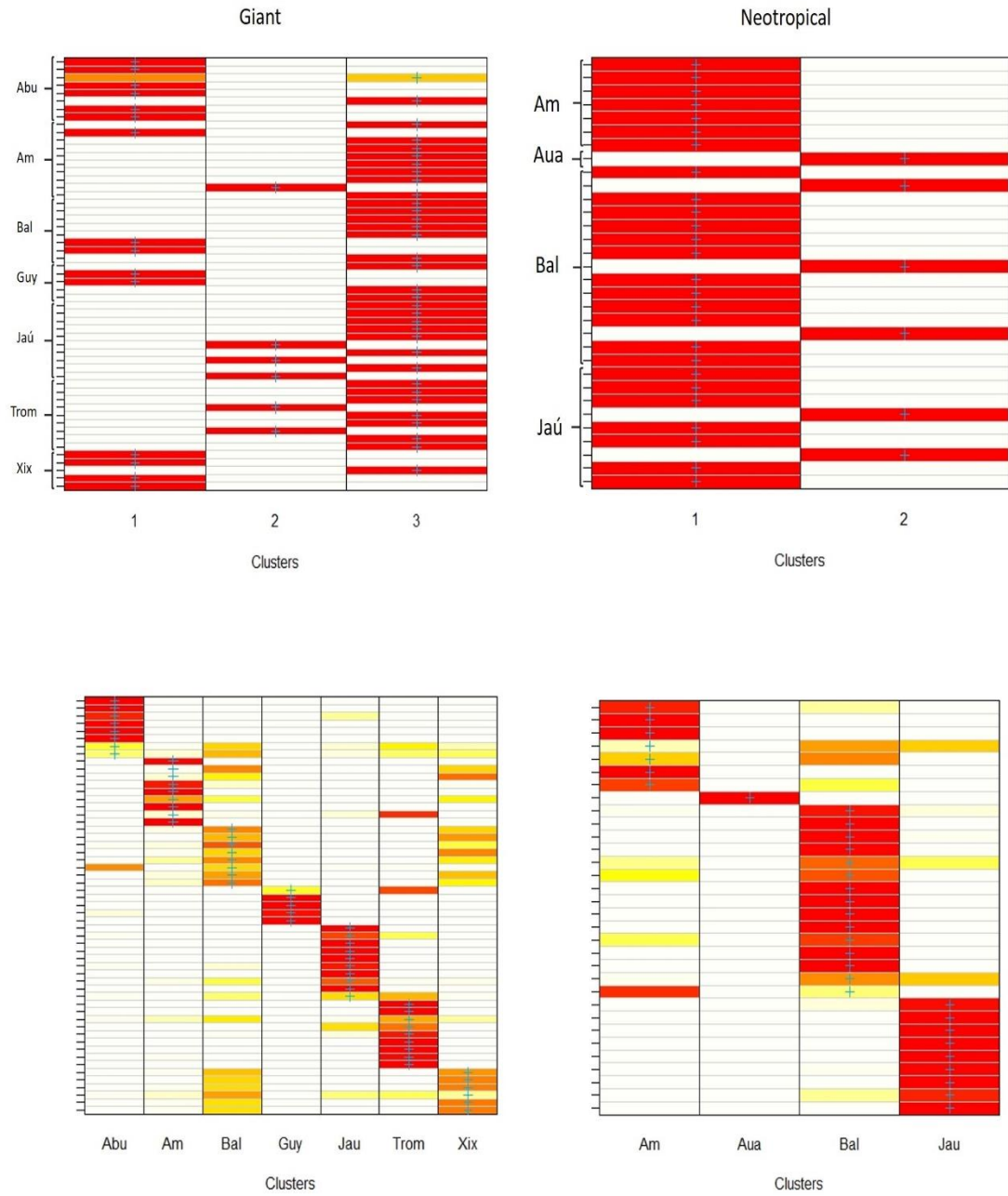


Figure 3.9: Discriminant analysis of principal components, with Giant otter plots on the left and Neotropical otter on the right. Top: clusters assigned with the function `find.clusters` in `adegenet`; Bottom: clusters assigned considering a priori knowledge of locations. Each bar represents one individual. Darker colours indicate stronger assignment of individuals to clusters.

Results of the FCAs based on SNP genotypes are shown in Figs. 3.10 and 3.11.

For giant otters, 4 factors were supported in the analysis and after attempting all combinations between them, the most informative was with factors 2 vs 3; in the plot (Fig. 3.10), the horizontal axis (factor 2) accounts for 24.01 % of the total variance and the vertical axis (factor 3), 15.65 %. The clusters inferred with previous methods are also differentiated by FCA, and for better visualization Balbina and Xixuaú were already grouped as a single class in the plot. The only major difference is that, in this case, Jaú individuals were more prominently differentiated from others while in PCA, for instance, they were more scattered over the plot. Plots showing the combinations of factors 1vs 2 and 1 vs 3 were included in Appendix 3.3.

For Neotropical otters, the analysis only supported 2 factors, so factor 1 was plotted against factor 2. In Fig. 3.11, factor 1 accounts for 54.17% of the variation while factor 2 accounts for 45.83% in individual genotypes. The FCA analysis was again capable of identifying similar patterns as other methods, showing that Balbina individuals are differentiated from Jaú and Amanã, which are grouped more closely. In this analysis, however, those two groups can be better distinguished than in, for instance, the Admixture analysis.

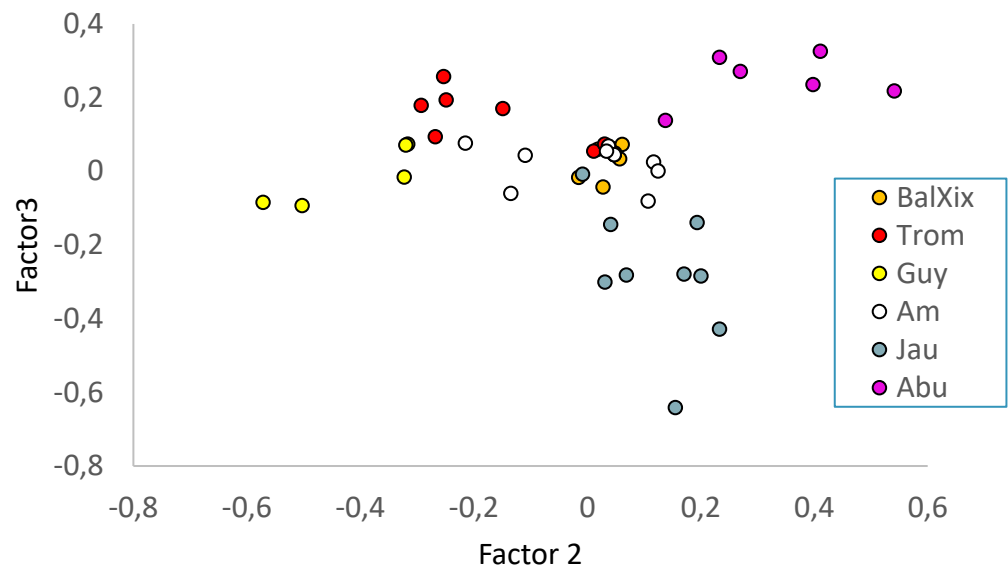


Figure 3.10: FCA plot from GENETIX, using SNPs from giant otter called genotypes.

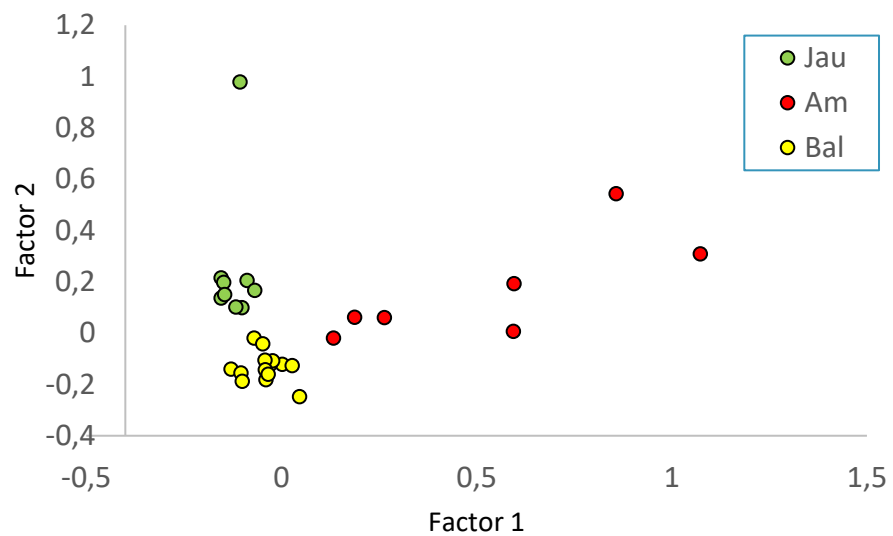


Figure 3.11: FCA plot from GENETIX, using SNPs from Neotropical otter called genotypes.

3.3.2 Genetic Diversity

Considering the admixture results and geographical proximity (with hydrographic connection), individuals from the adjacent locations Balbina and Xixuaú were merged into a single group for SNP allele frequency-based analyses and diversity metrics calculations, to increase the number of individuals in the same population (in particular due to small sample size of Xixuaú). Individuals from Guyana were excluded due to the smallest sample size (N=5).

All SNP loci were in Hardy-Weinberg equilibrium. Comparing giant and Neotropical diversity metrics based on SNPs (Table 3.8), results of the latter suggest a higher genetic diversity for this species in the populations studied. Heterozygosity levels, for instance, were generally low for giant otters compared to Neotropical otters. The negative Tajima's D values suggest a possible excess of rare alleles in the dataset, but the approach used in realSFS does not test for significance of this metric.

Table 3.8: Median Tajima's D, Watterson's theta (θ), average observed (H_o) and expected (H_e) heterozygosity based on SNP loci across giant (Pb) and Neotropical (Ll) otter populations.

Species / Population	N	Tajima's D	θ	H_o	H_e
Pb Ama	10	-1.71	0.34	0.125	0.200
Pb Bal-Xix	13	-0.04	0.06	0.097	0.106
Pb Jau	10	-1.59	0.25	0.294	0.260
Pb Abu	8	-1.37	0.34	0.227	0.305
Pb Trom	9	-1.23	0.30	0.262	0.236
Ll Ama	7	0.009	0.84	0.433	0.371
Ll Bal	15	-2.04	0.54	0.317	0.248
Ll Jau	9	-0.7	0.46	0.389	0.309

3.3.3 Mitochondrial DNA Analyses

Since not all the samples amplified the full CR fragment intended, haplotype identification was based on regions of 132 and 139 bp (final length of the 220 bp sequence after excluding sites with gaps or missing data) obtained with the internal primer pair and shared among all sequenced individuals of giant and Neotropical otters, respectively.

The Bayesian trees generated with mtDNA data from this study's samples (Figs. 3.12 and 3.13) give some further support to population structure findings based on SNPs. In the giant otter tree (Fig. 3.12), it is noticeable that most individuals from Balbina are grouped together, showing a stronger overall differentiation for this population. In Fig. 3.13, similar results are observed for Neotropical otter; although not showing a strong structure for any of the groups, a few clusters of individuals from the same locations (Amanã and Jaú) with well-supported branch values can be observed.

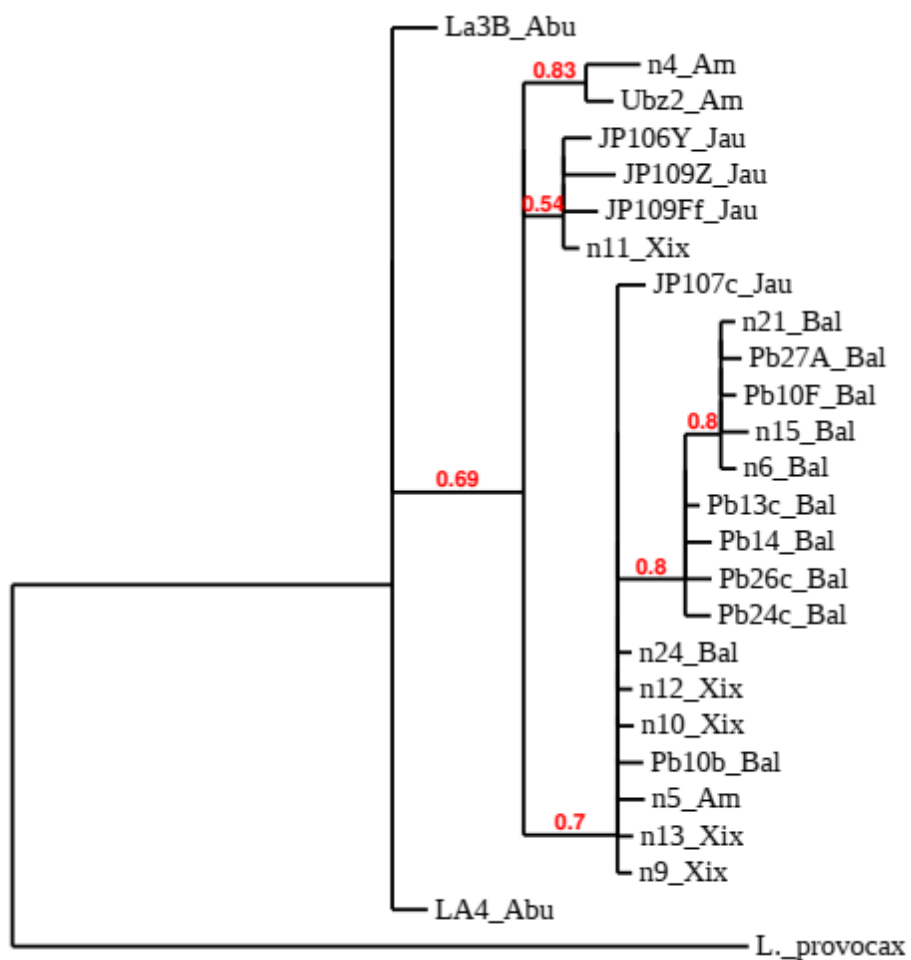


Figure 3.12: Bayesian tree based on partial sequences of mitochondrial control region for giant otter individuals. Branch support values are shown in red.

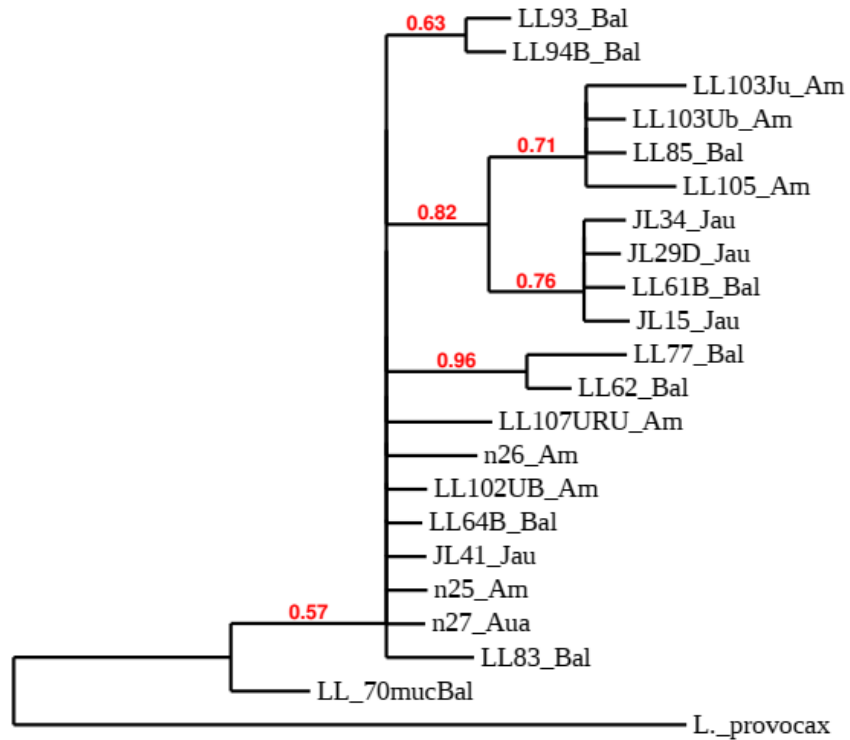


Figure 3.13: Bayesian tree based on partial sequences of mitochondrial control region for Neotropical otter individuals. Branch support values are shown in red.

In giant otters, 6 different haplotypes were identified from this study's samples, based on 7 variable sites. Mean haplotype diversity (H_d) was 0.723 ± 0.07 and nucleotide diversity π was 0.012 ± 0.002 . Haplotype 2 was the most frequent (Fig. 3.14), being found in four different locations (Balbina, Amanã, Xixuaú and Jaú). The Abufari samples both showed distinct haplotypes, while the remaining locations have shared at least one haplotype in common.

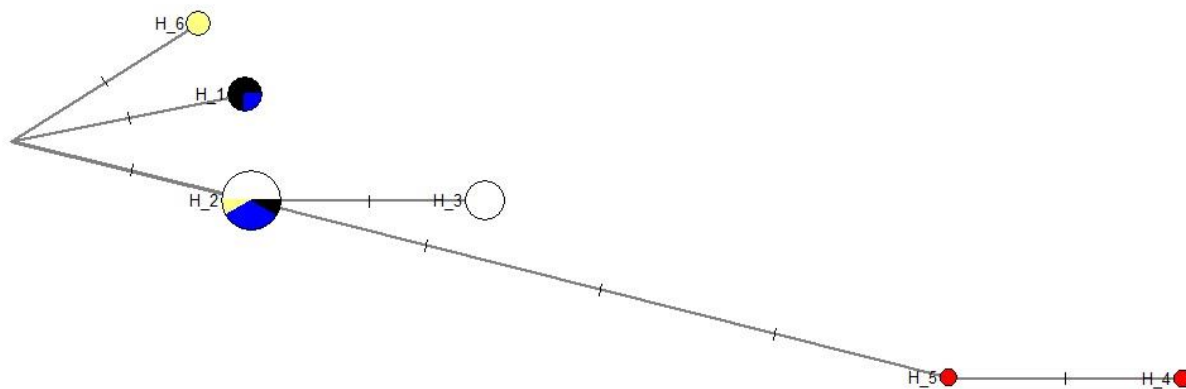


Figure 3.14: Median-joining network of giant otter haplotypes considering only samples from this study. Each circle corresponds to one haplotype, and circle sizes correspond to haplotype frequencies within the whole sample. The hatch marks on network lines indicate numbers of mutations. Colours within the circles denote the different geographic locations, as following: yellow – Amanã; black – Jaú; blue – Xixuaú; white – Balbina; and red – Abufari.

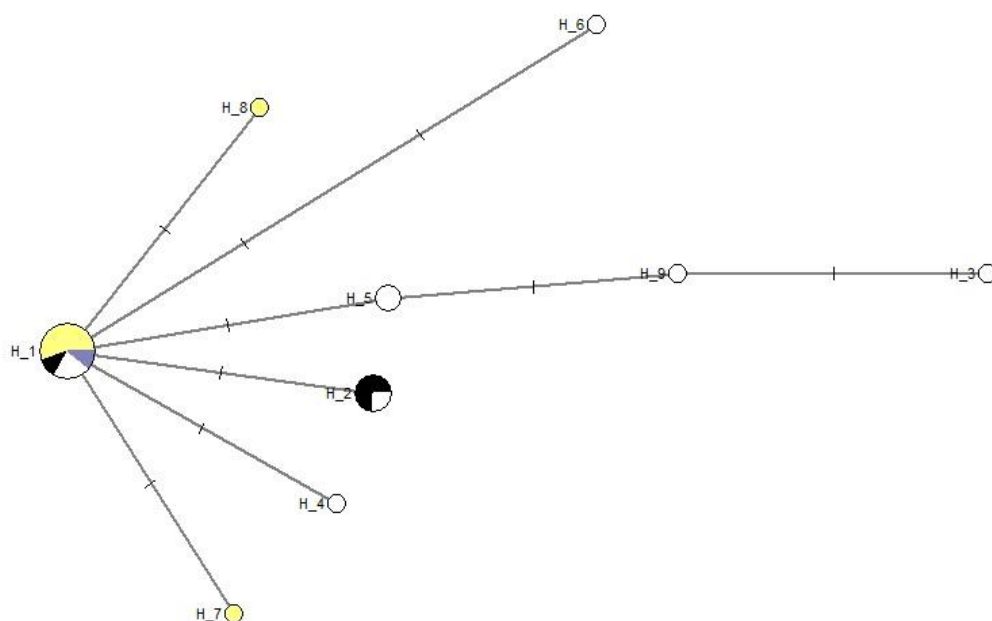
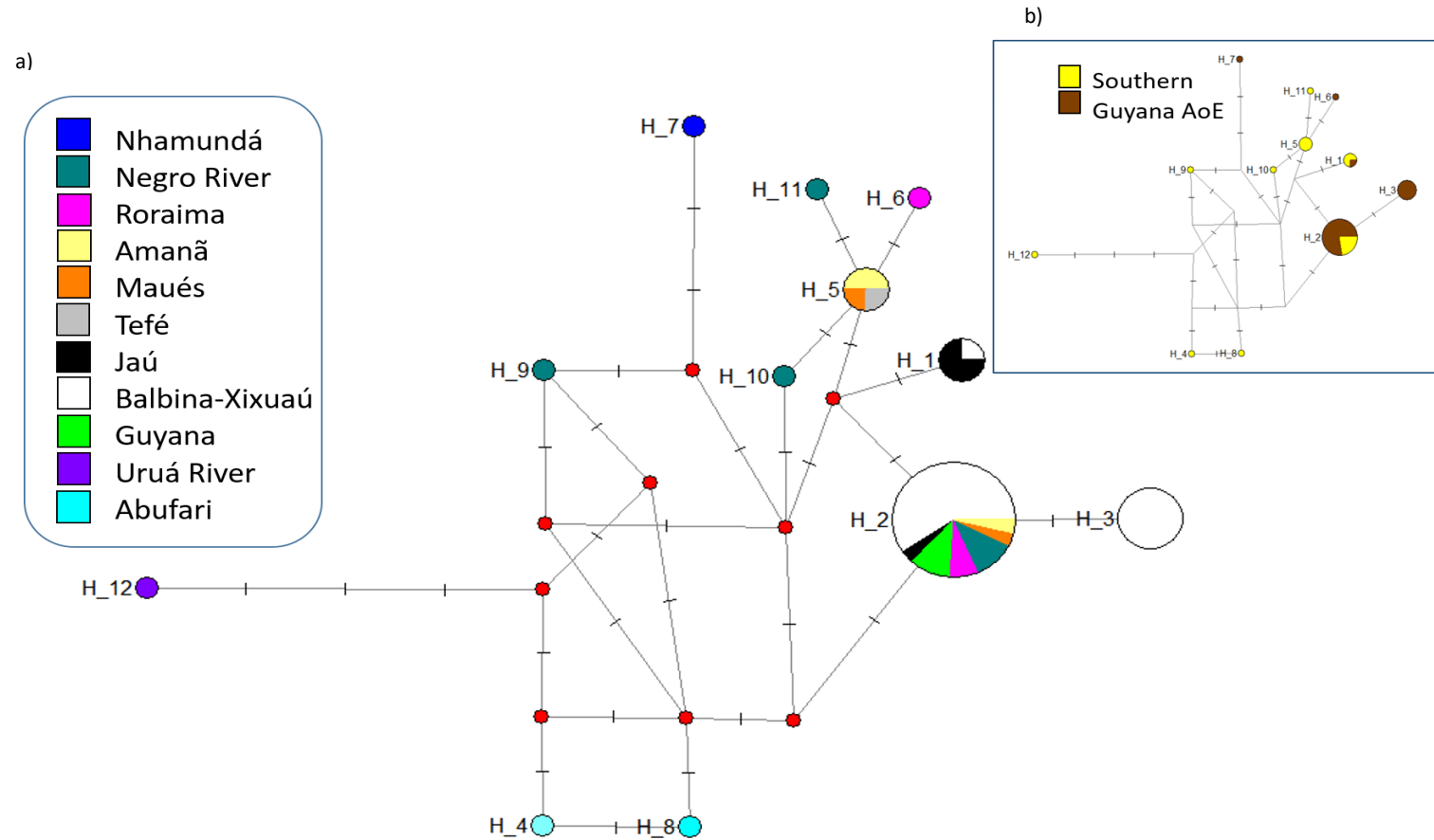


Figure 3.15: Median-joining network of Neotropical otter haplotypes considering only samples from this study. Each circle corresponds to one haplotype, and circle sizes correspond to haplotype frequencies within the whole sample. The hatch marks on network lines indicate numbers of mutations. Colours within the circles denote the different geographic locations, as following: yellow – Amanã; black – Jaú; white – Balbina; and purple – Ati-Paraná.

1



2

3 Figure 3.16: Giant otter haplotype network with added Genbank sequences. a) Haplotype circles coloured according to location; b) Haplotype circles according to broader
 4 classification in “Southern” group (N=20) and Guyana AoE (Area of Vertebrate Endemism) group (N=31).

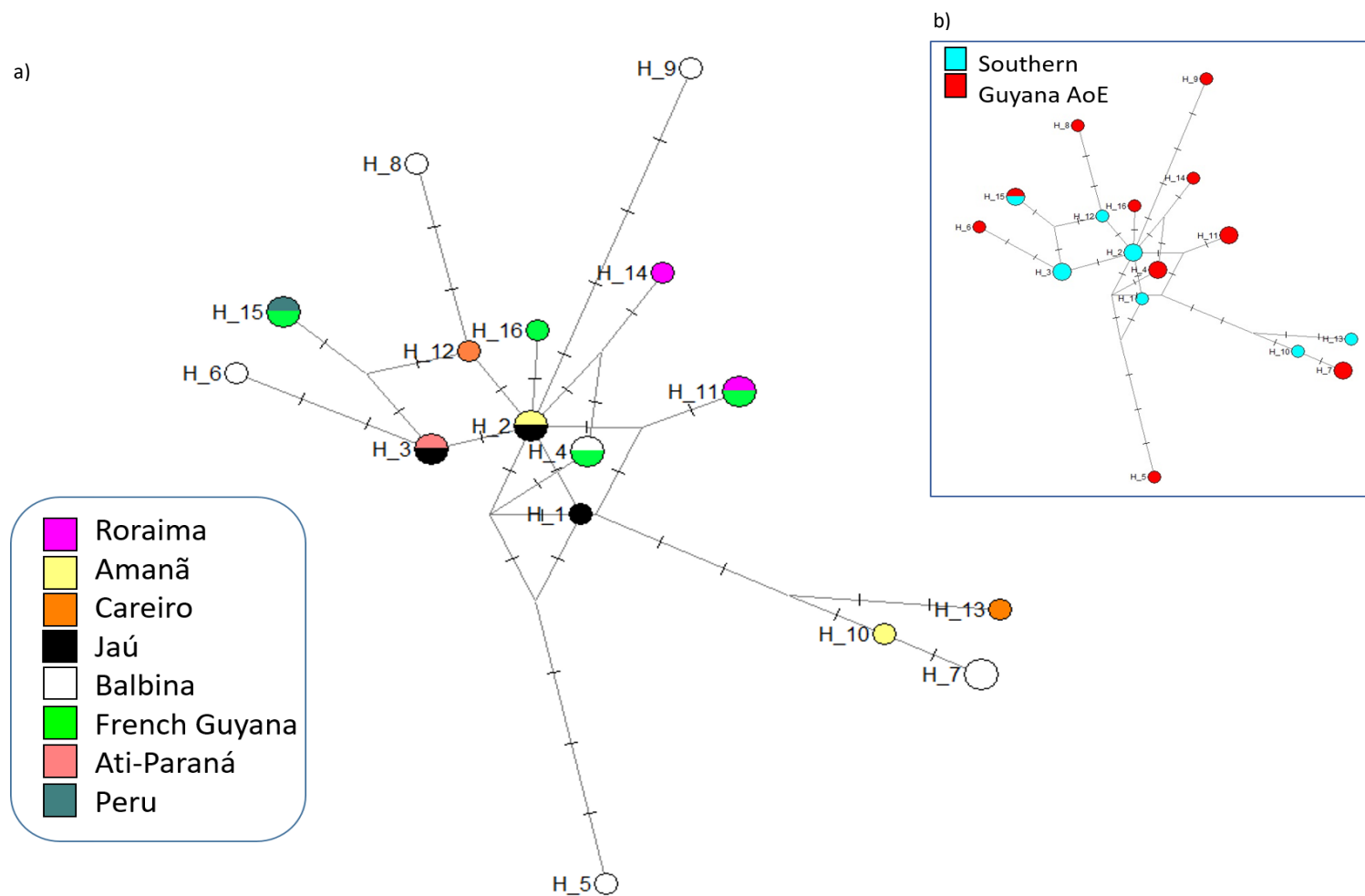


Figure 3.17: Neotropical otter haplotype network with added Genbank sequences. a) Haplotype circles coloured according to location; b) Haplotype circles according to broader classification in “Southern” group (N=8) and Guyana AoE (Area of Vertebrate Endemism) group (N=14).

Neotropical otters sampled in this study had a total of 9 haplotypes (Fig. 3.15), based on 9 variable sites. The overall haplotype and nucleotide diversity were similar to giant otters ($Hd=0.795\pm0.07$; $\pi=0.01\pm0.002$). Haplotype 1 was the most frequent, being shared by individuals from all the locations included (Amanã, Ati-Paraná, Balbina and Jaú). The majority of the haplotypes ($N=5$) were exclusive from Balbina. Amanã showed two distinct haplotypes (H7-8), while Jaú individuals showed only shared haplotypes.

Both haplotype networks also show an overall concordance with the previously shown results, based on NGS data. Abufari, for instance, had quite distinct clustering patterns for giant otter SNPs, and again it showed its distinct haplotypes in the mtDNA analysis. Neotropical otters from Balbina were also strongly clustered both with SNPs, and had the higher haplotype variability within the samples analysed.

The second analysis, including the sequences from Genbank, resulted in a higher number of haplotypes for both species (Figs. 3.16 and 3.17). Giant otters had a two-fold increase on the number of haplotypes identified ($N=12$, based on 13 variable sites out of 132bp) with an Hd of 0.693 ± 0.06 and $\pi=0.01\pm0.002$. Neotropical otters too had an increase to 16 haplotypes (with 20 variable sites in a 427bp sequence - after excluding gaps and missing data sites from the original 516bp segment), resulting in an Hd of 0.97 ± 0.01 and $\pi=0.01\pm0.001$.

In Figs. 3.16b and 3.17b is possible to see that there is a small proportion of shared haplotypes between locations from Guyana AoE and the Southern group. The only shared haplotype between the two groups in Neotropical otter - H15 – is shared by two individuals quite apart from each other (see map in Fig. 3.5): one from French Guyana and the other from the Peruvian Amazon (both sequences retrieved from

Genbank). Nevertheless, F_{ST} comparisons showed that this differentiation was only significant for giant otters ($F_{ST}=0.24$; $p= 0.0001$).

3.4 Discussion

The aim of this study was to compare patterns of diversity and population structure of Neotropical and giant otters in Central Amazonia, in order to provide relevant information and transferable inference for the conservation and management of species. Previously, no studies were able to detect signals of genetic structuring for Amazonian otters at finer/regional scales (e.g., at minor river sub-basins level – see Table 3.1 and further discussion below). This study was directed as an attempt to fill this gap, performing a sampling scheme at a regional scale encompassing several sub-basins and incorporating NGS methods for the use of high-resolution genetic markers.

3.4.1 *Giant otters*

Using sets of 469 and 134 SNPs (identified with the GL approach and conventional approach respectively), combined with mtDNA data, it was possible to identify population genetic structure and assess diversity metrics of giant otters in Central Amazonia. This is the first time that a structuring pattern has been identified within this region.

Evolutionary history and phylogeographic patterns of giant otters over different portions of the Amazonian biome were previously addressed using mostly mitochondrial DNA markers, as in the works by Garcia et al. (2007), Pickles et al. (2011), Caballero et al. (2015) and Ruíz-García et al. (2018). Patterns of population structure were also investigated using 13 microsatellite loci using 59 samples (mostly scats) from

populations in the Upper Amazon, Guyana, northwest Orinoco basin and Bolivia (Pickles et al. 2012). In general, all of these studies cited found relatively high levels of genetic diversity for this species at the Amazonian biome scale with the molecular markers used, proposing the existence of a large-scale genetic structure with a few phylogroups, between which they suggest widespread gene flow (without barriers' influences). But normally, such patterns of high diversity in phylogeographic studies are the reflex of diversity among locations, when haplotypes are sampled among a broad spatial range - especially when the sample sizes per location are low.

Analysing partial sequences of the control region and gene cytochrome b (Cyt-b), Garcia et al. (2007) identified 11 haplotypes within their Amazonian sample, and obtained an average haplotype diversity (Hd) of 0.867 (this estimate includes samples from Pantanal, where 1 additional haplotype was found). In the present study, both analyses performed with mtDNA (with and without Genbank sequences) had smaller values of Hd. Nonetheless, the present study had a larger number of samples from locations at a finer scale - within almost the same spatial range, Garcia et al. analysed 22 samples, while here 51 samples were used, i.e., an almost two-fold increase in sampling density. Taking Balbina as an example, as this was the location with the larger sample size (N=18), Garcia et al. 2007 had only 5 samples. Hence, if several of the sampled individuals originate from the same matriline, they will share the same haplotypes, which would consequently reduce the overall haplotype diversity – and in turn could explain the current results. In fact, the Hds obtained for the CR fragment here (0.72 and 0.79) were close to the overall Hd reported by another study that also used a partial CR sequence (of 258 bp - Caballero et al. 2015). Their overall Hd was 0.71, and the Hd reported in the same study for the phylogroup of Puerto Carreño in Colombia (which,

like here, also comprised a large number of samples, $N=35$, concentrated at a finer scale) was 0.70.

The overall nucleotide diversity estimate reported in this chapter ($\pi=0.01$) for giant otters appears high considering the moderate H_d values, but nevertheless it is again close to that obtained by Caballero et al. (2015) with a partial CR sequence ($\pi=0.012$) and with the one obtained by Garcia et al. (2007) when considering the CR only, which was also 0.012.

Garcia et al. (2007) found significant genetic (Φ_{st}) differentiation between individuals from Balbina Lake area and the Negro River, indicating the possibility of population structuring within central Amazonia at finer scales than normally contemplated by phylogeographic research (i.e., among minor river basins). Other population pairs in Amazonia were also compared by Garcia et al. (2007), but inferences were limited since some of their populations were represented by a single or a couple of individuals (see Table 3.6). But since then, no other work has tackled the matter of assessing genetic patterns of the species within this central region, which includes the intersections of several areas of vertebrate endemism (cf. Silva et al. 2005, Borges 2004), having therefore a biogeographical relevance. With the set of SNP loci obtained by NGS in this study, it was in fact possible to detect some degree of population structuring in giant otters across this region.

One of the identified clusters based on SNP analyses appears to pool together most individuals from the locations Balbina and Xixuaú, which shared a predominant common ancestry. These two areas are situated in different river sub-basins. Xixuaú is in the middle course of Jauaperi River, a tributary of the Negro. The Balbina study area comprises the Balbina Lake - a 2360 km² hydroelectric reservoir (formed by the

damming of Uatumã river, a tributary of the Amazon) and the lower/medium course of the river Pitinga (tributary of Uatumã). Xixuaú and Balbina are ca. ~200 km apart in a straight line, but the two sub-basins are connected by smaller tributaries of Alalaú river (a western tributary of Jauaperi) and Cuariaú/Camanaú rivers, so it is likely that individuals use them as a dispersal route, facilitating gene flow between these areas. This could explain the high admixture between the two sites, which might well constitute a single population.

The likely connection between Balbina and the Jauaperi River is important because the impact of large dams on populations of giant otters is not well known. Palmeirim et al. (2014) have suggested that the Balbina Lake provides a low-quality habitat for otters, arguing that despite an estimated increase in population size, overall giant otter density has decreased after the reservoir filling compared to pre-filling densities (i.e. - the population did not grow in the same expected proportion as the amount of available habitat). There is, therefore, much concern about the impacts of dams on biodiversity (Lees et al. 2016) and connectivity among Amazonian rivers (Anderson et al. 2018). With the present results, it can be suggested that, at least for giant otters, connectivity between river basins seems to be maintained so far, despite the potential barrier imposed by the large dam to the lower course of Uatumã River and its potential connections to other sub-basins and to the Amazon River, towards where Uatumã flows.

On the other hand, the Balbina/ Xixuaú population had relatively low heterozygosity compared to the other putative populations (see Table 3.8). Some past or ongoing process might be influencing genetic diversity of this population, and the possible influence of the reservoir cannot be discarded. As reported in the study by Palmeirim (2014), the giant otter population in Balbina was estimated to undergo a two-

fold increase over the last 25 years following the dam filling. It is possible that the new habitat conditions, including a temporary pulse in the prey biomass available during the initial years of the dam closure (Santos & Oliveira 1999) may have influenced giant otter demographic processes, for instance leading to higher litter survival, and eventually leading to an increase in inter-group relatedness. Nevertheless, pre-dam events could also be responsible for the patterns observed, and with the data obtained it is not possible to infer the causes and processes that led to the current status; more focused studies are needed in order to test different hypotheses.

Balbina and Xixuaú are both located in the Guianan AoE, along with two more sampling sites in this study: Trombetas and Guyana. Trombetas showed a strong clustering of its individuals, with common ancestry coefficients between them. Trombetas, like the Uatumã River, is also a tributary of the left (northern) bank of the Amazon. In terms of Euclidian distance, the two sites are located around 320 km apart. However, the hydrographic connections from Trombetas sub-basin to Uatumã might not be as direct, as two more major watercourses (Nhamundá and Jatapu rivers) flow in parallel between the two areas. It is thus less likely that direct gene flow would occur between those sites, and the results presented suggest that giant otters from the Trombetas River might constitute another separate population.

The Guyana individuals, on the other hand, showed more admixed ancestry coefficients and did not cluster. This was not expected, considering that this location was the most distant from all others, being located in the Essequibo basin, which flows towards the Caribbean and is separate from the Amazon basin. One possible issue with this group could be the low quality of the data available for the few individuals analysed. First, only 5 individuals yielded enough reads to allow further analysis - and only two of them had less than 30% of missing data for the SNP loci used. Plus, no mtDNA data was

obtained. But one hint could come from the DAPC analysis, which was based on the smaller set of SNPs obtained by genotype calls: in the DAPC assignment plot, all the Guyana individuals indeed showed strong assignment to this group, except for one, which had a stronger assignment to the Trombetas cluster instead (see Figure 3.9). The Guyana samples all cluster together in the FCA analysis (see Figure 3.10). It is not possible to confidently infer relationships between the Trombetas and Guyana clusters without an increased sample size. However, connectivity could be possible since the Trombetas sub-basin originates in Guyana.

The other group of individuals showing evidence for separate clustering was Abufari. This site is located on the middle of Purús – an extensive lowland white-water river and major tributary of the Solimões (Amazon) river, before its confluence with Negro. It is included in another sub-division of the endemism centers: Inambari, and is the southernmost study site among the whole sample-set. The shortest Euclidian distance from Abufari is to the Amanã site is approximately 360 km, but the sub-basins are centrally separated by the Amazon and by the Jutáí-Purus interfluve, and the more complex watercourse networks between them might hamper a continuous gene flow. Hence, a clustering of individuals from this area was not unexpected, and the mtDNA results give further support to suggest that this population has less genetic similarity to the others studied.

Finally, the individuals from Amanã and Jaú showed overlap in the PCA and Admixture analyses, but some separate clustering for DAPC, FCA and mtDNA. The two areas are located before the confluence of Negro and the Amazon, in an interfluve which is also considered an area of endemism, Imeri - or Negro, according to some authors (e.g. Ribas et al. 2012). On the north, this area is delimited by the Negro River and on the south by the Amazon. The fact that Amanã and Jaú are situated in a middle geographic

position between Abufari and the northernmost sites (Balbina, Xixuaú, Trombetas, Guyana) could explain the higher admixture found, as they could have indirect connectivity to both “sides”. Amanã is a lake formed by several tributaries that provide year-long connections to the white-water Japurá and Amazon rivers on the west, and seasonal connections to the Negro sub-basin on the east. The latter seasonal links allow the connection between Amanã and Jaú, though perhaps some level of isolation as well. To some extent the Imeri/Negro interfluvium may serve as an intermediate area important in maintaining gene flow between the Guiana AoE and the southern AoEs.

3.4.2 Neotropical Otters

Results obtained for Neotropical otters using SNPs and mtDNA datasets have also suggested the existence of population structure for this species within the study area in Central Amazonia. The clustering of the Balbina population was well supported in the PCA. Admixture analysis found two clusters, one of them clearly dominated by the Balbina individuals. Jaú, Amanã and the single individual from Ati-Paraná have shared ancestry proportions of the two clusters identified; nevertheless, all three appear to have a higher proportion of ancestry from the same cluster. The FCA analysis was able to cluster all three putative populations separately. Although limited, the mtDNA dataset helps to corroborate the NGS findings, since Balbina had the majority of exclusive haplotypes in the sample. Therefore, the study results suggest that Neotropical otter populations in Central Amazonia also show signs of genetic differentiation, with a very similar pattern as seen for giant otters for the populations sampled in common.

Previous studies with mtDNA data have been able to identify main lineages and phylogroups of the species over large scales (Trinca et al. 2012, Hernandez-Romero et al. 2018, Ruiz-Garcia et al. 2018), but no clear evidence of population structure at regional

or local scales. A recent study, however, has found a clear indication of population structure of Neotropical otters between three different river basins in eastern Mexico, by genotyping 49 individuals with 11 microsatellite loci (Latorre-Cárdenas et al. 2020_b). Buglione et al. (2020), using the same number of microsatellite markers, have found analogous results for *Lutra lutra* (a similar species in terms of morphology, ecology and behaviour). The authors observed the sub-structuring of populations mostly according to different river basins in southern Italy (Buglione et al. 2020). The results of the present study suggest that the same happens in central Amazonia, and it can be hypothesized that gene flow can be more restricted between sub-basins.

Unlike the case with giant otters, for Neotropical otters there was no data available from closer populations to Balbina, such as Xixuaú. It would be important to sample this and/or other populations potentially connected to Balbina, in order to assess if this population is really isolated (due, for instance, to the influence of the dam) or if there is evidence of gene flow and genetic connectivity with other locations. But, once again, Amanã and Jaú areas showed a similar pattern of admixture as for the giant otter, highlighting the potential of this region as a connection between sub river basins. Ordination analyses in DAPC and FCA could isolate Amanã and Jaú clusters, but not as clearly as for Balbina.

3.4.3 Comparative genetic diversity and structure patterns

Population structure was found for both species, but due to the limited number of sampling locations achieved for Neotropical otter, it was not possible to compare whether the degree of structuring is reduced for this species when compared to giant otters, as hypothesized. Therefore, the role of sociality in promoting or reducing connectivity and gene flow could not be assessed with the current data. Still, considering

the three locations in common for both species, the patterns are quite similar, with structure being found in the Balbina area, while Amanã and Jaú locations were more admixed with shared ancestries. Although the role of sociality cannot be either inferred or discarded, these preliminary results might suggest that other extrinsic factors can contribute to population genetic structure.

The diversity metrics found indicate a greater genetic diversity for the Neotropical otter than for the giant otter, consistent with the greater demographic impacts of hunting on the populations of the latter. These results corroborate the findings of Pimenta et al. (2018) on the greater resilience of the Neotropical otter to the decades of intensive fur trade, evidenced through historical records that did not show a decrease in the exploitation of this species over time, unlike the observed for giant otters.

It was long thought that giant otters might have undergone a genetic bottleneck. However, to date, other studies have found moderate levels of diversity for the species not consistent with a loss of rarer alleles by a bottleneck. Ribas et al. (2015) and Pickles et al. (2012) performed specific tests for bottleneck detection with microsatellite loci, but did not detect evident signs of such an event in either Pantanal or Amazonian populations. Pickles et al. (2012) found only weak evidence in one of the groups studied in the Amazon (Iténez), but they acknowledge that the small sample size impairs the ability to detect a possible bottleneck (especially such a recent one). With the data available in this study, it was also not possible to perform a specific test. Neutrality tests performed with mtDNA data can provide some clues, in this case the significant negative Tajima's D for the haplotypes from Guyana AoE can indicate a process of population expansion following a reduction, due to excess of rare alleles which is an expected pattern after a bottleneck.

Also, the reported values of diversity based on the sets of SNPs were low - this might indicate that the Amazonian populations of the species were not able to maintain moderate to high diversity levels, as has been a consensus in the literature to date considering phylogeographic studies. Nonetheless, H_o and H_e values reported here for the giant otter, despite low, are in fact similar to other vertebrate studies using SNPs, including for instance terrestrial and aquatic mammals (e.g., island fox - Funk et al. 2016, harbor porpoise - Lah et al. 2016) and the pirarucu fish in Amazonian rivers (Torati et al. 2019).

In addition, considering haplotype diversity results, the overall mitochondrial DNA diversity is quite similar for both species and indicates a reasonable level of genetic variation over Amazonia. Patterns observed with nuclear markers, though, might tell a slightly different story and, as the present results suggest, giant otter populations could be currently less diverse and more structured than those of Neotropical otters.

Still, mitochondrial DNA markers are undoubtedly useful for detecting phylogeographic patterns and studying evolutionary aspects and history of species and populations (Rubinoff & Holland 2005), among many other applications. In fact, an interesting result in common for both species was the distribution pattern of the haplotypic diversity observed when including Genbank sequences. For Giant otters, there was a significant distinction between haplotypes found in the “Southern” group (which included all individuals to the south of the Amazon and west of Negro Rivers) and the “Guiana” group (including all individuals sampled within the Guiana area of endemism). This strengthens the hypothesis that large Amazonian rivers might indeed have a role in shaping genetic diversity patterns not only in terrestrial vertebrates (Antonelli et al. 2010), but even in mobile, semi-aquatic species such as otters. In fact, a recent study has found two distinct lineages of the dwarf caiman, a semi-aquatic reptile, which are

separated in four different populations structured among major river limits in central Amazonia (Bittencourt et al. 2019). At finer scales, population structuring within river basins have been found in other semi-aquatic mammals, such as the Pyrenean desman *Galemys pyrenaicus*, the water rat *Nectomys squamipes*, and capybaras (Querejeta et al. 2017, Maroja et al. 2003, Byrne et al. 2015).

Due to experimental limitations, though, any conclusions from the present results should be drawn with caution. Despite the major sampling effort in the field, the low quality and scarcity of DNA in scat samples has reduced the final sample size. Having few samples sequenced per study area weakens the predictive power of some bioinformatic analyses, and hampers certain estimates and hypotheses that could have been tested with a more complete sample size and dataset. Still, the combination of SNPs loci obtained by NGS with mtDNA sequences allowed the identification of current population structure in both species in the studied region, using modern contemporary samples.

3.5 Conclusion

This study constitutes the first focused attempt in assessing comparative population genetic patterns for otters in the Brazilian Amazonia at a regional scale. Results presented in this chapter suggest the existence of population structure for giant and Neotropical otters among Amazonian river sub-basins, and possibly among known areas of vertebrate endemism delimited by major Amazonian rivers.

Wide-ranging species can sometimes hide cryptic structure or isolation by distance (IBD) patterns that might only be detected at finer scales and/or under an

intensive sampling scheme (Quaglietta et al. 2012, Escobar et al. 2015, Bittencourt et al. 2019), and the sampling design proposed here aimed to cover both points. Previous works have evoked the dense hydrography – and thus putatively high connectivity - of the Amazonian basin to explain large-scale phylogeographic diversity in otters (Trinca et al. 2012, Pickles et al. 2011, Ruiz-Garcia et al. 2018). But the network of watercourses in the Amazon basin can be as complex as it is dense; from the viewpoint of a semi-aquatic animal, maybe not every river is a route. Agreeing with Latorre-Cardenas et al. (2020_b), it is likely that the population structure found in some of the Amazonian sub-basins studied here is related to the hierarchical character of the riverine landscape, in a way that gene flow can be lower among drainage basins than within them (Hughes et al. 2009, Esmaeili et al. 2020). The complex characteristics of rivers, considering flow direction, width, vegetation cover, among many other aspects, might have a main role in promoting or restraining dispersal and gene flow within and among basins or sub-basins.

This work also brings some relevant conservation implications for the species studied. Because population structure was found, this highlights the need for maintaining a good mosaic of protected areas, to allow connectivity between populations. It was found that genetic diversity of giant otters might still be reflecting past anthropogenic exploitation, and that some populations might be more genetic depauperate than others. More specifically, attention should be given to the giant otter population in the area of influence of Balbina hydroelectric dam, because despite its apparent health, genetic data suggests that this population could be experiencing more risky levels of genetic isolation. Of course, the same caution should be taken into consideration for other large dams, and the findings highlight the importance of genetic monitoring of freshwater species potentially affected by this kind of developments.

3.6 References

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3.7 Appendices

Appendix 3.1 List of target loci designed for the capture protocol.

Appendix 3.2 Figure illustrating the Amazonian areas of endemism. Republished figure from Ribas et al. (2012) with permission of the Royal Society (Great Britain), from the Proceedings of the Royal Society B: Biological Sciences 279(1729); permission conveyed through Copyright Clearance Center, Inc.

Appendix 3.3 Giant otter FCA plots.

Appendix 3.1

```
>Giant.XPO4_1009bp_GC:_32.5%
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TCCTTAATTGATCTTTCTCATTAGCTGGAGTTTCTTCCATCCTGACCTTACACTTCCTTCAAAAATAATCTTTCTACTA
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TGCATACACCTGTGTAACCAGGCCATGTTAAGATACAGAATATAACCATACATAATCTCTGAAAGCTCCCTCATTTTCT
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TTAAAATGACACTTTTTTATGGGCATATATTTTATTATCATGGATAAAATACCTAGGAGTAGAATCCTATTTTCATGGAAC
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>Giant.TXNDC5_1017bp_GC:_37.6%
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CAGGTCATAGAGTAGCTCTATTTTAAATTTCTTTTTTAAAAATATTTTATTTATTTTATTTGACAGAGA
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>Giant.TBC1D9B_992bp_GC:_41.4%
```

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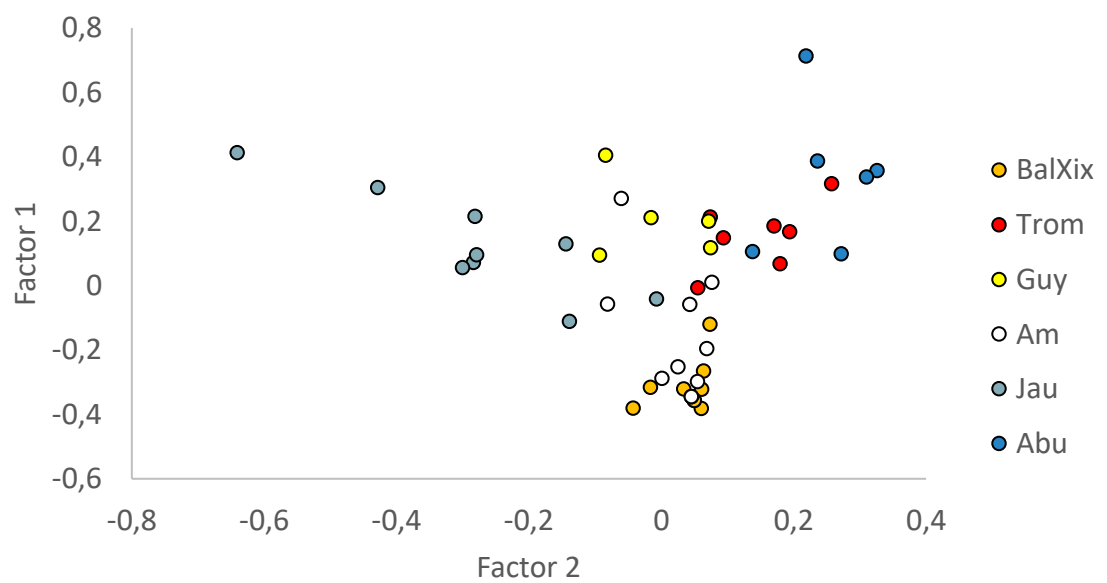
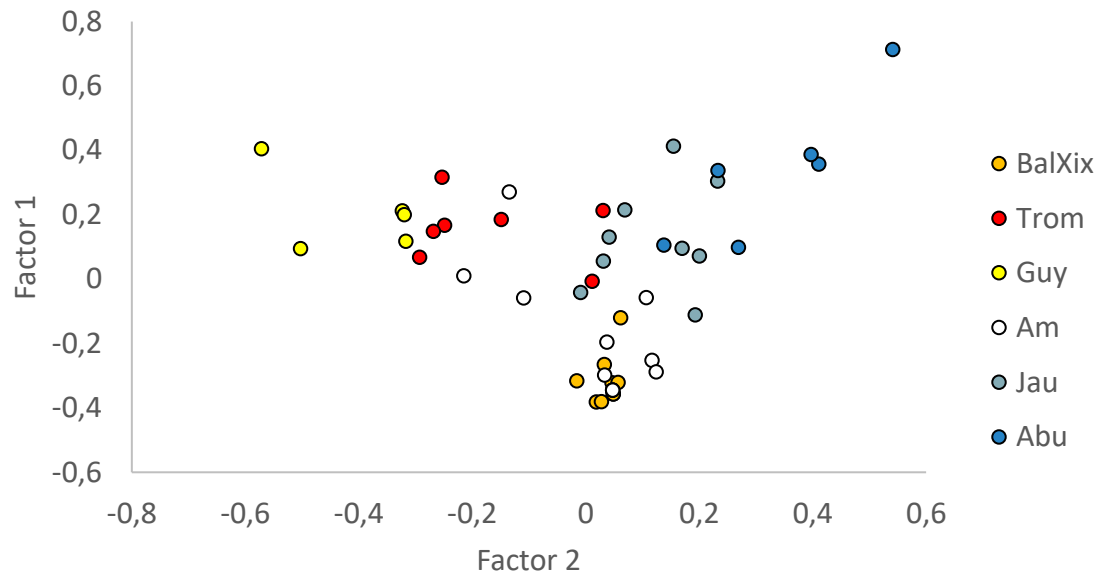
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Appendix 3.2



Appendix 3.3



Chapter 4

Reconstructing Carnivora evolutionary relationships with a particular focus on the Lutrinae using a novel dataset of nuclear loci



Photo © 2013 “Mike” Michael L. Baird (<https://www.flickr.com/photos/mikebaird/9137174915/in/album-72157634330789112/>)

4.1 Introduction

4.1.1 *The Order Carnivora*

Carnivora is a diverse order of eutherian mammals, encompassing 286 extant species distributed in 16 families and over a hundred genera (Eizirik et al. 2010). The remarkable diversity in this group is not only linked to the number of species, but also to their array of dietary habits, social systems, locomotion styles and morphologies (Macdonald 1983, Van Valkenburgh 2007, Samuels et al. 2012). No other mammalian group has such a distinct range of body mass between its members - the minuscule least weasel (*Mustela nivalis*) can weigh between 0.025 - 0.3 kg (Hunter & Barret, 2018), while at the other extreme, male southern elephant seals (*Mirounga leonina*) can weigh as much as 3 t (Hindell & Perrin 2009). Not surprisingly, carnivorans can explore many different niches and are well adapted to a huge variety of both terrestrial and aquatic habitats, being found in all continents of the world.

Basicranial characters – in particular the auditory bulla – have been considered important diagnostic features within Carnivora since early studies from the 19th century (Flower, 1869), which recognized some main differences firstly categorized into three superfamilies (Arctoidea, Cynoidea and Aeluroidea). Following further development in such studies, in 1945 Kretzoi formalized the main Carnivora dichotomy that has been accepted since then: the superorders of Feliformia and Caniformia. Almost all except for a few basal members of Feliformia present two-chambered auditory bullae, divided by a septum; while caniforms' bulla has a single chamber, with an absent or partial septum (Hunt Jr. 1974, Ivanoff 2019).

Since the advent of molecular techniques, there have been increasingly more studies focused on refining and elucidating the evolutionary relationships among the

order Carnivora. Between 30 and 40 years ago, researchers could mainly use differences in amino acid sequences for certain proteins (such as hemoglobin and cytochrome C) to establish relationships between species (e.g., de Jong et al. 1977, Baba et al. 1982). Later, mitochondrial genes, such as 16S, 12S and cytochrome b, became widely used in phylogenetic studies (Johnson & O'Brien 1997, Masuda & Yoshida 1994, Ledje & Arnason 1996). Mitochondrial DNA has a high rate of mutations, lack of recombinations and is relatively easy to amplify, even from older or degraded material. Its use has been target of criticism though, largely because it is a short portion of the whole genome, maternally inherited, and phylogenies will basically represent a single gene tree instead of a species tree (see Baloux 2010, Dool et al. 2016). Furthermore, comparisons between nuclear and mitochondrial based molecular phylogenies have shown significant discrepancies caused by factors such as incomplete lineage sorting and introgression, and might lead to ambiguous results (Shaw 2002, Hurst & Jiggins 2005).

4.1.1.1 Divergence time estimates

Time of divergence between the two main lineages Feliformia and Caniformia remained unresolved in the last couple of decades due to disparities between studies. In addition, restricted fossil evidence from the critical period between Late Cretaceous and early Paleocene hampers better calibrations and estimates (Rose, 2006). According to some authors, the two clades diverged during early to middle Eocene – between 38 and 47 Ma, estimates obtained both by morphology-based phylogenies (Wesley-Hunt & Flynn 2005, Tomiya 2011) and by molecular data from nuclear genes (Kumar & Hedges 1998). Other molecular-clock approaches have suggested older ages of divergence that fall within early Eocene or late Palaeocene: 55 Ma (Springer et al. 2003) and between 58-59 Ma (Eizirik et al. 2010). Finally, the most recent estimate comes from Nyakatura and Bininda-Emonds' study (2012), with a meta-analysis which accounts for both

morphology-based phylogenies and the addition of their own new molecular data. This study presented the oldest (and likely most accurate) estimate of all, 64.9 Ma (shortly after the Cretaceous-Paleogene boundary).

4.1.2 *Feliformia*

Feliformia sub-order started its radiation in early Eocene between ~50-57 Ma (Nyakatura & Bininda-Emonds 2012, Hedges et al. 2015). Nimraviidae, an extinct family of false sabre-toothed cats, is considered the most basal clade of feliforms and has possibly originated in Asia during the middle Eocene (Averianov et al. 2016). Zhou et al. (2017) suggested that the first feliforms, ancestors to extant taxa, indeed dispersed from South Asia and Africa to Europe, North Asia and North America. There are now seven extant families included in this “cat-like” clade: Nandiniidae, Felidae, Prionodontidae, Viverridae, Hyaenidae, Eupleridae, and Herpestidae. Of these, Nandiniidae, represented by only one species, is considered the most basal, sister group to all other families (Eizirik & Murphy 2009).

Evolutionary history of Feliformia appears closely associated with climatic changes that occurred from Eocene through Pliocene (Zhou et al. 2017). Such changes caused variations in sea level that possibly favoured continuous events of vicariance and speciation by separating dispersal routes and isolating populations when sea levels rose, and then providing new opportunities for dispersal when levels dropped (Zhou et al. 2017). Some periods of rapid diversification have been identified in this sub-Order during the Late Eocene, Early Oligocene and Late Miocene (Eizirik et al. 2010). The early Oligocene radiation, between 32-33 Ma, happened in two lineages leading to (Hyaenidae + Herpestidae + Eupleridae + Viverridae) and Felidae; and is particularly interesting, as it coincides precisely with the “Grande Coupure” in Eurasia, a major

faunal turnover event when many mammalian species went extinct in Europe and were supposedly replaced by immigrant taxa from Asia (Eizirik 2012, Van Valkenburgh 1999).

4.1.3 Caniformia

In Caniformia, earlier radiations were roughly synchronous to those of Feliformia, between ~49-61 Ma (Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012), when there was a basal split between the infra-orders Cynoidea (that includes a single family, Canidae) and Arctoidea. The lineage leading to Canidae originated in North America (Van Valkenburgh 1999), and is the most basal within Caniformia (Yu & Zhang 2006).

Recent estimates of divergence time for the Canidae family range between ~8-16 Ma (Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012), however, although these estimates seem appropriate for the only extant group (subfamily Caninae), they disregard well-known divergence events described between the late Eocene - early Miocene for extinct subfamilies in North America (Wang & Tedford 2008, Goswami 2010, Slater 2015). For instance, the oldest canid fossil, genus *Hesperocyon*, is aged around 43 Ma (Storer 1984). Two earlier major radiations occurred between late Eocene and early Miocene, within the subfamilies Hesperocyoninae and Borophaginae; and the third and last within the subfamily Caninae, from late Miocene until the Plio-Pleistocene (Wang & Tedford 2008).

The three canid subfamilies coexisted in North America for ca. 20 million years, but both Hesperocyoninae and Borophaginae went extinct, one after the other, and only Caninae species persisted. A recent comprehensive study on fossil occurrences using a Bayesian framework has shown that the extinction of these subfamilies was caused by clade competition, both within the family (especially between Hesperocyoninae-

Borophaginae) and with felids, following their arrival in North America (Silvestro et al. 2015). Evidence on the effects of competition between Caniformia and Feliformia had as well been demonstrated by Pedersen et al. (2014), providing an example of how biotic interactions can shape evolutionary histories and diversity patterns.

For a prolonged time (about 30 Ma) Canidae members were thus restricted to North America, until the geological changes that occurred later in the Miocene and Pliocene allowed for their spread and a rapid diversification of the taxon (which at that point was only represented by Caninae species). The land connection between North and South America, for instance, gave way to several speciation events within a relatively short time-frame of 2.5 million years (Van Valkenburgh 1999). Presently, even after Plio-Pleistocene extinctions, 10 extant species of Canids remained in South America only, representing the largest diversity of the family over all continents (Tchaicka et al. 2016) and showing how well this taxon has adapted and radiated into recently colonized environments.

Arctoidea, the second sub-order of Caniformia, includes a large number of families: Ursidae, Phocidae, Otariidae, Odobenidae, Ailuridae, Mephitidae, Procyonidae and Mustelidae. Intra and inter-familial relationships within Arctoidea have been historically complex to resolve. Ursids constitute the most basal clade, dating back to around 40 Ma with its earliest known fossils, *Parictis* sp., being aged between 37-43 million years old (Konizeski 1961, Ostrander 1985). It has been long debated whether giant pandas (*Ailuropoda melanoleuca*) belonged in this taxon and in what position, representing in fact one of the most controversial discussions in mammalian systematics (O'Brien et al. 1985, Bininda-Emonds 2004). Such disputes were partly due to the similarities between giant and red pandas (and their likewise problematic phylogeny - see below), but currently it is well established that giant pandas belong to Ursidae, being its

most basal extant representative (Yu & Zhang 2006, Arnason et al. 2007, Eizirik & Murphy 2009) while red pandas belong to their own monotypic family, Ailuridae.

Another example of a conflicting ancestry is the clade Pinnipedia. It is not yet clear whether this superfamily is more closely related to Ursidae or to Musteloidea (a superfamily including the red panda, skunks, racoons and otters; see Yu et al. 2011 and Berta et al. 2018). A potentially important clue so far comes from a recent study by Doronina et al. (2015) who used for the first time retroposon elements to reconstruct Caniformia phylogeny, in order to elucidate such discordances in Arctoidea. The advantage of using this class of molecular markers is that they can distinguish phylogenetically informative sites from conflicting signals in comparison to traditional markers, such as nuclear or mitochondrial genes, because they are unique genome insertions which are nearly homoplasy-free (Shedlock and Okada 2000, Doronina et al. 2015). Doronina et al. (2015) results suggest a closer relationship between Pinnipedia and Musteloidae. In addition, they showed that such historical incongruences possibly result from incomplete lineage sorting, especially during the basal Arctoidea radiations. Moreover, a new study by Paterson et al. (2019) reached the same conclusions on this sister-group relationship, by using total evidence analysis and including multiple extinct taxa.

Pinniped monophyly has nevertheless been widely accepted and supported, through both molecular and morphological datasets (Sato et al. 2006, Dragoo & Honeycutt 1997, Flynn et al. 2005, Eizirik et al. 2010, Berta et al. 2018). Pinnipedia includes the extant families Odobenidae (walrus), Phocidae (true seals) and Otariidae (fur seals and sea lions), and had its origins in the North Pacific (Berta et al. 2018). Earliest pinnipeds date from the late Oligocene (ca. 30-23 Ma – Berta et al. 2018), and their fossil

record shows a much higher species diversity than remains in the extant lineages (Valenzuela-Toro et al. 2019).

4.1.4 Musteloidea and phylogenetic incongruences

Musteloidea is another superfamily of Arctoidea, formed by the extant families Mustelidae (otters, weasels, ferret), Procyonidae (racoons, coatis), Mephitidae (skunks and stink badgers) and Ailuridae (red panda). Musteloids first appeared in Asia around 30 Ma (Sato et al. 2012). Basal positions within this group have been focus of debates and are still fairly confounding (Eizirik & Murphy 2009, Doronina et al. 2015, Koepfli et al. 2017). Mephitidae was once considered part of Mustelidae as a sub-family (Mephitinae), but Ledje and Arnason (1996) found that skunks (*Mephitis mephitis* and *Spilogale putorius*) were genetically distant from the other mustelid species, characterizing a paraphily of the group as it was. Later, Dragoo & Honeycutt (1997) proposed their family level classification based on a total-evidence analysis (molecular and morphological data), which remains the accepted version.

Ailuridae, as mentioned before, was a source of debate due to its similarities with the giant panda. Sato et al. (2009) found strong support for Ailuridae as a sister group to (Procyonidae + Mustelidae), being further confirmed by Eizirik et al. (2010) with molecular data and by Law et al. (2018) with a combination of molecular and fossil data. Consequently, Ailuridae is now established as a monotypic family. Nonetheless, uncertainties remain regarding the relative positions of Ailuridae, Mephitidae and the clade formed by (Procyonidae +Mustelidae) (Koepfli et al. 2017). Both Ailuridae and Mephitidae have previously been placed as the most ancient lineage of Musteloids in different studies, so this position was unclear. Now, some of the latest findings seem to

have reached an agreement on Mephitidae as the first branching clade (Sato et al. 2009, Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012, Luan et al. 2013).

Despite these common positioning issues in Arctoidea, there is a solid consensus regarding the sister-group relationship between Procyonidae and Mustelidae, whose lineages diverged from a common ancestor around 27 Ma (Eizirik et al. 2010, Sato et al. 2012). Procyonids started their radiation about 23 Ma, and appear to have originated in Western Eurasia (Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012, Koepfli et al. 2006). Today, this family includes 14 extant species distributed in six genera, and became restricted to the Americas. Interestingly, extinct genera of procyonids (*Cyonasua* and *Chapalmalania*) were the first carnivorans to colonize South America during the Late Miocene, before the formation of the Panama isthmus – possibly, using island arcs to disperse (Marshall et al. 1982). This early colonization provided a good opportunity for establishment and speciation, since they fulfilled a previously unoccupied dietary niche (Engelman & Croft 2019).

Mustelidae is the largest family in the whole Carnivora order, with over 60 extant species, and its evolutionary history is considered a remarkable example of adaptive radiation in mammals (Koepfli et al. 2008a). Many charismatic and well-known animals belong to this family, such as otters, badgers, ferrets and wolverines. Extant species of mustelids are globally distributed, with the exception of Antarctica (although, in Oceania, they were introduced for pest control in the 19th Century – King et al. 2009), being adapted to a variety of environments and climates and showing a broad range of locomotion types (Samuels et al. 2012). The earliest fossil records for this family date from the transition between Eocene and Oligocene (ca. 35 Ma), and its first radiations from ancestral lineages took place in Asia in the Miocene (Sato et al. 2012), later dispersing to other continents in multiple events (Koepfli et al. 2008a). In the subset of

17 extant mustelid genera included in the work of Sato et al. (2012), only six were shown to have non-Asian ancestries: one from North America (*Lontra*), two from South America (*Lyncodon* and *Galictis*) and three from Africa (*Ictonyx*, *Poecilogale* and *Vormela*); in addition, two clades within the genus *Mustela* were of European origin.

Although most South American species of mustelids seem to have originated after the interchange across the Panamanian land bridge, there is a standing hypothesis that tayras (genus *Eira*) could well have arrived to the continent before the isthmus was complete, as did the procyonids (Ruíz-García et al. 2017).

Even if biogeographic patterns of origin seem well-defined, the main divergence age for crown mustelids is not well resolved, as there is discrepancy between estimates from different authors: from as recently as 13 Ma (Eizirik et al. 2010) and 16 Ma (Sato et al. 2012) to as early as 30 Ma (Nyakatura & Bininda-Emonds 2012). Extant representatives of the most ancient radiations are mainly badgers, martens and the wolverine, while other subfamilies, such as Mustelinae (weasels, minks, polecats) and Lutrinae (otters), diverged later in time (Marmi et al. 2004).

4.1.5 Otter phylogeny

Lutrinae is a subfamily constituted by the 13 extant species of otters. Semi-aquatic or fully aquatic habits are characteristic of this clade, and otters present several life-history and morphological adaptations to this lifestyle. *Mionictis* sp. is the oldest known fossil otter, dating back from the Late Miocene (ca. 23 Ma – Matthew, 1924). Most of our knowledge regarding phylogenetic relationships amongst extant otters comes from the works by van Zyll de Jong (1987), Koepfli & Wayne (1998) and Koepfli et al. (2008b). The latter two studies were the first to use molecular data to specifically

understand those relations within Lutrinae, and some main findings are summarized below.

Koepfli & Wayne (1998) used the full cytochrome *b* gene sequence and identified three main monophyletic lineages of otters. They also found evidence for a topological proximity between Lutrinae and the Mustelinae subfamily, but the mitochondrial data used did not provide enough resolution to fully resolve their relationships. Giant otters (*Pteronura brasiliensis*) were placed in a separate monotypic clade (among the three main clades observed), that likely diverged from other Lutrinae in the Miocene, between 10-14 Ma. However, this topology was not considered fully resolved; in fact, it was not possible to confidently resolve the monophyly of the subfamily Lutrinae as a whole with the mitochondrial gene data. In a following study of Mustelidae phylogeny, the same authors employed a combination of nuclear markers (type I sequence-tagged sites from 5 genes) and cytochrome *b*, with a total sequence size of 3,180bp, and this time they could corroborate the hypothesis of Lutrinae as a monophyletic group (Koepfli & Wayne 2003).

Ten years after the first otter study, Koepfli et al. (2008b) revisited and expanded their previous work with different analytical approaches, including more otter species and using sets of multiple loci (nuclear and mitochondrial). The three primary otter clades recognized before were confirmed: one including the sea otter and river otters of Eurasia and Africa; the second with North and South American river otters (genus *Lontra*); and finally, the monotypical clade of *Pteronura*. Another finding was the evidence of *Pteronura* being the first to diverge from other extant Lutrinae. Phylogenetic relationships of Southeast Asian species were also examined for the first time using genetic data.

A few more studies, although not focused on otters, have analysed otter evolutionary relationships in broader contexts. Marmi et al. (2004) have used cytochrome *b* sequences and a complex repetitive flanking region (*Mel08*) to build Mustelidae phylogeny. Their combined Bayesian-inferred tree supported monophyly of Lutrinae as well as its sister grouping with Mustelinae. It is worth noting, though, that they only included four otter species in this analysis. In contrast, the “cytochrome *b* – only” trees by the same authors (that, for this case, included more species) had no support for Lutrinae monophyly, as the giant otter (not included in the combined tree) was placed in a sister branch to Mustelinae. Other studies that found strong support for the Lutrinae clade monophyly were Flynn et al. (2005), Sato et al. (2012) and Law et al. (2018), all using combinations of nuclear and mitochondrial sequences, although the first two had a limited representation of otter species, and the latter was the only one including the giant otter.

Cytochrome *b* sequences were again used later by Agnarsson et al (2010) to reconstruct Carnivora phylogeny analysing the majority of extant species (N=222), including most otter species as well. One noteworthy outcome of their Bayesian inference was the paraphyly of Lutrinae - the results pointed to a separation between the giant otter in a clade apart from the remaining otter species, which were monophyletic. Nyakatura & Bininda-Emonds (2012) have also questioned the monophyly of otters within their Carnivora supertree, once again observing the splitting of other Lutrinae and giant otters in a separate branch. In addition, a rather curious result was obtained in their partitioned maximum likelihood supermatrix analysis: the tayra (*Eira barbara*), normally classified within Guloninae, was instead grouped with otters.

More recently, Beichman et al. (2019) included the giant and the sea otter (*Enhydra lutris*) in a comparative phylogeny reconstruction with 10 other carnivoran

species using high-resolution datasets, obtained from whole genome sequences; the tree was based on 4-fold degenerate sites from 784 single-copy orthologous genes. Although very limited in terms of species diversity, the tree topology was similar to previously reported ones (e.g Eizirik et al. 2010), and the authors did not find evidence of gene flow from the giant otter lineage into sea otter lineages (Beichman et al. 2019).

4.2 Study goals

The rapid advance in molecular techniques over the last decades and the increasing facility in obtaining new genetic data facilitated great progress in our understanding of the evolutionary histories of organisms. Despite this, it is evident that many questions remain in the reconstruction of organism phylogenies, as is the case with the Carnivora order.

The overall aim of this chapter was to generate and propose the use of a novel set of nuclear phylogenetic markers, using data from a target-enrichment experiment on Neotropical and giant otters (see Chapter 3) and published reference genomes from other Carnivora species. To validate these markers, the phylogeny of the order Carnivora was reconstructed. The goal was to compare results with previous phylogenies (produced with other types of genetic markers), with a focus on Mustelidae and in particular Lutrinae. A secondary aim was to better understand times of divergence between carnivoran lineages and their degree of divergence. The final aim, by using multiple samples from different populations of giant otter *Pteronura brasiliensis* and Neotropical otter *Lontra longicaudis* from Amazonia, was to attempt a better clarification on the positioning of these taxa - especially the giant otter, which remains in an uncertain position that generates confusion regarding the monophyly or paraphyly of lutrines. The

use of multiple samples will also allow inferences about species diversity, and to test the hypothesis of a lower overall diversity in giant otters caused by population declines in the 20th century.

4.3 Methods

Detailed descriptions of sampling and laboratory protocols, as well as target loci selection and bioinformatics pre-processing of data can be found in Chapter 3. Analyses in the present chapter were based on a subset of the target loci designed for the study.

4.3.1 Selection of loci for phylogenetic estimations

A smaller subset of target regions was selected after sequencing for phylogenetic analyses. This selection was necessary considering the read depth per sequence – without enough read depth in a region, it would not be possible to obtain a consensus sequence for it, since we worked with short sequencing reads (<100 bp after trimming) and most target loci were around 1kbp.

The function `coverage.target` in the R package TEQC (Hummel et al. 2011) was used to obtain the number of reads in each target locus for each sample. Sample bam files were visually inspected in the program Tablet v.1.19 (Milne et al. 2013) in order to estimate an approximate number of reads necessary to obtain coverage over the whole (or most of) extent of a target sequence. From this, it was considered that a minimum of ~50 reads would be needed, and therefore only loci with an average read depth of 50 (over all samples for both species) would be considered - resulting in 34 loci that were eligible for further filtering.

The individual consensus sequences from samples for all 34 loci were called with `bcftools` (Li 2011). The same sequences were used as queries in a BLAST+ (Camacho et

al. 2009) search with genomes from 40 carnivoran species (see Table 4.1), using the dc-megablast task, suitable for interspecies comparisons. At this stage, an additional selection of loci was needed, as not all the sequences could be found in all the species, and some searches retrieved sequences that were too short compared to the reference (e.g., less than 50% of the reference's length). After this last cut-off, 17 loci remained for the phylogeny analysis (a total of 16,496 bp). For Giant and Neotropical otter concatenated sequences, diversity metrics such as nucleotide diversity, Tajima's D and overall genetic distances were also computed.

Two samples of Neotropical otters had enough coverage over the selected loci in order to build consensus and perform alignments, and the reference genome (unpublished, kindly provided by Eizirik et al.) was also used. For giant otter, six samples were used, plus the reference genome (accession number GCA_004024605.1). Therefore, counting with the individuals from reference genomes, each species had a total of three and seven representatives respectively.

4.3.2 Phylogenetic Analyses

Sequences from giant/Neotropical otter samples and from the carnivoran species were aligned for each separate region, using the iterative refinement method implemented in MAFFT (Katoh et al. 2002). Resulting aligned sequences were cleaned with trimAL (Capella-Gutierrez et al. 2009), to trim poorly-aligned segments. Then, we applied a Bayesian inference (BI) approach for each of the 17 regions individually with MrBayes v.3.2.6 (Huelsenbeck & Ronquist 2001). This program uses the Markov chain Monte Carlo (MCMC) technique for approximation of the posterior probabilities of phylogenetic trees. The present analysis was done in 3 independent runs with 4 parallel MCMC chains for 2,000,000 generations, using a general model of nucleotide substitution

(GTR) with gamma-distributed rate variation across sites, as determined by the program ModelGenerator (Keane et al. 2006) using a Bayesian information criterion. Trees were rooted using pangolins (*Manis javanica* and *M. pentadactyla*) and domestic horse (*Equus caballus*) as outgroups (Genbank accessions GCA_000738955.1, GCA_000738955.1 and GCA_002863925.1 respectively). The first 25% of trees were discarded as a burn-in. Trees were visualized and edited in FigTree 1.4.4 (Rambaut 2018).

4.3.3 Supermatrix Tree, Calibration and Divergence Date Estimates

The 17 individual sequence alignments were concatenated in a single supermatrix with FASconCAT (Kück & Longo 2014). To reconstruct the phylogeny with this supermatrix, three different methods were used: a) a BI method implemented in BEAST v.2.6.2 (Bouckaert et al. 2019; b) BI with MrBayes v.3.2.6 (Huelsenbeck & Ronquist 2001); c) a maximum likelihood (ML) approach with RAxML (*Randomized Axelerated Maximum Likelihood*) (Stamatakis 2006).

The xml input file for BEAST was created using BEAUti v. 2.6 (Bouckaert et al. 2019). A Birth-Death model was used as tree prior, under a relaxed log-normal molecular clock model, and incorporating a standard GTR substitution model. The MCMC was run for 50 million generations, with a sampling frequency of 500, and discarding the first 10% as burn-in.

The same BEAST run was also used to estimate lineage divergence times. Four MRCA prior points were used for node calibration (with normal prior distribution): divergence dates for the clades Carnivora, Canidae, Pinnipedia and Mustelidae based on literature fossil records (Table 4.2). Convergence and effective sample size (ESS) values were inspected by checking BEAST log files in the program Tracer v.1.7.1. (Rambaut et al 2018). A Maximum clade credibility tree was generated in TreeAnnotator v.2.6.2

(Rambaut & Drummond 2007), discarding the first 10% of trees. The final output tree was visualized and edited in FigTree. In RaxML, the phylogeny was reconstructed with a rapid bootstrapping option and subsequent ML search, and the number of bootstrap replicates was inferred by using the autoMRE option under the -N flag.

Table 4.1: List of carnivoran reference genomes used in the study.

Species	Common name	Accession number or reference	ID
<i>Pteronura brasiliensis</i>	Giant Otter	GCA_004024605.1	GiantOtter
<i>Lontra longicaudis</i>	Neotropical Otter	Eizirik et al. (provided by authors)	NeoOtter
<i>Lontra canadensis</i>	Northern American river otter	GCA_010015895.1	NARivOtter
<i>Lutra lutra</i>	Eurasian otter	GCA_902655055.2	EurOtter
<i>Enhydra lutris</i>	Sea Otter	GCA_002288905.2	Sea_Otter
<i>Mustela erminea</i>	Stoat	GCA_009829155.1	Stoat
<i>Mustela putorius furo</i>	Domestic ferret	GCA_000215625.1	Ferret
<i>Neovison vison</i>	American mink	GCA_900108605.1	American_mink
<i>Martes zibellina</i>	Sable	GCA_012583365.1	Sable
<i>Gulo gulo</i>	Wolverine	GCA_900006375.2	Wolverine
<i>Mellivora capensis</i>	Ratel or honey badger	GCA_004024625.1	Honey_badger
<i>Taxidea taxus</i>	American badger	GCA_003697995.1	AmBadger
<i>Spilogale gracilis</i>	Western Spotted Skunk	GCA_004023965.1	WSpSkunk
<i>Bassariscus sumichrasti</i>	Cacomistle or Ringtail	DNA Zoo (Dudchenko et al. 2018)	Cacomistle
<i>Procyon lotor</i>	Common raccoon	DNA Zoo (Dudchenko et al. 2018)	Raccoon
<i>Nasua narica</i>	White-nosed coati	DNA Zoo (Dudchenko et al. 2018)	Whitenosed_Coat
<i>Ailurus fulgens</i>	Lesser panda or red panda	GCA_002007465.1	Red_Panda
<i>Ursus maritimus</i>	Polar bear	GCA_000687225.1	Polar_bear
<i>Ursus americanus</i>	American black bear	DNA Zoo (Dudchenko et al. 2018)	Blackbear
<i>Ursus arctos horribilis</i>	Brown bear or Grizzly bear	GCA_003584765.1	Brown_bear
<i>Ailuropoda melanoleuca</i>	Giant panda	GCA_002007445.2	Panda
<i>Zalophus californianus</i>	California sea lion	GCF_900631625.1	Cal_SeaLion
<i>Odobenus rosmarus</i>	Pacific walrus	GCA_000321225.1	Walrus
<i>Mirounga leonina</i>	Southern elephant seal	GCA_011800145.1	SouthElSeal
<i>Phoca vitulina</i>	Harbor seal	GCA_004348235.1	HarbSeal
<i>Puma concolor</i>	Puma or Mountain Lion	GCA_003327715.1	Puma
<i>Acinonyx jubatus</i>	Cheetah	GCA_003709585.1	Cheetah

Table 4.1 – continued

Species	Common name	Accession number or reference	ID
<i>Felis catus</i>	Domestic cat	GCA_000181335.4	Cat
<i>Lynx canadensis</i>	Canada Lynx	GCA_007474595.2	Canada_Lynx
<i>Panthera pardus</i>	Leopard	GCA_001857705.1	Leopard
<i>Panthera onca</i>	Jaguar	GCA_004023805.1	Jaguar
<i>Neofelis nebulosa</i>	Clouded leopard	DNA Zoo (Dudchenko et al. 2018)	Clouded_Leopard
<i>Paradoxurus hermaphroditus</i>	Asian palm civet	GCA_004024585.1	AsianPalmCivet
<i>Crocuta crocuta</i>	Spotted hyena	GCA_008692635.1	SpHyena
<i>Suricata suricatta</i>	Meerkat	GCA_006229205.1	Meerkat
<i>Mungos mungo</i>	Banded mongoose	GCA_004023785.1	BandedMongoose
<i>Cryptoprocta ferox</i>	Fossa	GCA_004023885.1	Fossa
<i>Canis lupus familiaris</i>	Domestic dog	GCA_008641055.3	Domestic_dog
<i>Canis lupus</i>	Wolf	GCA_007922845.1	Wolf
<i>Lycaon pictus</i>	African Wild dog	GCA_001887905.1	AfWildDog
<i>Vulpes vulpes</i>	Red fox	GCA_003160815.1	Red_fox

Table 4.2: Node calibration dates used in Beast analyses.

Clade	Divergence date used	Reference
Carnivora	64.6±1.35	Fox et al. 2010
Canidae	39.74±0.07	Robinson et al. 2004
Pinnipedia	26.0±1.0	Valenzuela-Toro et al. 2019
Mustelidae	28.95±1.35	Clark & Beerbower 1967

4.4 Results

4.4.1 Individual Locus Trees

Phylogenies inferred for individual loci presented similar topologies with an overall pattern consistent with other Carnivora phylogenetic trees (see Appendices 4.1 – 4.17), although branches could present moderate to low support values. A typical single



Fig. 4.3: Detail from Locus 17 BI tree obtained in MrBayes, showing only the Mustelidae family. Mustelines are highlighted in yellow inside the polytomy containing otter species.

Two loci had topologies that were most distorted compared to the other loci: Locus 2 (Fig. 4.4) and Locus 6 (Fig. 4.5). The tree generated for Locus 2 has its general topology in agreement with current classifications, but the lineage including the ferret, stoat and American mink (i.e., representing the subfamily Mustelinae) has much longer branch lengths than for all other taxa (Fig. 4.4). The branches show a high support value, and average nucleotide substitution rates were 0.092 and 0.052. As this might indicate some sort of selective pressure, the location of the locus was inspected in Ensembl genome browser (<http://www.ensembl.org>) to check for any possible overlaps or proximity to coding regions. In Figure 4.6, it is possible to see that this locus (marked

with black arrows) is only about 1kb apart from a zinc finger protein gene (ZNF646) in the ferret genome.

Locus 6 tree also presented an unusual topology, with the family Canidae positioned as a sister clade to all Feliformia (Fig. 4.5). This locus overlaps with the gene GFRA1 (Fig. 4.7), that encodes one of the glial cell line-derived neurotrophic factor receptor (GDNFR) family of proteins. Interestingly, the dog genome shows two splicing variants for this gene according to Ensembl genome browser (which were not observed in species from other families). To investigate potential functions of the genes associated with the loci in question, databases such as the International Mouse Phenotyping Consortium (IMPC) (Dickinson et al. 2016), Entrez Gene (Maglott et al. 2011) and Online Mendelian Inheritance in Man (OMIM) (Hamosh et al. 2004) were searched for ontologies and possible phenotypes. According to the QuickGO (<https://www.ebi.ac.uk/QuickGO/>) database, GFRA1 is a plasma membrane component involved in signalling receptor activity, and ZNF646 is a nuclear protein that enables DNA-binding transcription factor activity among other molecular functions. Mutations in GFRA1 were reported to have phenotypical effects on mouse, especially regarding the renal/urinary system and abnormal development and/or morphology of some organs and systems (e.g., Davis et al. 2013, Tomaca et al. 2000, Uesaka et al. 2007, Cacalano et al. 1998).



281

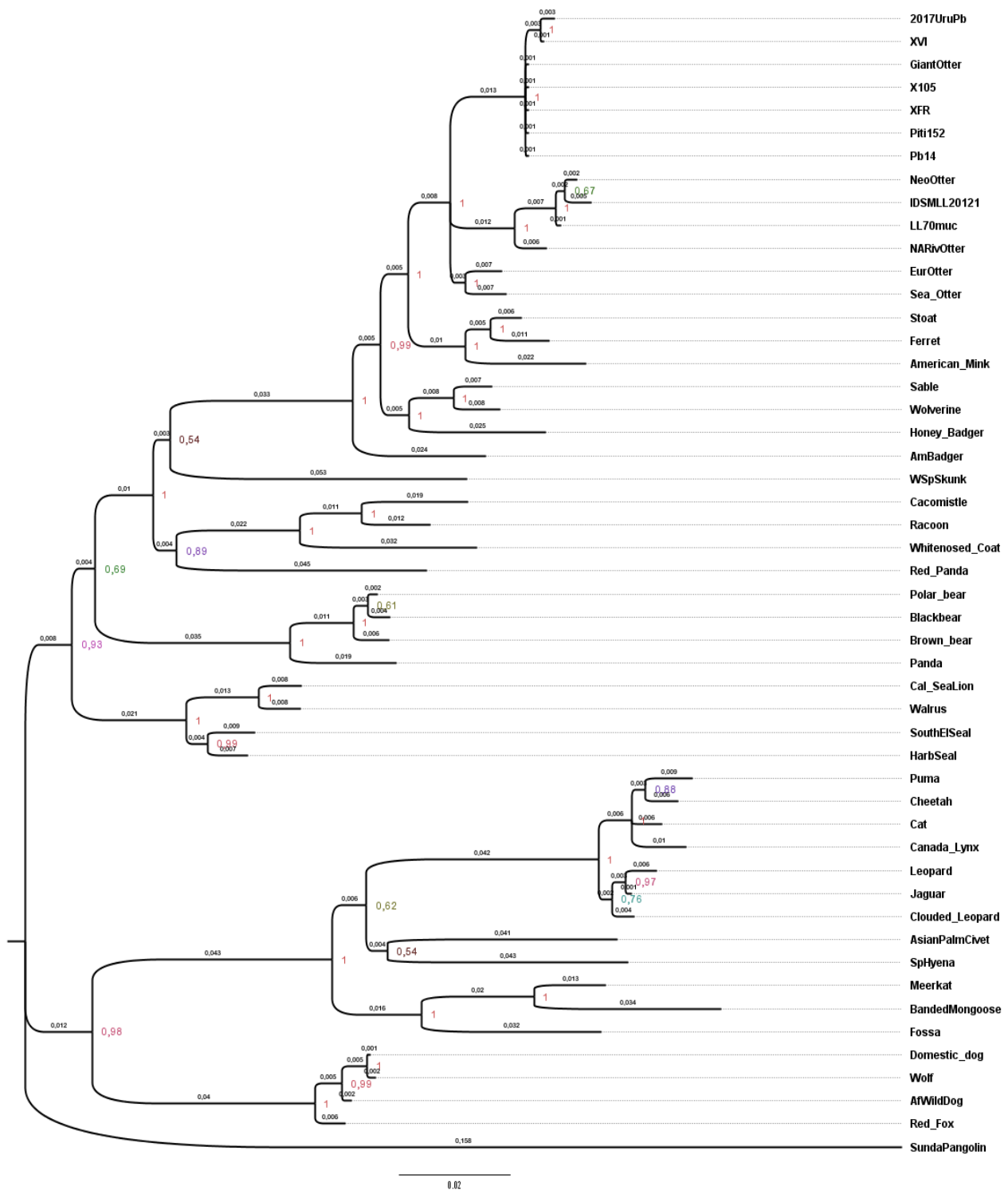


Figure 4.5: Phylogenetic relationships of Locus 6 for Carnivora species. Coloured numbers indicate support values for each node, and on top of each branch numbers in black correspond to branch lengths (measured in expected substitutions per site).

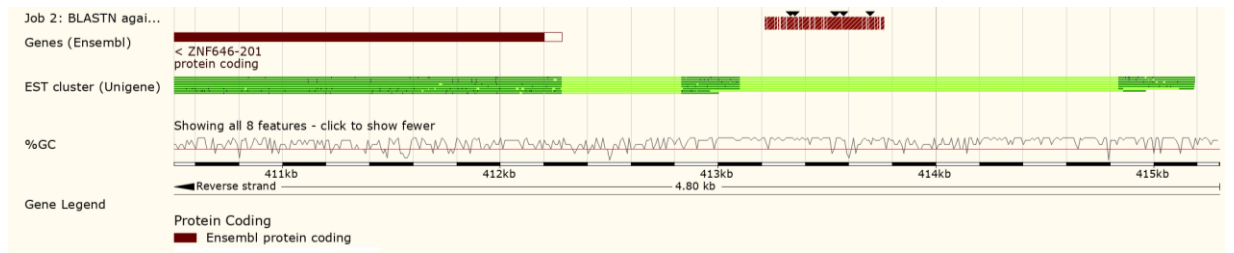


Figure 4.6: Ensembl Genome browser showing the location of Locus 2 (in red, indicated by black arrows) and the ZNF646 gene in the domestic ferret (*Mustela putorius furo*) genome assembly.

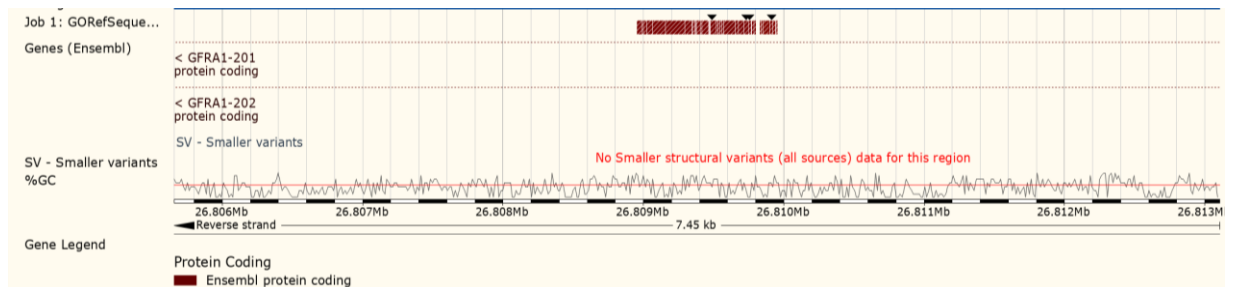


Figure 4.7: Ensembl Genome browser showing the location of Locus 6 (in red, indicated by black arrows) overlapping with the GFRA1 gene (dashed line) in the domestic ferret (*Mustela putorius furo*) genome assembly.

4.4.2 Supermatrix Tree and Date Calibration

After concatenation of the 17 sequences, the supermatrix consisted of a complete dataset of 16,496 base pairs. The BI (MrBayes) and ML (RaxML) phylogenetic trees are presented in Figures 4.8 and 4.9. Due to the distinct topologies presented by Loci 2 and 6 in the individual BI trees, an additional tree was generated in MrBayes without including those loci (Fig. 4.10). The overall topology was not changed with their exclusion and so they were retained in further analyses. The supermatrix phylogenetic tree generated by Bayesian inference in BEAST is shown in Fig. 4.11. All nodes showed high posterior probability support.

No prominent differences were observed between trees generated by the three different methods. Note that in Fig. 4.9 (ML tree), some of the internal nodes are rotated in a different manner, but the pattern is the same. There was a distinct separation between the suborders Caniformia and Feliformia. Feliformia clades are separated according to the existing families for which there were representative species in the present study: Felidae, Viverridae, Hyaenidae, Eupleridae and Herpestidae. Within the Felidae family, the cheetah (*Acinonyx jubatus*) and the Puma (*Puma concolor*) form a monophyletic clade, which in turn is sister to a clade including the domestic cat (*Felis catus*). Here, there was a slight difference between this study and Nyakatura & Bininda-Emonds' (2012) and Zhou et al. (2017): in their trees, the cat was positioned in another clade (with other *Felis* species) and with *Prionailurus* spp. (leopard cats) as its sister group, so it did not form a monophyletic group with *Lynx* spp. branch. The latter, instead, was a sister clade to (*Acinonyx* + *Puma*) in both aforementioned studies. This could, though, be related to the more limited taxon sampling for the present analyses.

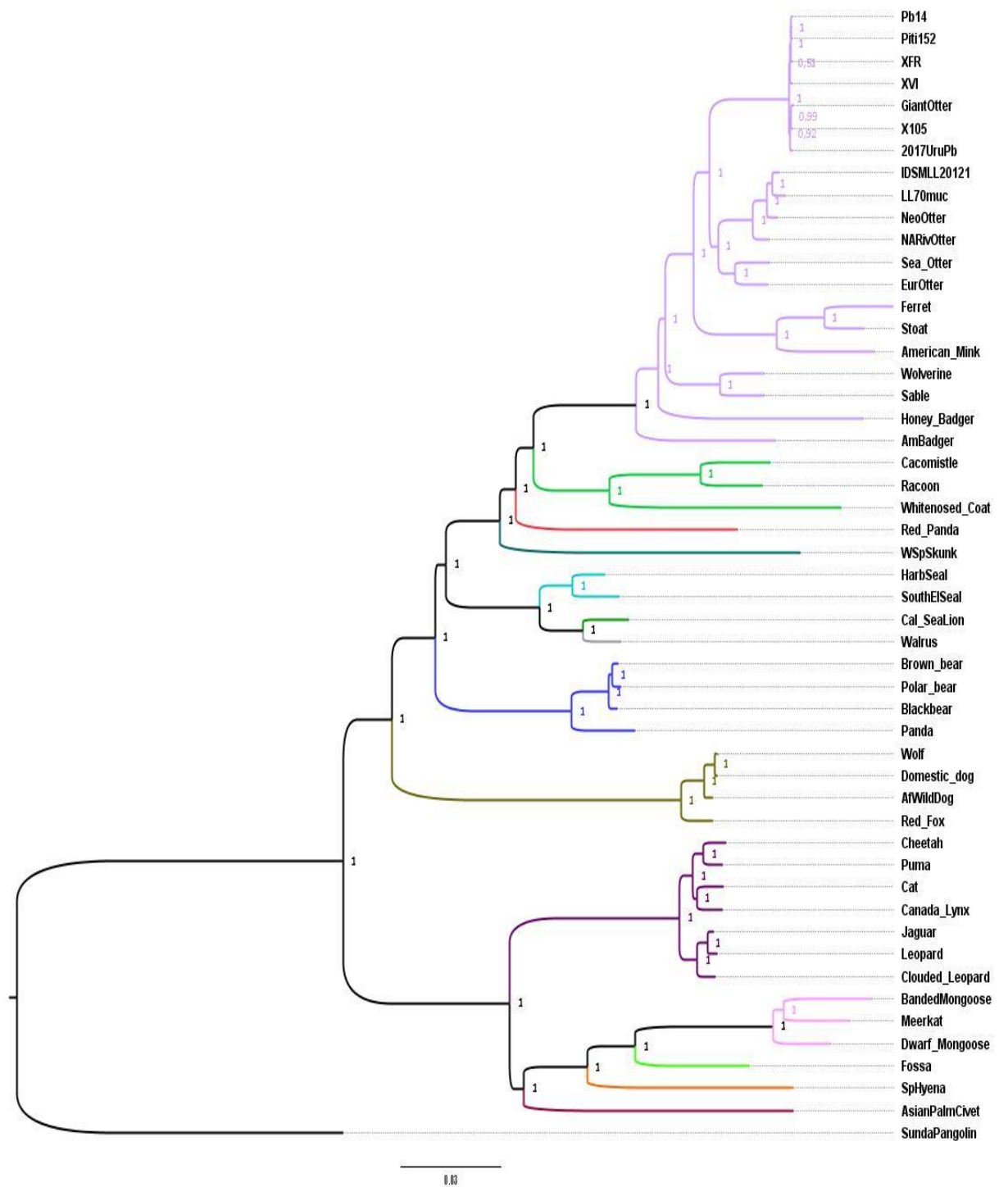


Figure 4.8: BI phylogenetic tree generated in MrBayes. Each node shows its respective posterior probability value, and Carnivora families are displayed in different colours.

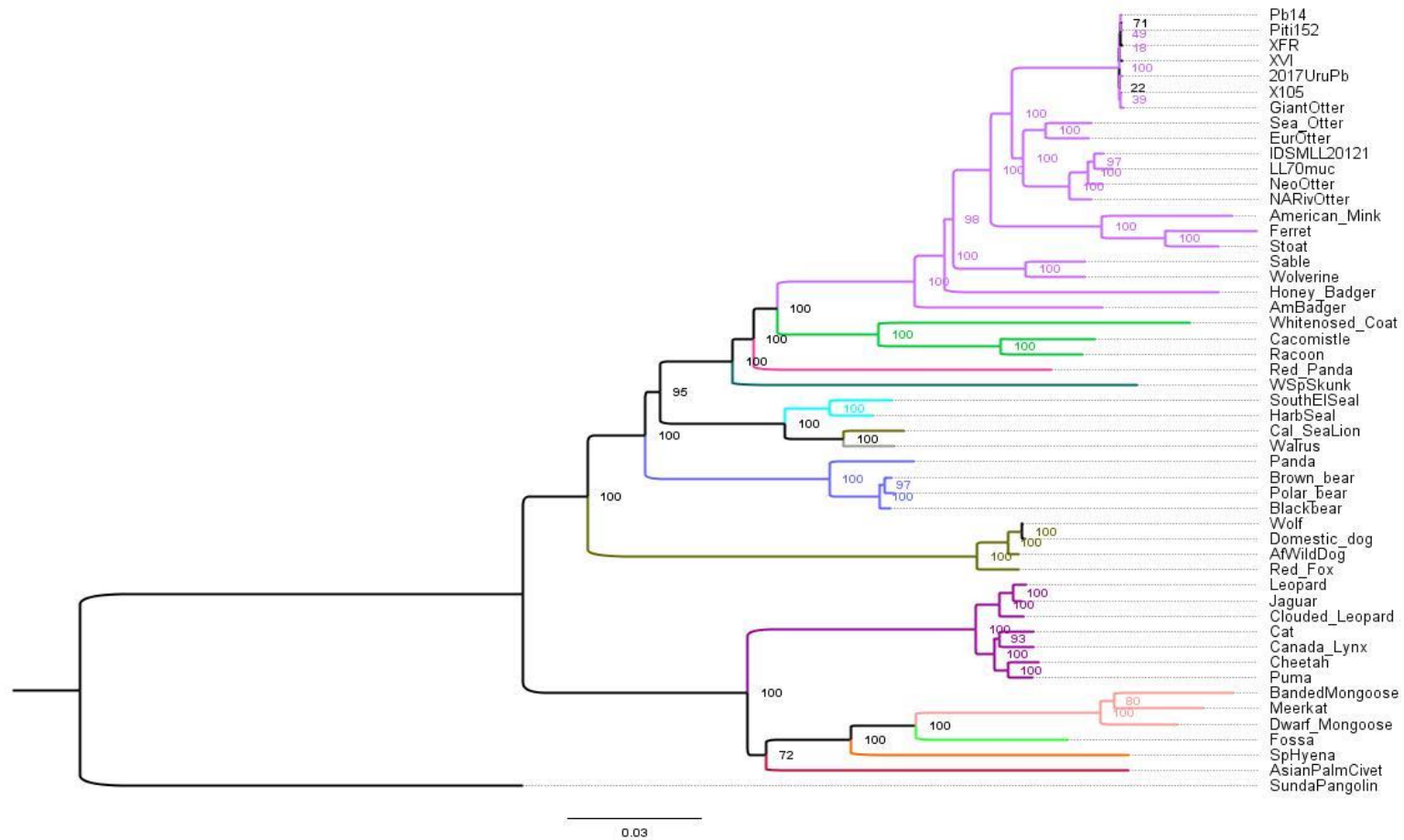


Figure 4.9: Maximum likelihood tree produced in RaXML for the order Carnivora. The bootstrap support values are shown for each node , and Carnivora families are displayed in different colours.

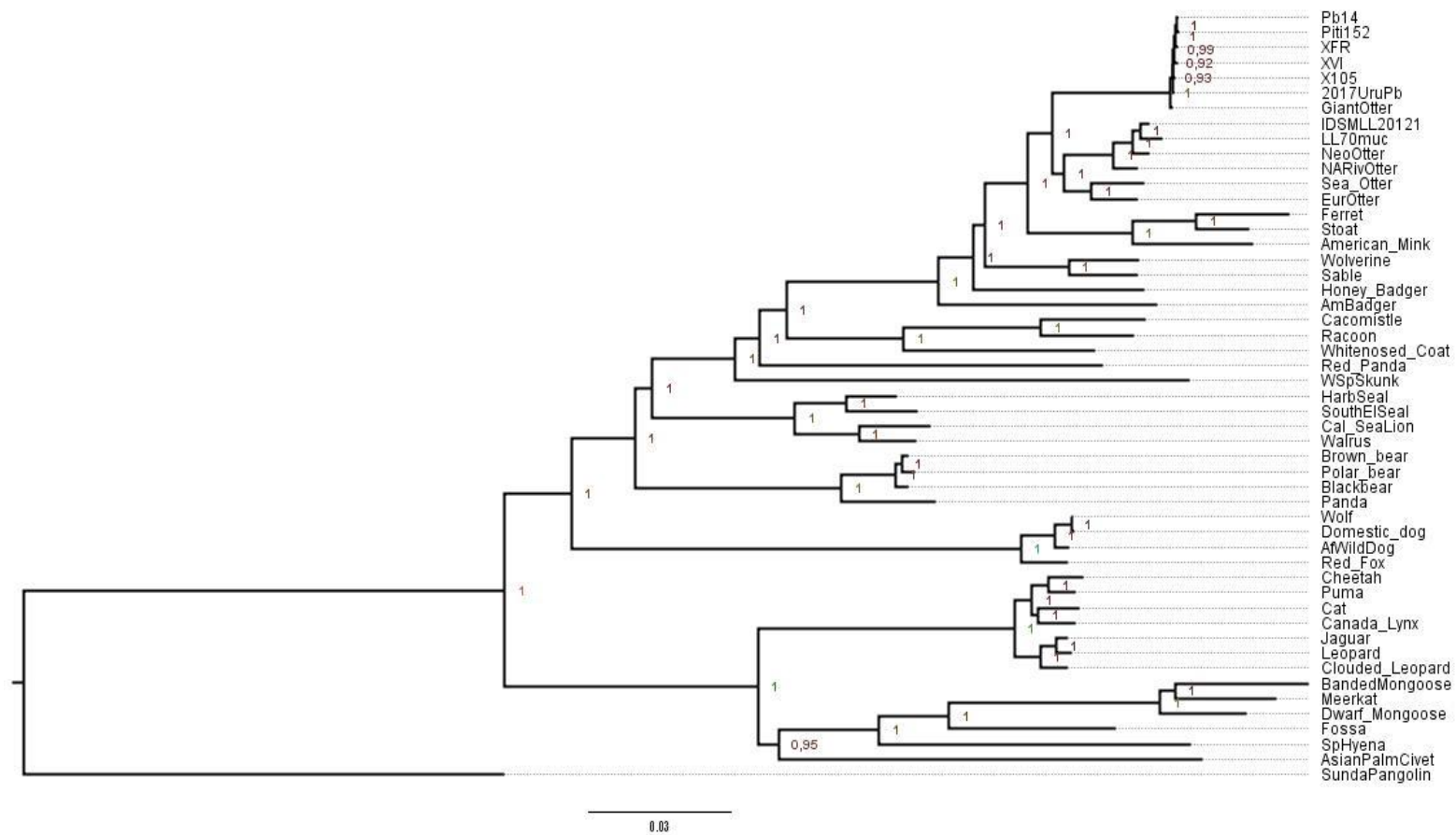


Figure 4.10: BI tree produced in MrBayes. Posterior probability values are shown for each node.

In the Caniformia suborder, the supermatrix analysis was effective in splitting the two main superfamilies, Cynoidea and Arctoidea. Cynoidea has only Canidae as an extant representative family. The inferences from Canidae lineage are limited in face of the small number of species used, but its topology is consistent with canid evolutionary history, with *Canis* (dog and wolf) forming a monophyletic group together with the African wild dog *Lycaon pictus*, and separated from the clade composed by the red fox (*Vulpes vulpes*).

Ursidae was the first diverging lineage in Arctoidea, with the giant Panda diverging earlier than the other bear species, which together form a single monophyletic clade. The supermatrix tree also supports the monophyly of Pinnipedia, that diverges in two main lineages, one formed by true seal species (Phocidae) and with the other branch leading to Odobenidae (walrus) as a sister group to the California sea lion *Zalophus californianus* (representing the family Otariidae).

The Musteloidea is then next lineage derived following Pinnipedia in these phylogenies. With the Western spotted skunk (*Spilogale gracilis*) in the most basal position, it is possible to confirm the placement of family Mephitidae as the closest relative of pinnipeds. Ailuridae, the red panda family, is the sister group to the Procyonidae+Mustelidae lineage. The internal branches of Procyonidae were equally highly supported.

Finally, regarding the topology of Mustelidae family, the Bayesian inference has strongly recovered Taxidiinae (American badgers), Mellivorinae (honey badger), Guloninae (sable and wolverine), Mustelinae (stoat, mink, ferret and ferret) and Lutrinae (all otters included in the analysis) as monophyletic groups. Taxidiinae was the earlier derived branch. Lutrinae was divided into a clade containing the giant otter and another

clade further split in two branches: one with the representatives of *Lontra* genus, and the other grouping the sea otter (*Enhydra lutris*) with the Eurasian otter (*Lutra lutra*).

The split between Feliformia and Caniformia suborders was estimated to have happened 56 Ma, and their basal radiations were dated at 40.3 and 51.8 Ma respectively. It was not possible to determine divergence dates for all families, since in many cases only a single species per family was used (Viverridae, Eupleridae, Mephitidae, Hyaenidae). Some nodes were closely spaced within a short time, suggesting a rapid period of diversification; for instance, the first Arctoidea radiation (the split of Ursidae and Pinnipedia), occurring between 45.3 and 42.6 Ma; and several internal nodes within Musteloidea.

4.4.3 Giant and Neotropical otter Diversity

Since only three individuals of Neotropical otters (two from this study and one reference genome) were used in this phylogeny, little can be inferred from their data. Nevertheless, inspection of the phylogenetic tree shows that Neotropical otter branches were clearly longer than those of giant otter, which likely indicates a higher diversity of the former. For the seven giant otter individuals (including the reference genome), nucleotide diversity π was 0.00144, and Tajima's D statistic was 0.102. Among the same seven samples, there were 47 segregating sites and 26 parsimonious informative sites; and the overall Kimura-2P mean genetic distance was 0.001451 ± 0.0002 .

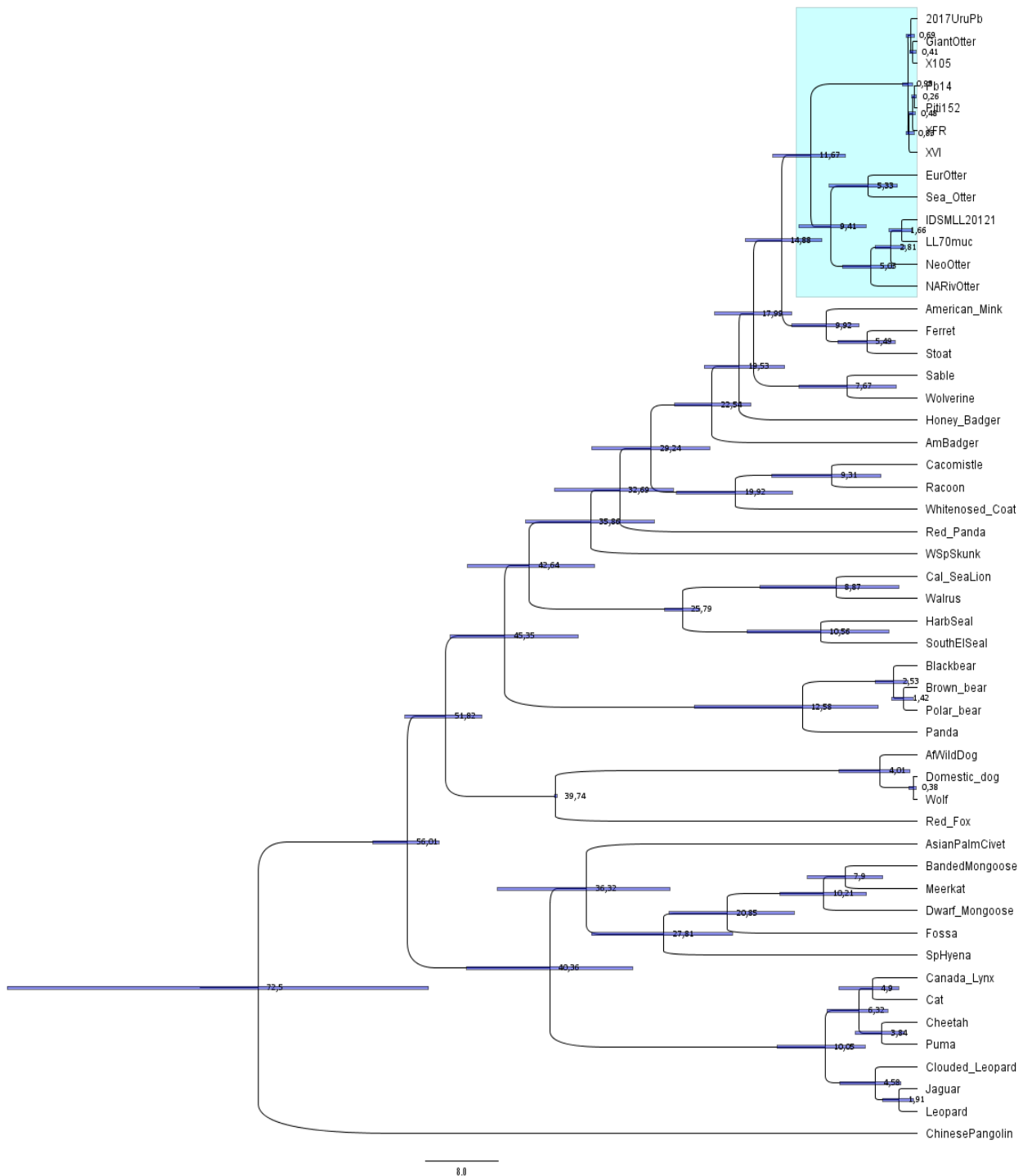


Figure 4.11: Phylogeny resulting from Bayesian analysis of the supermatrix in BEAST. Node bars represent 95% confidence interval for node ages (which are displayed at each node in Ma). The Lutrinae are highlighted in blue.

Neotropical otters also have shown an older temporal split for its lineages (between 2.8 – 1.66 Ma). The divergence event that separated the ancestors of the two samples from Balbina reservoir (LL70muc) and Tefé Lake (IDSMLL2012) occurred around 1.66 Ma (CI 2.6 -0.8 Ma), and the split between their lineage and the branch of the reference genome (which is also sequenced from an Amazonian individual – V. de Ferran, personal communication) was 2.8 Ma (CI 4.3-1.31 Ma).

Giant otter temporal splits ranged between 0.26 and 0.69 Ma; the first, leading to two different basal lineages in the studied samples happened ca. 0.98 Ma (1.58 – 0.58 Ma). Then, the first one diverged at ~830 Ka leading to two more consecutive splits, with the most recent arriving to the ancestors of the two samples from Balbina (Pb14 and Piti152). Interestingly, individuals from the Xixuaú area were split in the two most basal branches: XVI and XFR were grouped with the Balbina individuals, having descended from earlier ancestors; while X105 was positioned in the other basal lineage, having shared its most recent common ancestor with the reference genome individual. This ancestor was from a sister lineage with the ancestors of 2017UruPb, the only sample from the Amanã Lake area.

4.5 Discussion

4.5.1 Phylogenies and divergence times

At present, researchers commonly use combinations of mitochondrial and nuclear sequence data to elucidate evolutionary relationships, and progress is being made on identifying new potentially informative markers, including Ultra conserved elements (UCES), *Alu* elements in primates, exome capture and retroposon insertions (Jiang et al.

2016, Zarza et al. 2018, Courcelle et al. 2019, Doronina et al. 2015). This study used a novel set of nuclear loci (encompassing putatively anonymous non-coding regions), and assessed their potential in reconstructing the phylogenetic relationships of members of the order Carnivora.

The 17 loci used, comprising 16,496 bp (and with 11 chromosomes represented, considering the domestic dog reference genome – see Appendix 4.18), have allowed a robust reconstruction of the phylogeny of carnivorans. The supermatrix phylogenetic tree generated had high posterior support values for all the nodes recovered, and showed patterns consistent with previous findings in the literature. In the family Felidae, branching patterns were concordant with the phylogenies presented in Agnarsson et al. (2010), Nyakatura & Bininda-Emonds (2012) and Flynn et al. (2005). Regarding non-felid feliforms, there was again a good overall agreement with previous studies (Zhou et al. 2017, Agnarsson et al. 2010, Nyakatura & Bininda-Emonds 2012, Eizirik et al. 2010), with Viverridae being the most ancient family among the ones included here, and a monophyletic clade containing the representatives of families Hyaenidae, Eupleridae and Herpestidae. Unfortunately, there are no available genome assemblies of the African Palm Civet (the only species of family Nandiniidae), which would allow confirmation of its basal divergence within Feliformia. Nevertheless, even if the representation of feliform species was small, it was still possible to recover and identify the main radiation patterns of the group at the family level.

For Caniforms, the phylogeny results were also consistent with earlier studies. In the family Canidae, the branching pattern indicated subdivision into tribes Canini and Vulpini, which was also recovered, with a larger number of species, by other authors (Nyakatura & Bininda-Emonds 2012, Agnarsson et al. 2010).

Another evidence in favour of the utility of this set of loci is that some historically doubtful or conflicting nodes in the Arctoidea superfamily were successfully recovered in the phylograms generated, and are in agreement with the current scientific consensus. For instance, the uncertainty regarding the position of pinnipeds in relation to Ursidae or Musteloidea, which has been in discussion until quite recently (see Berta 2018). In the present inference, Pinnipedia was recovered as a monophyletic group in a sister position to Musteloidea, confirming and supporting previous results obtained in recent studies by Doronina et al. (2015) and Paterson et al. (2019).

One more issue that has been extensively discussed in the literature is the position of Ailuridae (represented by its only extant species, the red or lesser panda *Ailurus fulgens*; e.g. Flynn et al. 2000, Arnason et al. 2007, Yu & Zhang 2006, Sato et al. 2009). For a long time, it remained ambiguous in relation to other taxa, in particular Mephitidae and Procyonidae, at the basal positions of the superfamily Musteloidea. With the loci employed here Ailuridae was positioned as a sister group to (Procyonidae+Mustelidae), which corresponds to the current academic consensus (Eizirik et al. 2010, Nyakatura & Bininda-Emonds 2012). This was also able to resolve the related conflict on the position of Mephitidae, here shown to be ancestral within Musteloidea consistent with other authors (Nyakatura & Bininda-Emonds 2012, Luan et al. 2013, Law et al. 2018).

Within Lutrinae one of the main remaining questions regarding its phylogeny is whether or not it is a monophyletic group. This confusion is based mainly on the positioning of giant otters *Pteronura brasiliensis*, because other lutrine species seem to be overall consolidated into a monophyletic group, according to most studies. Here I found a high node support for giant otters internally to Lutrinae, consistent with monophyly.

Nonetheless, this result should be interpreted with caution. Law et al. (2018) and Koepfli et al. (2008b) also supported monophyly for the otter subfamily, however both included the majority of otter species in their analyses. Two recent studies where Lutrinae was recognized as a paraphyletic group (Agnarsson et al. 2011 and Nyakatura & Bininda-Emonds 2012) also included a large number of otter species (and likewise a large number of Mustelinae, otter's putative closest relatives). This was not possible in this study since whole-genome assemblies were needed to retrieve the target loci, and so far only five otter whole genomes were sequenced out of 13 species, and only 4 out of 17 Mustelinae. It is noteworthy, though, that in Agnarsson et al. (2011) *Pteronura* was in a monotypic branch between Lutrinae and the Chinese ferret badger *Melogale moschata*; whereas in the supertree by Nyakatura & Bininda-Emonds (2012), it was placed within a polytomy with the African striped weasel *Poecilogale albinucha*, Saharan striped polecat *Ictonyx libyca* and the two Neotropical species of grisons (*Galictis*). In Eizirik et al. (2010), another *Ictonyx* species (*I. striatus*) was recovered as a sister lineage of Lutrinae, but unfortunately, their study did not include the giant otter. Therefore, it seems that internal nodes at the mustelid subfamily level need more genetic resolution and should still be resolved, particularly between Mustelinae and Lutrinae.

With respect to the main Carnivora divergence dates, they will be mainly discussed considering and contrasting results to two studies that also have recently estimated divergence times over the whole order: Eizirik et al. 2010 and Nyakatura & Bininda-Emonds 2012. Origins of Carnivora inferred in this chapter date back to 72.5 Ma, but the 95% CI was large (54.5-99.5Ma). Nyakatura & Bininda-Emonds have estimated this origin as 89.6 Ma (83.1 - 96.2 Ma), but they suggest that this age could be younger since they did not include a Pholidota (pangolins) species as outgroup. Here, the

Malayan pangolin was used to root the tree, and indeed our estimate of Carnivora age was slightly younger than theirs, though the confidence intervals overlapped extensively.

The estimated age of divergence between Caniformia and Feliformia (56 Ma – 95% CI 59.5–52.5 Ma) was similar to that obtained by Eizirik et al. (2010), 59.2 Ma (CI 51.6–64.7), but younger than the one estimated by Nyakatura & Bininda-Emonds (2012), 64.9 Ma (CI 62.3 - 67.5). For all Families, dates of origin and divergence were within the range of estimates of both studies, with a single exception – the node corresponding to the radiation of Canidae, that here was dated as 39.74 Ma (95% CI 39.72–39.78), whereas in Eizirik et al. it was dated as 7.8 Ma (5.9–11.5) and in Nyakatura & Bininda-Emonds, 16.3 Ma (13.9–18.5). This also had the narrowest 95% CI obtained for all nodes, and is compatible with dates from the fossil record, since the oldest canid fossil is around 43 Ma (Storer 1984). As discussed earlier, this young radiation of Canidae makes sense if one considers the extant subfamily. But here, node calibration was done using the age of a *Hesperocyon* fossil, which belongs to the extinct subfamily Hesperocyoninae. If the node calibration had been done considering a fossil from the Caninae subfamily then it is likely that the estimate would be much younger. Indeed, Eizirik et al. used the oldest *Canis* fossils as calibration constraints, which are dated at only 5.3 Ma.

Considering the family Mustelidae and the focal subfamily Lutrinae, here the estimated age of divergence between Lutrinae and the sister clade Mustelinae (14.88 Ma) was very close to the age estimated by Beichman et al. (2019) using a high-resolution set of loci (4-fold degenerate sites from 784 single-copy orthologous genes): 14.4 Ma (10.4–20.1), considering the split between otters (giant and sea otter) and the ferret. The age of divergence between the lineage leading to sea otter (or remaining otters) and the giant otter lineage were also close comparing this study and the ones by Beichman et al.

(2019), Marmi et al. (2004) and Law et al. (2018): 10.1 Ma (6.6-15.4), 10.6 - 7 Ma, and 9.96 Ma (8.47-11.63), respectively.

4.5.2 Loci 2 and 6 Gene ontologies

Loci 2 and 6 resulted in atypical gene trees. According to the gene ontology, the gene ZNF646, 1kb apart from Locus 2, (according to Ensembl genome browser) is involved in DNA transcription processes. In human RNA Seq profiles, ZNF 646 was found to be considerably more expressed in the testis (although it is expressed in other tissues as well) (Fagerberg et al. 2014). The phylogeny generated for this locus (Figure 4.3) suggests more rapid divergence for the lineage including the stoat, mink and ferret, possibly driven by selection. Although this cannot be resolved further with available data, further research may suggest a mechanism. GFRA1, where Locus 6 is completely overlapping, encodes a transmembrane receptor protein for glial cell line-derived neurotrophic factor (GDNF), which is involved in the control of neuron survival and differentiation. In humans, it is a candidate for Hirschsprung disease, a congenital disorder of the colon that causes chronic constipation. The relevant point for this region might reside in the fact that Canids show a splicing variant for that gene; Locus 6 tree was distorted indeed due to the odd position of Canidae as a sister lineage to Feliformia. Therefore, this gene might have some particular function for the dog family that influenced in this gene's evolution, perhaps being currently under selection. Although clinical phenotypes have been identified after mutations in the mouse GFRA1 gene, it is difficult to make any assumptions about potential adaptive value of this region for dog relatives.

4.5.3 Giant and Neotropical otter diversity and phylogenetic inferences

Previous studies have revealed that the Neotropical otter has an overall high genetic diversity throughout its distribution (Trinca et al. 2007,2012, Hernández-Romero et al. 2018), and especially in Western Amazonia (Ruiz-Garcia et al. 2018). Even with a small sample size, the present phylogenetic inference seems consistent.

The estimated divergence dates between Neotropical otter lineages (1.66 Ma and 2.8 Ma) were both similar to divergence estimations reported in Ruíz-Garcia et al. (2018). Furthermore, these estimates are young enough to have happened after the completion of the Panama isthmus in the late Pliocene - early Pleistocene 2-3 Ma, when Neotropical otter ancestors colonized and spread across the South American continent.

Many hypotheses have been postulated regarding the origins of diversity in Amazonia and consequent taxonomic radiations during the Plio-Pleistocene periods (see Haffer, 1997). In fact, substantial changes in the Amazonian drainage system that shaped the current landscape occurred relatively recently, in the last 3-2 million years (Ribas et al. 2012). The results presented here, although with limitations due to the small sample size, seem to be concordant with Ruíz-Garcia et al. (2018), who have also reported a high haplotypic diversity for the species in Amazonia based on three mitochondrial genes (Cyt-b, COI and COII). High haplotype diversity in Amazonia was also observed by Trinca et al. (2012) based on 1471bp from the mitochondrial control region and the genes *ATP8*, *ATP6* and *ND5*. Moreover, as documented by Pimenta et al. (2018), Neotropical otters have revealed a notable resilience to the impacts of commercial hunting for the pelt trade in the 20th century; so, it would be unlikely to experience any durable effects of such events in the species genetic diversity (such as a genetic bottleneck).

Giant otters, instead, have suffered worse consequences of the pelt trade. There was a documented decline in their populations (Duplaix et al. 2015, Pimenta et al. 2018), with many becoming locally extinct (e.g. Lima et al. 2014), which could have led to impacts in the species genetic diversity. Nevertheless, so far, weak evidence for a genetic bottleneck effect has only been noted for one population in the Iténez/Guaporé sub-basin (Bolivian Amazonia) with mitochondrial control region and Cyt-b sequences (Pickles et al. 2011). Nevertheless, nucleotide diversity of mitochondrial sequences estimates reported for the species in Central Amazonia were low (Garcia et al. 2007 - $\pi = 0.006$). In contrast, populations in the Colombian Orinoco (Caballero et al. 2015), showed higher levels of both haplotype and nucleotide diversity when compared to other populations, again based on mitochondrial DNA data (258bp of the control region).

In this analysis, relatively low nucleotide diversity was observed for giant otters compared to the available samples of Neotropical otter. Again, due to a limited sample size and samples from few populations on a smaller geographic range, inferences are also constrained. The age of splits in the ancestral lineages of giant otters were younger than those reported by Ruíz-García et al. (2018) in Colombia, Mamoré (Bolivia), Peruvian Amazonia and Orinoco. However, Ruíz-García et al. (2018) identified another cluster which had younger split ages similar to this study (between 0.03–0.96 Ma), and this cluster in fact included two individuals from the Brazilian Amazonia (rivers Negro and Javari).

This timeframe could also indicate that those splits are related to Pleistocene events. According to Ruíz-García et al. (2018), unlike Neotropical otters, giant otters were probably more affected by vicariance effects, landscape barriers such as rapids, and past geological events. Another relevant finding from the same study was the identification of patches of genetic similarity among the 59 samples analysed, that were

of about 600 km for giant otters – with more mitochondrial similarity than would be expected by chance. Considering that the samples used here were within a maximum distance of ~500 km, this could also explain the low diversity and overall genetic distance observed.

Finally, a possible effect of demographic reduction during the fur trade cannot be discarded as a factor reducing giant otter genetic diversity in the Brazilian Amazonia. Although a bottleneck effect has only been suggested in one study and for a particular region using mtDNA data (Pickles et al. 2011), some points should be taken in consideration. First, considering the historical records gathered by Pimenta et al. (2018), it is plausible to infer that the pelt trade was more significant in the Brazilian Amazonia than in other regions. The port of Manaus, from where animal hides were heavily exported, was directly linked to Europe and the United States, and became one of Brazil's main trading posts during the "Amazon rubber booms". It is reasonable, then, to hypothesize that most hunting to supply the international wildlife hide market could have been centred in Brazilian Amazonia. Consequently, the hunting pressure on giant otters might have been smaller in other parts of the giant otters' distribution. Another aspect to take in consideration is the choice of molecular markers used in different studies. Severe bottlenecks might be easier to detect, but moderate bottlenecks, which are likely more common, might go undetected if resolution provided by the markers of choice is not powerful enough (Peery et al. 2012). Mitochondrial markers, which have been used in most genetic studies with the species (Garcia et al. 2007, Pickles et al. 2011, Caballero et al. 2015 and Ruíz-García et al. 2018), are less likely to provide such level of resolution. Hoban et al. (2013) have suggested an increased number of loci (rather than samples) to increase power in bottlenecks detection.

4.6 Conclusion

This chapter has focused on the evolutionary history of two otter species within the broader context of the whole order Carnivora. A revisited phylogeny of the order was studied using Maximum Likelihood and Bayesian inference methods with a new set of nuclear loci, developed within the framework of this thesis.

The custom loci dataset was able to generate a robust phylogenetic tree with high support values. It was possible to assess some historically conflicting points in Carnivora phylogeny, confirming some of the current scientific consensus, but also contributing with new evidence that highlight the need of further clarification on some aspects of the current classification. For instance, it is evident that interspecies relationships should be better assessed in Lutrinae, especially regarding the position of *Pteronura* and its effect on the paraphyly or monophyly of the subfamily.

The time calibration applied has allowed the dating of most tree nodes with confidence, and provided relevant insights about the lineage splits in the giant and Neotropical otter branches. Even with a limited sample size, it was possible to make some pertinent inferences on the species evolutionary history and its relationship with current diversity patterns. Future studies should focus on the northern Brazilian populations of giant otters using nuclear markers, in order to find more evidence for reduced genetic diversity in those populations and assess a possible bottleneck effect. In fact, a negative Tajima's D estimate was obtained for giant otter haplotypes from the Guyana shield rivers (Chapter 3) which could be an indicative of a past population decline such as a bottleneck, and the overall nuclear genetic diversity levels estimated with SNPs were likewise low for the species.

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4.8 Appendices

Appendix 4.1. Individual Bayesian gene tree for Locus 2 generated in MrBayes.

Appendix 4.2. Individual Bayesian gene tree for Locus 3 generated in MrBayes.

Appendix 4.3. Individual Bayesian gene tree for Locus 4 generated in MrBayes.

Appendix 4.4. Individual Bayesian gene tree for Locus 5 generated in MrBayes.

Appendix 4.5. Individual Bayesian gene tree for Locus 6 generated in MrBayes.

Appendix 4.6. Individual Bayesian gene tree for Locus 7 generated in MrBayes.

Appendix 4.7. Individual Bayesian gene tree for Locus 8 generated in MrBayes.

Appendix 4.8. Individual Bayesian gene tree for Locus 9 generated in MrBayes.

Appendix 4.9. Individual Bayesian gene tree for Locus 10 generated in MrBayes.

Appendix 4.10. Individual Bayesian gene tree for Locus 11 generated in MrBayes.

Appendix 4.11. Individual Bayesian gene tree for Locus 12 generated in MrBayes.

Appendix 4.12. Individual Bayesian gene tree for Locus 13 generated in MrBayes.

Appendix 4.13. Individual Bayesian gene tree for Locus 14 generated in MrBayes.

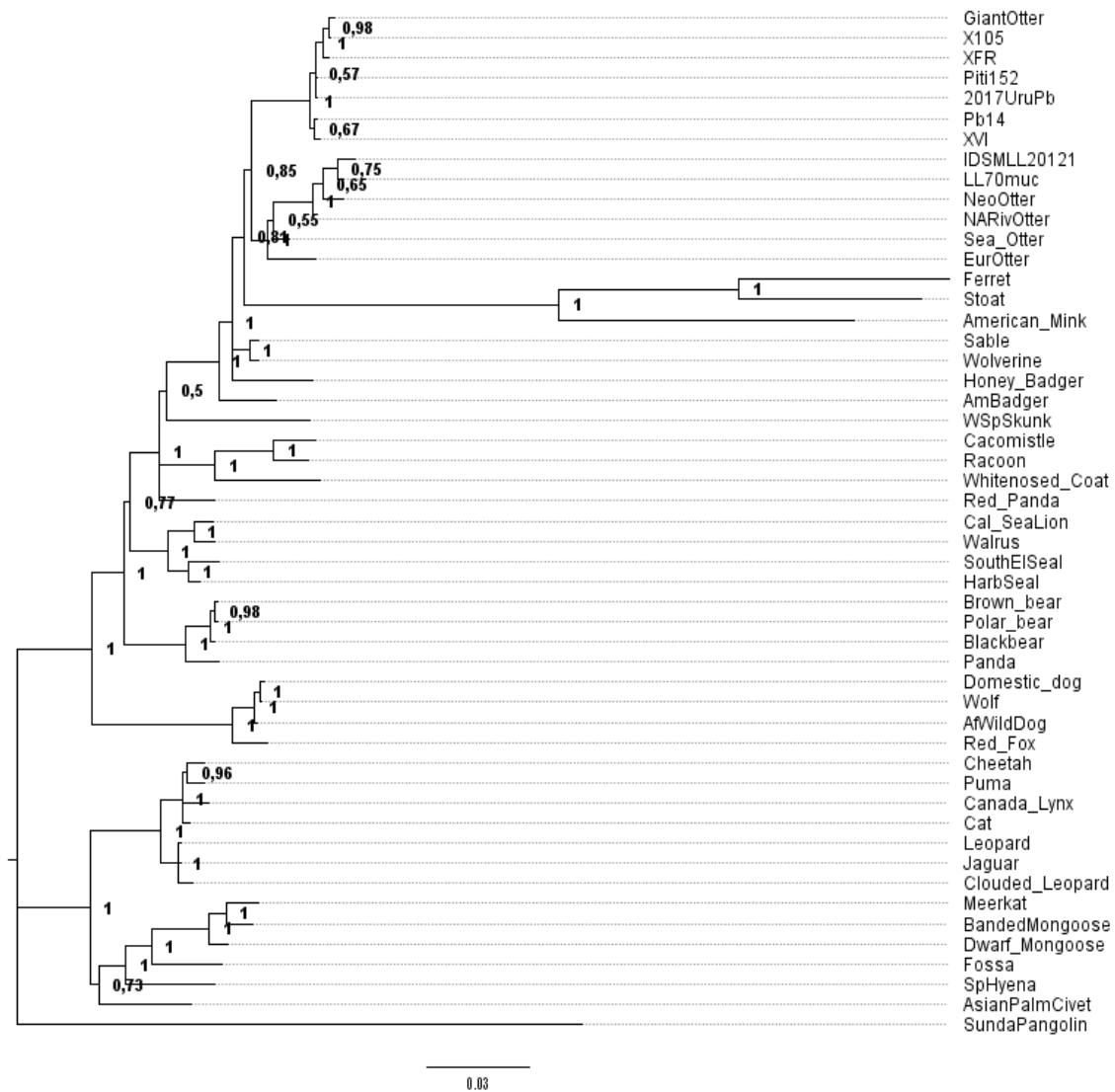
Appendix 4.14. Individual Bayesian gene tree for Locus 15 generated in MrBayes.

Appendix 4.15. Individual Bayesian gene tree for Locus 16 generated in MrBayes.

Appendix 4.16. Individual Bayesian gene tree for Locus 17 generated in MrBayes.

Appendix 4.17. List of the 17 loci used in the analyses and their positions considering the reference dog genome assembly (CanFam 3.1)

Appendix 4.1



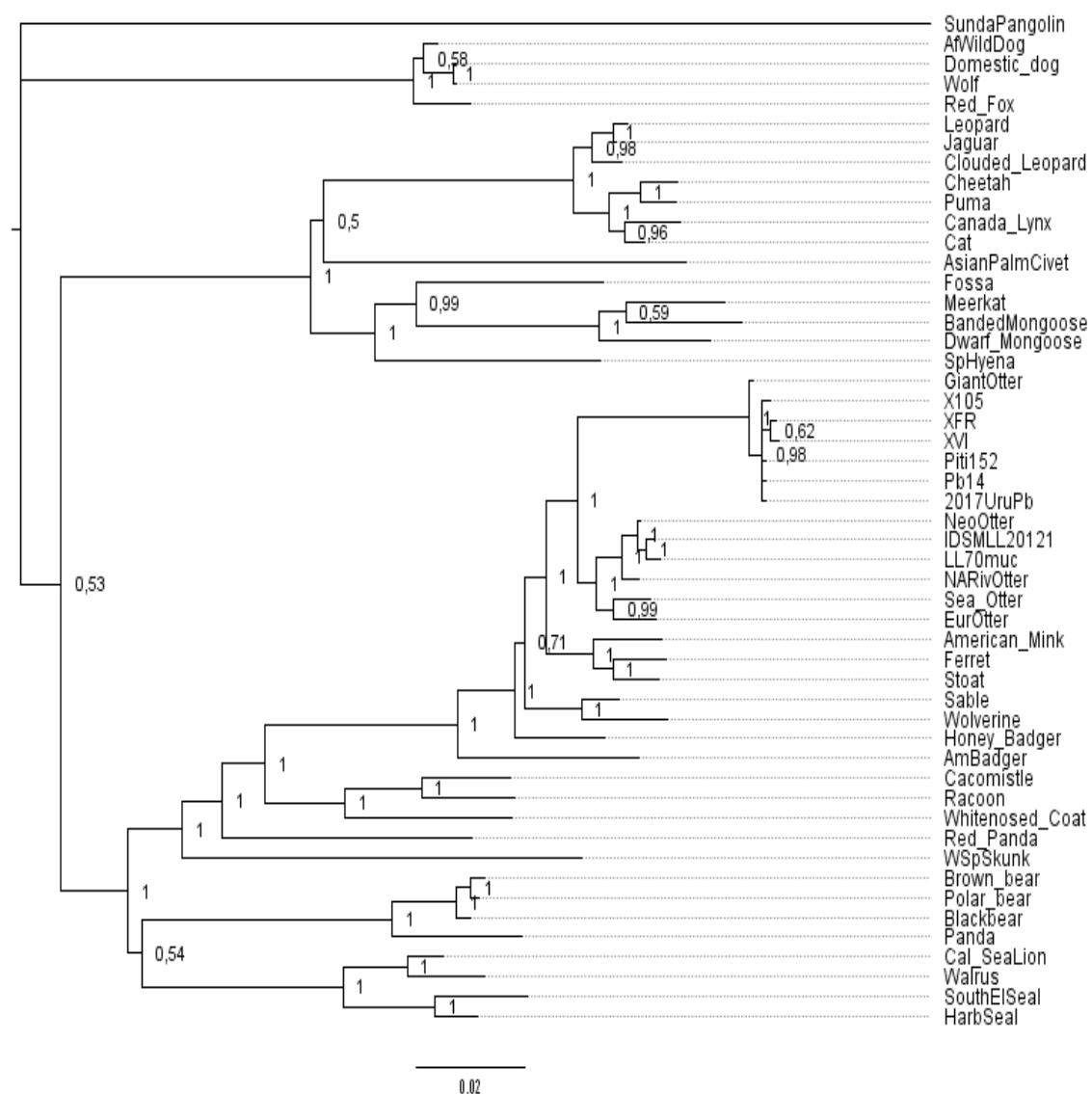
Phylogenetic tree showing relationships between various species based on mitochondrial cytb sequences. The tree is rooted at the bottom left and branches upwards. Bootstrap values are indicated at the nodes.

Species listed (from top to bottom):

- Piti152
- Pb14
- GiantOtter
- X105
- 2017UruPb
- XFR
- XVI
- LL70muc
- IDSMML20121
- NeoOtter
- NARivOtter
- EurOtter
- Sea_Otter
- Stoat
- Ferret
- American_Mink
- Honey_Badger
- Sable
- Wolverine
- AmBadger
- Cacomistle
- Raccoon
- Whitenosed_Coat
- Red_Panda
- WSpSkunk
- Cal_SeaLion
- Walrus
- SouthElSeal
- HarbSeal
- Brown_bear
- Polar_bear
- Blackbear
- Panda
- Domestic_dog
- Wolf
- ArWildDog
- Red_Fox
- Canada_Lynx
- Cat
- Puma
- Cheetah
- Leopard
- Jaguar
- Clouded_Leopard
- AsianPalmCivet
- Meerkat
- Dwarf_Mongoose
- BandedMongoose
- Fossa
- SpHyena
- SundaPangolin

Scale bar: 0.03

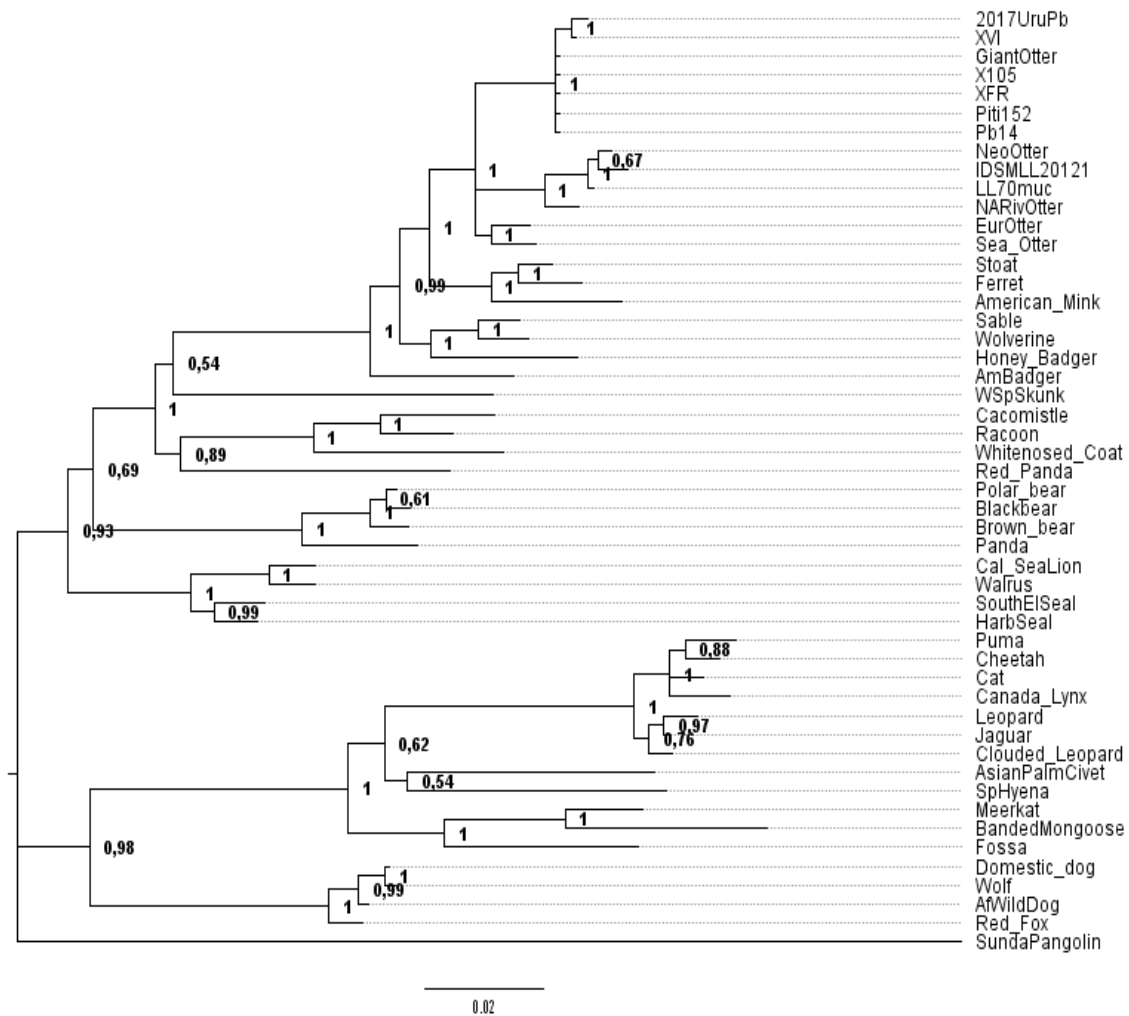
Appendix 4.3



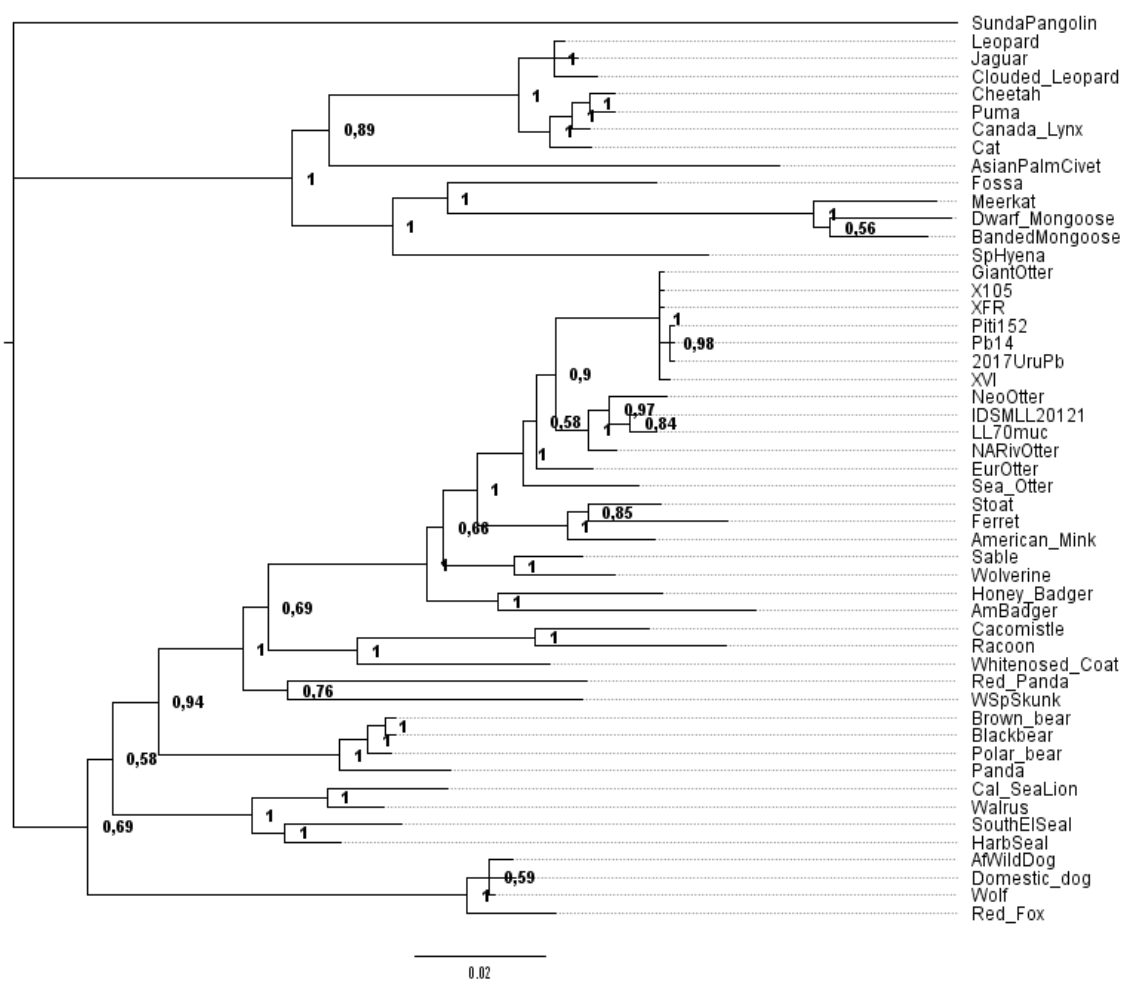
A phylogenetic tree illustrating the evolutionary relationships among various species, primarily focusing on carnivores and related groups. The tree is rooted at the bottom left. Bootstrap values are provided for numerous internal nodes, indicating the confidence in the branching order. The species names are listed vertically on the right side of the tree.

- X105
- XFR
- GiantOtter
- Piti152
- Pb14
- 2017UruPb
- XVI
- EurOtter
- Sea_Otter
- NARivOtter
- NeoOtter
- IDSMLL20121
- LL70muc
- Stoat
- Ferret
- American_Mink
- Sable
- Wolverine
- Honey_Badger
- AmBadger
- Red_Panda
- Cacomistle
- Raccoon
- Whitenosed_Coat
- WSpSkunk
- Domestic_dog
- Wolf
- ArWildDog
- Red_Fox
- Cheetah
- Puma
- Canada_Lynx
- Cat
- Leopard
- Jaguar
- Clouded_Leopard
- BandedMongoose
- Dwarf_Mongoose
- Meerkat
- Fossa
- SpHyena
- AsianPalmCivet
- Brown_bear
- Blackbear
- Polar_bear
- Panda
- Cal_SeaLion
- Walrus
- SouthElSeal
- HarbSeal
- DomesticHorse

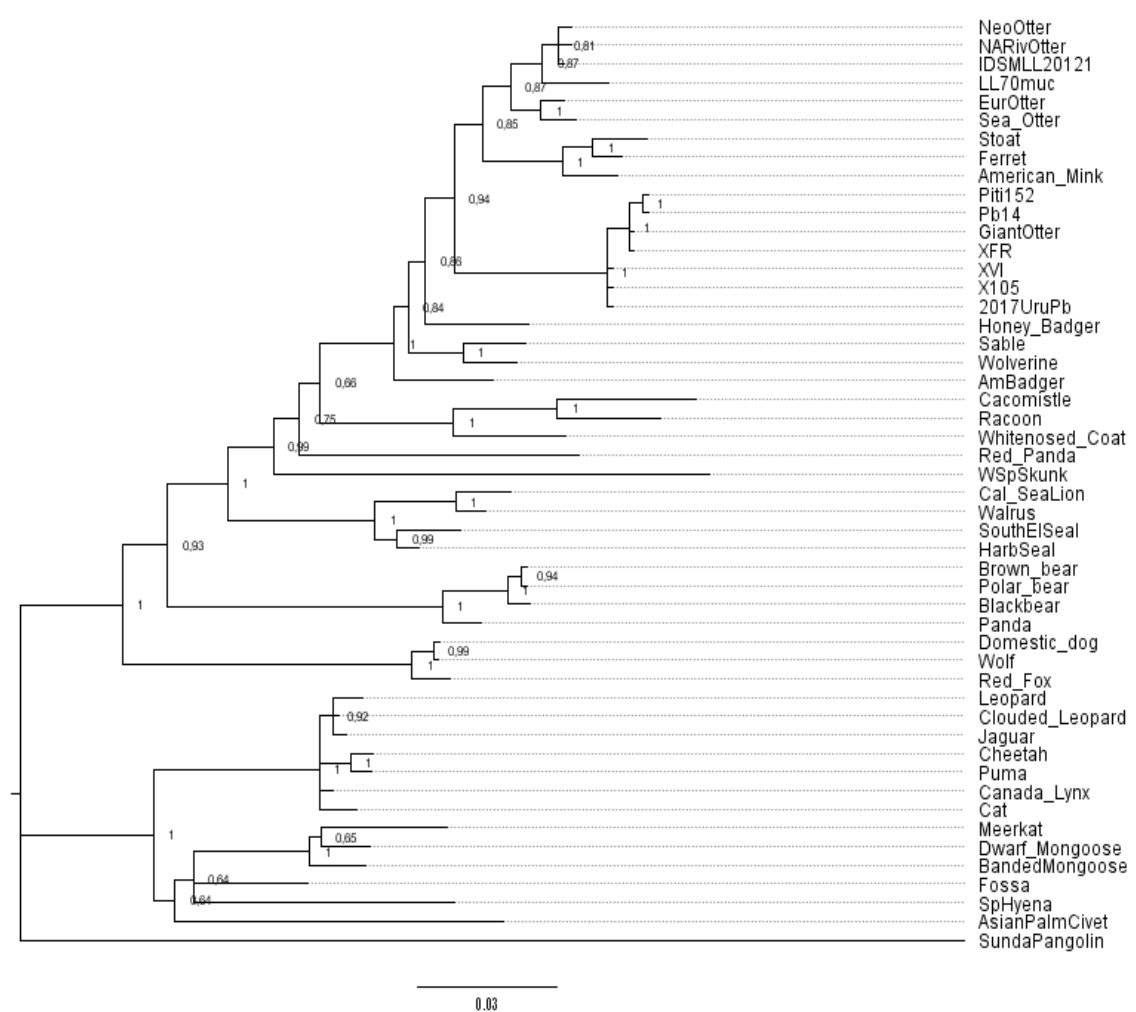
Appendix 4.5



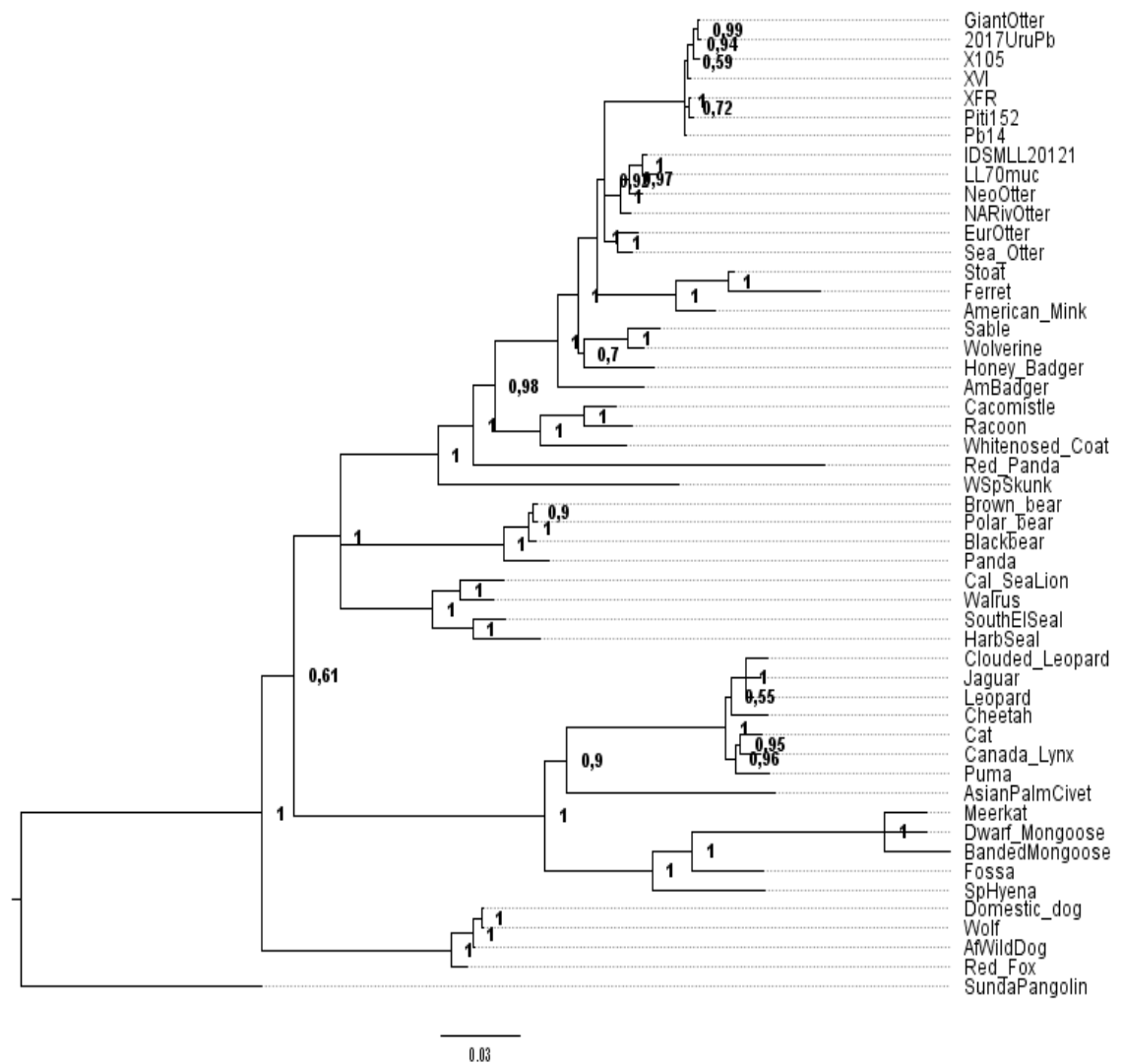
Appendix 4.6



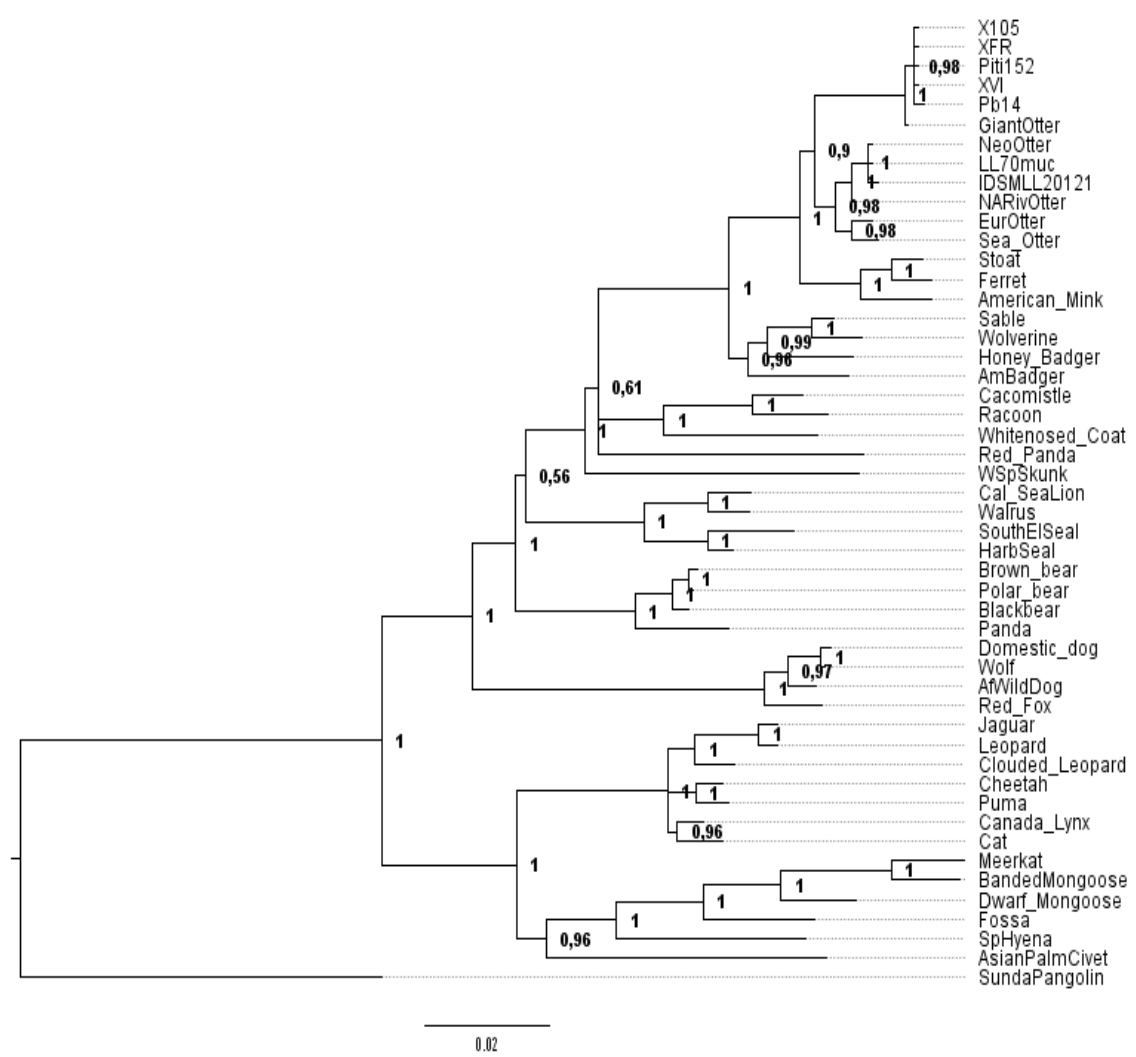
Appendix 4.7



Appendix 4.8



Appendix 4.9

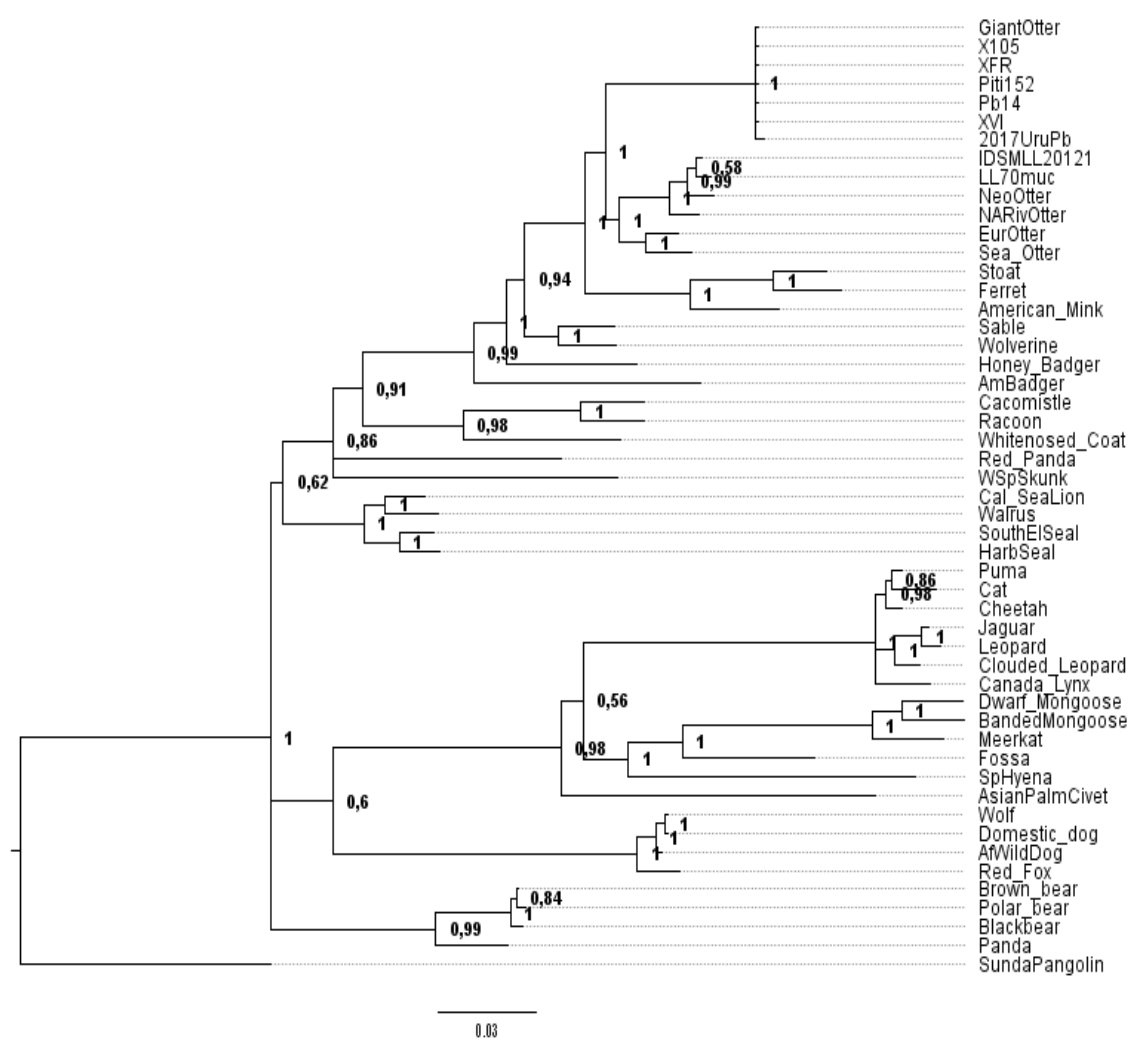


A phylogenetic tree illustrating the evolutionary relationships among various species. The tree is rooted on the left and branches out to the right. Bootstrap values are provided for many of the internal nodes, indicating the confidence in the branching order. The species names are listed along the right side of the tree.

- GiantOtter
- Pb14
- 2017UruPb
- XFR
- Piti152
- X105
- XVI
- EurOtter
- Sea_Otter
- LL70muc
- NeoOtter
- IDSMLL20121
- NARivOtter
- Stoat
- Ferret
- American_Mink
- Sable
- Wolverine
- Honey_Badger
- AmBadger
- Cacomistle
- Raccoon
- Whitenosed_Coat
- Red_Panda
- BandedMongoose
- WSpSkunk
- Brown_bear
- Blackbear
- Polar_bear
- Panda
- Cal_SeaLion
- Walrus
- SouthElSeal
- HarbSeal
- Wolf
- Domestic_dog
- AfWildDog
- Red_Fox
- Cheetah
- Puma
- Canada_Lynx
- Cat
- Leopard
- Jaguar
- Clouded_Leopard
- Meerkat
- Dwarf_Mongoose
- Fossa
- SpHyena
- AsianPalmCivet
- SundaPangolin

Scale bar: 0.02

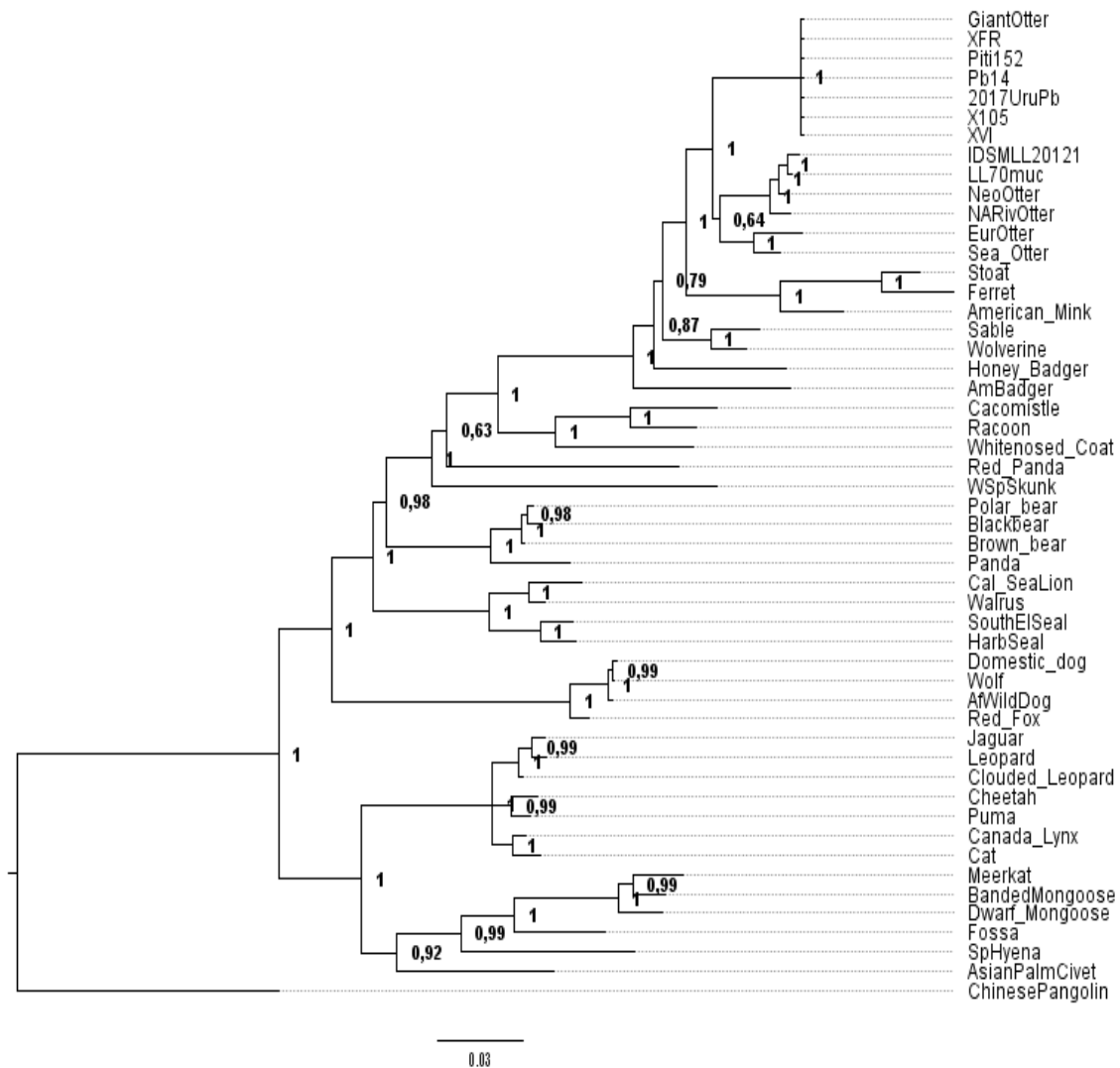
Appendix 4.11



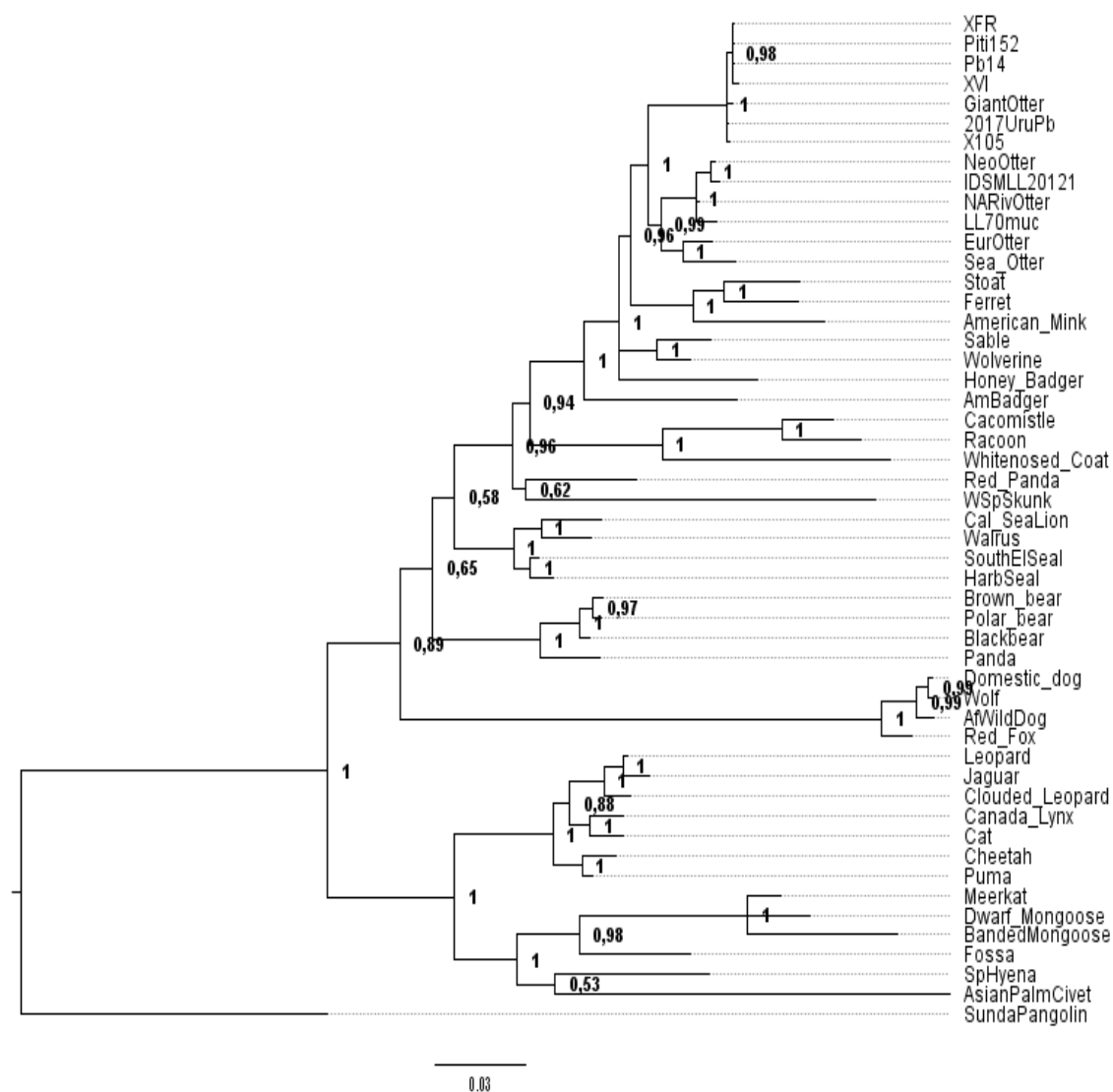
A phylogenetic tree illustrating the evolutionary relationships among various species. The tree is rooted on the left and branches out to the right. Bootstrap values are provided for many of the internal nodes, indicating the confidence in the branching order. The species names are listed along the right side of the tree.

- GiantOtter
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- Puma
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- Leopard
- Clouded_Leopard
- Meerkat
- BandedMongoose
- Dwarf_Mongoose
- Fossa
- SpHyena
- AsianPalmCivet
- DomesticHorse

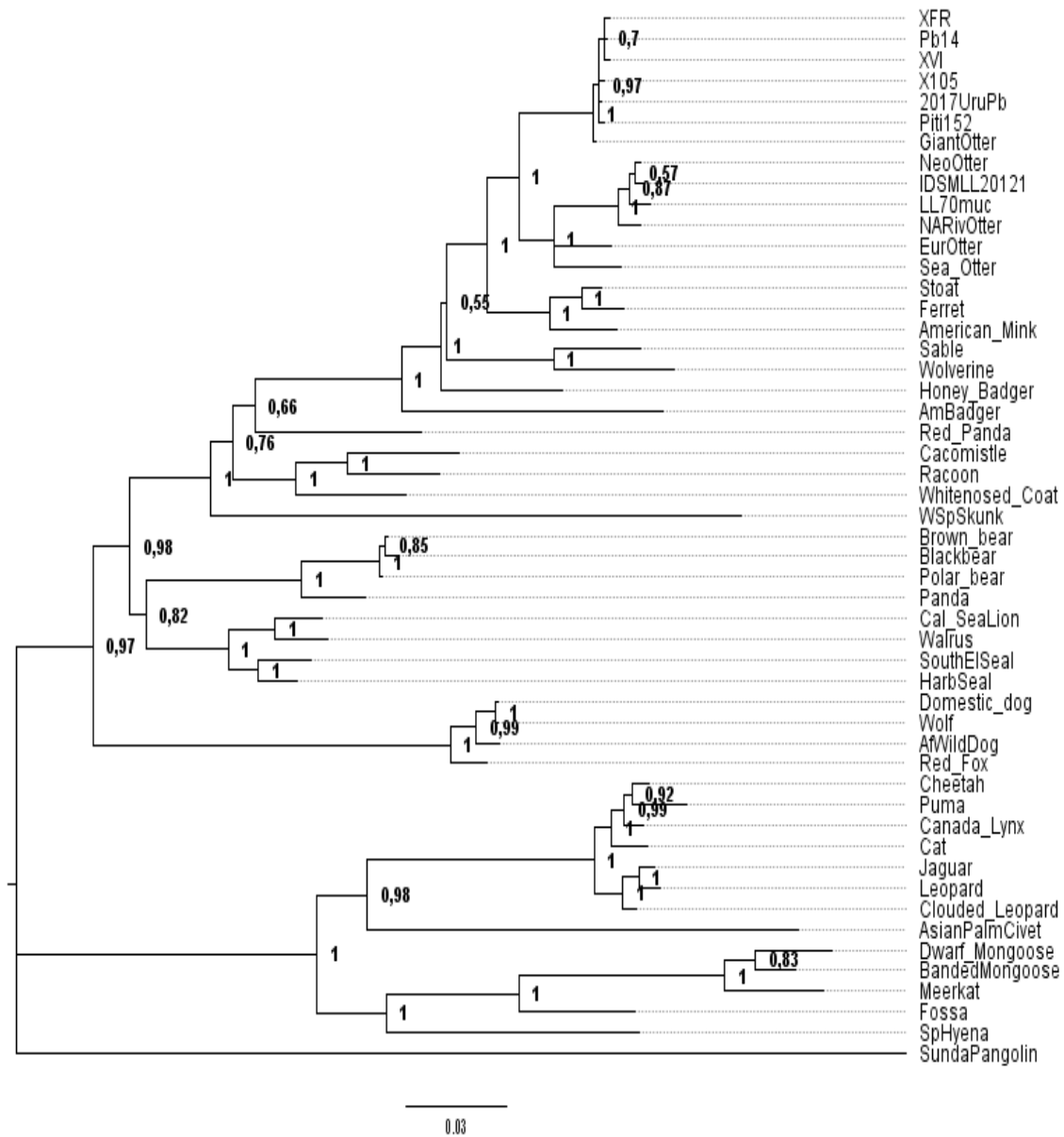
Appendix 4.13



Appendix 4.14



Appendix 4.15



Appendix 4.16



Appendix 4.17

Locus	Chromosome	Coordinates
1	28	26808912-26809842
2	22	52168901-52169503
3	6	17157117-17157570
4	10	27197036-27197432
5	17	33643513-33644549
6	1	1737257-1737701
7	6	34887758-34888378
8	22	33219827-33220532
9	1	92281733-92282574
10	14	39076541-39077084
11	6	18702830-18703869
12	28	28690217-28690608
13	27	33783564-33784522
14	6	2976493-2977204
15	2	34447674-34448182
16	31	37945961-37946420
17	29	40768180-40768460

Chapter 5

General Discussion



Photo: V.C. Fonseca da Silva

This study is a contribution to our knowledge of the ecology and status of giant and Neotropical otter populations in the Brazilian Central Amazonia. Through the description and analysis of potential connectivity patterns, combining occurrence data with molecular data on population genetic diversity and structure, the aim was to identify key points relevant to the management and conservation of the two species, in a region where they are relatively under-studied - despite it being the largest refuge of continuous habitats for both. This final Chapter integrates the main findings of the thesis in the context of the broader literature and points out recommendations for future research.

5.1 Summary and discussion of main findings

In Chapter 2, I assessed potential distribution and suitability over watercourses in Central Amazonia for both species, based on recent occurrence data registered in this study and in the literature. In the context of the thesis, this approach provided a general picture of potential connectivity within and between drainages that could be related to genetic patterns (further addressed in Chapter 3).

With a different perspective compared to previous studies that modelled distribution and habitat suitability of the two species in their total area of occurrence (e.g., Rheingantz et al. 2014, Cianfrani et al. 2018), I have focused on a regional scale within Amazonia, restricting the geographic background of the modeling (Acevedo et al. 2012). Moreover, I considered only the riparian environment rather than a continuous extent. This was done in order to visualize the results in a more coherent way, considering: i) the otters' semi-aquatic habits; and ii) the fact that is not realistic to extrapolate a single level of suitability for the total length of a watercourse or drainage, since characteristics vary among different regions (Carone et al. 2014, Quiñonez et al. 2018).

Overall, the predicted distribution range in the study area was similar for both otters; but considering finer resolution patterns, differences were noted, suggesting a partial spatial niche separation. Such differentiation is in line with reported habitat preferences for these species (e.g., Muanis et al. 2011, Smith et al. 2020), for other Lutrinae members in sympatry (Kruuk et al. 1994), and for other co-existent semi-aquatic small mammals (Galliez & Fernandez 2012).

According to the results obtained in Chapter 2, considering the predicted suitability maps, Neotropical otter populations in the study area may have a lower intra-basin connectivity than giant otters, but their inter-basin connectivity seems to be stronger, covered by areas with higher suitability. The suitable habitat in giant otter maps is more widespread, but appears to be reduced or lacking when looking at major rivers that provide connection routes between several sub-basins.

Still, there is a difference between a) structural connectivity, such as that predicted by SDMs and other habitat/landscape models; and b) functional connectivity, which depends on behavioral and intrinsic characteristics of each species, including dispersal patterns (Baguette & Dyck 2007, Beninde et al. 2016). Thus, spatial modeling (as potential distribution and suitability, or based on resource selection functions) is a good starting point for assessing connectivity (Beninde et al. 2016), and its predictions can be better validated by behavioral (e.g., obtained by telemetry, as in Fattebert et al. 2015) or genetic data (Beninde et al. 2016, Milanesi et al. 2017). Genetics can be even more informative, because directly detected dispersal events may not always be effective in contributing to gene flow, in case the dispersing individual is not able to mate and produce offspring (Quaglietta et al. 2013).

In Chapter 3, I investigated genetic structure and diversity patterns, and hence the findings can be contrasted and compared with SDM outcomes (Chapter 2). For the first time, next-generation sequencing was employed to the study of wild Brazilian otter populations, and results revealed an unknown population structure for both species across the study area in central Amazonia, that suggests neither species is panmictic across this range.

The comparison of structure patterns was limited by the fact that Neotropical otter data was available for only three out of the seven locations for which giant otter data was analysed. Therefore, it was only possible to consider an overlapped portion of their range, for which structure was quite similar. If functional connectivity patterns were directly related to the structural connectivity predicted by SDMs, one could expect to find a stronger structure pattern in Neotropical otter populations, consistent with the hydrological hierarchy of basins (see Chapter 3). Giant otters would probably show a lower degree of structuring, in part due to isolation by distance and, to a minor extent, caused by the weaker connectivity over major rivers that connect sub-basins. In the second case, differences would mainly be seen across drainages divided by wider rivers, especially white-water rivers such as the Amazon (Chapter 2).

Regardless of the aforementioned limitations, points concerning each separate species can be considered in order to corroborate or not the structural connectivity estimates from Chapter 2. For the Neotropical otter, molecular data suggests that Balbina is a separate population with little admixture; but Amanã and Jaú (and the single individual from Ati-Paraná) are more strongly admixed. This was not expected by SDM predictions, since potential hydrographic connections, especially between Jaú and Amanã, are patchy, having very low or null suitability values (Chapter 2). But, as pointed above, functional connectivity relies heavily on species behaviour and intrinsic biological mechanisms.

Virtually nothing is known about Neotropical otter dispersal behaviour - but if dispersers use sub-optimal habitat as dispersal routes, like observed in other species of Carnivora (Vanbianchi et al. 2018, Carvalho et al. 2018), that could be an explanation for the contrast between the genetic results and distribution modelling approach. Besides, this species is relatively solitary (see Chapter 1), and so dispersing individuals will likely tend to invest movement efforts seeking vacant territories, as observed in the Eurasian otter (Quaglietta et al. 2014). Santini et al. (2013) have shown, indeed, that social mammal species tend to disperse shorter distances than solitary ones. In giant otters, the occurrence of “transient groups”, i.e., groups of non-breeding unrelated individuals, with no established territory, is likely common, as observed in the Brazilian Pantanal and in Peru (Ribas et al. 2015, Groenendjik et al. 2014). This may reflect a greater tolerance among conspecific dispersers in this species, which is less likely to happen in a species tending to a more solitary behavior like the Neotropical otter.

Regarding giant otters, the wider reach of the study sites allows for more inference concerning the integration of results from Chapters 2 and 3. I found evidence that suggests genetic structure over the locations studied, unlike earlier work that has mainly focused on wider scales and identification of lineages through mitochondrial DNA markers (Garcia et al. 2007, Pickles et al. 2011, Caballero et al. 2015, Ruiz-Garcia et al. 2018).

Genetic patterns for giant otters in this case seem to partly correspond to expectations derived from SDMs. If the structural connectivity predicted by the SDM is reflected in population structure, Abufari and Trombetas sites would indeed show a higher differentiation from other locations. This pattern was corroborated by the genetic structure findings - these two locations, as well as Guyana and Trombetas, seem to have a stronger local ancestry compared to others. Connectivity between Balbina, Xixuaú, Amanã and Jaú sites seems to be functionally more complex than expected considering general habitat

predictions. If genetic patterns corresponded to such predictions, it is likely that a gradient of genetic variation would be observed in a continuum over those sites, but not enough to generate clusters as in fact observed (Chapter 3). This opens further space for the importance of taking into account the sociality factor (Parreira & Chikhi 2015), which has indeed been potentially linked to genetic structure in otter populations not facing any evident physical barriers (e.g., *Lontra canadensis* – Blundell et al. 2002, Latch et al. 2008; *Lutra lutra* – Quaglietta et al. 2013).

A gradient of variation could be in part true for Amanã and Jaú, as these were the most admixed groups, as seen likewise for Neotropical otters. Balbina and Xixuaú otters, on the other hand, formed a separate cluster (with Balbina individuals showing a slight admixture); this is in accordance with structural connectivity, as suitable watercourses link the two locations, and DAPC analysis potentially indicates long-term admixture between these two locations. On the other hand, the SDM also predicted a suitable route between Jaú and Xixuaú, potentially promoting higher similarity between these two locations instead of the strong clustering of Xixuaú individuals observed. Nevertheless, the ancestry proportions (Fig. 3.7a) exhibited by Jaú individuals have shared co-ancestry with Xixuaú, showing that at least some minor degree of functional connection likely exists between the two sites.

Jaú and Jauaperi/Xixuaú sub-basins are located on opposite banks of the Negro River, being traversed by it. This particular stretch of the Negro, towards where these sub-basins flow, is relatively close (~230km) to the city of Manaus, the chief urban center in the Brazilian Amazon. Therefore, it likely experiences an intense daily traffic of vessels (transporting both cargo and passengers) between the ports of Manaus and interior municipalities of the Amazon State. As previously hypothesized (see Chapter 2), giant otters might be sensitive to human disturbance in rivers and avoid areas of higher human

activity (Oliveira et al. 2015), and this could be one putative factor that reduces connectivity across Negro River.

A similar pattern of differentiation and restricted gene flow between neighboring populations was also found in pink dolphins (Hollatz et al. 2011), between individuals from a population that includes the Amanã study site and from Tefé Lake, which are also located on opposite banks of a major drainage (in this case, the Amazon River). The authors suggest the combined influences of species behaviour and environmental differences in riverine habitats in generating the observed genetic pattern (Hollatz et al. 2011). The same might hold true for otters, but more studies on the species behavioral ecology, such as dispersal and habitat selection, are needed to clarify the processes driving population genetic structure. A further possibility builds on the ideas by Hollatz et al. (2011) on environmental differences as drivers of genetic structuring, since the studied locations included sub-basins with predominance of different water types. Black, white and clear waters of the Amazon basin show different physical-chemical properties (Ríos-Villamizar et al. 2014) and can exhibit distinct species assemblages of invertebrates (Roque et al. 2012) and fish (Saint-Paul et al. 2000, Bogotá-Gregory et al. 2020). Indirect or direct effects of water types on otters' spatial behaviour (that could affect dispersal and thus gene flow) cannot thus be rejected without more research.

In addition, and bearing in mind the limited sampled areas in common for both species, the presumed similar admixture pattern observed for both in the Amanã and Jaú areas could suggest the effect of common landscape drivers of genetic patterns. As mentioned above, the sites are located in an important interfluvial zone, close to the confluence of Negro and Amazon Rivers, and which is covered by three extensive protected areas (Jaú National Park, Unini Extractive Reserve and Amanã Sustainable Development Reserve). From this, I hypothesize that this area of connection between two

major Amazonian drainages, that is also highly protected, might be acting as an important contact zone between otter populations from different sub-basins.

Chapter 4 provided a further perspective on the two otters' phylogeography within a broader taxonomical context. Some of the same loci designed for targeted sequence capture (Chapter 3) were successfully used in reconstructing the phylogeny of Order Carnivora and integrating data from multiple individuals from the focal study species. The results obtained also aid in supporting findings from its preceding chapter. Possibly, Balbina and Xixuaú giant otters indeed share a common ancestor and have a long-term connection and admixture. In addition, considering the concatenated sequence used in the analysis, it appears once more that Neotropical otters are more genetically diverse than giant otters, as observed by the tree branch lengths of reconstructed phylogenies.

5.2 Limitations of the study

The sampling design proposed in this study was planned in such a way that I would be able to have an overall picture of how structured and related otter populations are, in the context of a complex river network landscape. I had sampling sites to the north and south of the Amazon River, in relevant interfluvial areas and across one of its main tributaries, the Negro River. The chosen locations also included sub-basins with all three main types of water found in Amazon basin rivers – black (Jaú and Jauaperi Rivers), white (Purus River), clearwater (Uatumã and Trombetas Rivers), and a site with influence from both black and white drainages (Amanã – white water from Japurá River and black water from Negro).

Nevertheless, despite a substantial field effort in order to collect a maximized number of scats over chosen sites, the sequencing and genotyping successes were low for both species, not allowing a final ideal number of samples per study sites as planned. Furthermore, Neotropical otter scats were not found at all in Abufari and Trombetas, and the few that were sampled in the Xixuaú area did not yield any data. I also had a completely failed study site, the Viruá National Park (located in the Branco River sub-basin, a main tributary of Negro River), where no samples were found for either species (although I could still use the occurrence data for giant otters, in Chapter 2).

Non-invasively collected scat samples are normally poor in both quantity and quality of target DNA. Moreover, they are subject to degradation and high concentrations of reaction inhibitors (Taberlet et al. 1999, Broquet et al. 2007). DNA from otter scats in particular is known to be problematic, with low success in extraction and amplification steps and prone to genotyping errors (e.g., Lampa et al. 2008, Ortega et al. 2012, Lerone et al. 2014). With the main chosen method for this study (target capture protocol), I was expecting to overcome most of these difficulties, based on successful cases from the literature (Carpenter et al. 2013, Snyder-Mackler et al. 2016, Hernandez-Rodriguez et al. 2017). Nevertheless, in this study, I eventually faced such issues after all – and jeopardizing factors can possibly be related to the sampling conditions in the Amazonian context, which are far from ideal. For example, Hájková et al. (2009) recommended the sampling of Eurasian otter scats in colder months in order to obtain a better-quality DNA (and consequently increased PCR success). This is obviously impossible in the rainforest, as average temperatures are always warm yearlong. In addition, facilities in field locations were limited and despite taking maximum storage precautions, such as keeping samples in a cooler box (with ice when available), it was

unmanageable to keep them refrigerated for the whole duration of field campaigns which may have contributed to further DNA degradation.

Hence, for both species - and especially for Neotropical otters - a lack of a sufficient sample size over the whole study area was a relevant limiting factor. As a consequence, deep inferences were limited, for instance, on important topics that require a comparative analysis, such as the influence of sociality or spatial behavior on population genetic patterns. The interpretation of the results in the light of sociality was still possible, though, considering the study's caveats. Small sample sizes also limit estimations and interpretations of important genetic diversity parameters, such as F_{ST} . Still, ordination and coalescent methods, such as the ones used here for determining structure, work well with small sample sizes, and have been successfully applied to my dataset.

The quality of the DNA libraries was likely an issue as well. Sequencing reads showed an overall low depth, which hinders the determination of SNPs in the dataset, and also contributes to an increased proportion of missing data over individuals (Marandel et al. 2020). So, a second limitation in the study can be owed to a low number of SNPs identified. Although reduced SNP datasets can be powerful enough to detect genetic structure and correctly assign individuals to clusters (Turakulov & Easteal 2003, Stetz et al. 2016, von Thaden et al. 2020), some useful analyses do rely on, or function better with, a more robust marker dataset, such heterozygosity estimates (Yao et al. 2020).

If more information was available in the literature concerning, particularly, the behavioral ecology of the species, this would have assisted in the interpretation and integration of my findings. For instance, if dispersal patterns were well known, more inference could be drawn regarding the differences between the connectivity depicted by SDMs and the potential functional connectivity inferred from genetic data. The

combination of molecular data with radio-tracking of multiple individuals in a Eurasian otter population, for example, has allowed a sound inference on the species dispersal and its likely effects on genetic structure (Quaglietta et al. 2013).

Moreover, apart from diet studies which have shown only a small trophic overlap between the two species in Amazonia (Silva et al. 2013, and author's unpublished data), little is known regarding their fine-scale mechanisms for coexistence. Ecological niche separation is a factor that can have an important role in the coexistence of species belonging to the same guild, encompassing one or more niche dimensions such as food or habitat use (Jácomo et al. 2004). Vanak et al. (2013) argued that dietary niche partitioning might be in fact a consequence of intraguild competition avoidance between carnivores, and fine-scale avoidance mechanisms can vary according to different areas and/or resource availability (Karanth et al. 2017). It is therefore reasonable to consider that cryptic patterns of interaction between the two species could also have an influence on their movements and ecology and, subsequently, on their gene flow patterns.

5.3 Conservation implications and suggestions for future research

The main motivation in this research was to lay groundwork for additional conservation and management policies for otters and other freshwater vertebrates in the Brazilian Amazonia. The present work expands upon our current knowledge of otter population structure and diversity in this biome while allowing for relevant conservation implications.

The results illustrate that both giant and Neotropical otter populations can show structure at fine-scale levels even in such an intricate and dense drainage network as the

Amazon basin. Gene flow between structured (sub) populations might be restricted either by species' intrinsic mechanisms such as dispersal patterns or by an interplay of environmental (including anthropogenic) and biological factors; and it is likely that the different social system of the two species also affects their genetic structure. The findings reported here stress the need to monitor wildlife populations with vast distributions, as cryptic structuring patterns might play a role in increasing their vulnerability to current and future threats. Rheingantz et al. (2017) have indeed emphasized this need for local and regional scale studies for Neotropical otters, to support the definition of task areas and planning of management and conservation actions. The occurrence of isolated populations can bring conservation concerns, as it increases the odds of extinctions due to the associated risks of reduction in effective population sizes and consequent effects of genetic drift and erosion of genetic diversity (Frankham 1995, Keyghobadi 2007).

Although it appears that most giant otter populations studied do experience at least some migrant contribution to the gene pool, the group including Balbina and Xixuaú individuals seems more isolated and less diverse than others. This population could be potentially suffering from impacts caused by the hydroelectric dam, despite an estimated population increase based on density of dens (Rosas et al. 2006, Palmeirim et al. 2014) giving a different impression. Rocha et al. (2019) have reported an irreversible change of the flooded *igapó* forest vegetation downstream to Balbina dam. These habitats are crucial for Amazonian fish species for reproduction, nursery and feeding (Henderson 1990, Goulding 1980, Saint-Paul et al. 2000). Fish are giant otter's prey base (Cabral et al. 2010), and any impacts on the prey will likely affect the predators as well. There should be an effort to monitor otter occurrence on downstream stretches of Uatumã River in order to clarify such potential impacts.

With increasing numbers of dams planned for Amazonia's headwaters (Anderson et al. 2018) and in the Brazilian Amazonia (Brasil, 2017), researchers must focus on actions that both detect and mitigate potential negative impacts of such developments - including the social-economic impacts to surrounding human populations, which are countless. Displacement (sometimes from sacred territories, in the case of indigenous people), scarcity of fishing resources downstream of the dams, loss of cultivatable land, lack of favorable alternatives, increased violence, are all possible consequences already observed after the implementation of large dams, such as the controversial Belo Monte dam on the Xingu River (Fearnside 2015, Marin et al. 2016, Grisotti 2016, Riethof 2017, Jiang et al. 2018, Anderson & Elkaim 2018). Effective conservation measures in such scenarios are only possible when considering the needs of human inhabitants (Erbaugh et al. 2020), and increased poverty and quality of life could also drive additional anthropogenic impacts, such as deforestation and poaching.

My thesis findings also highlight the importance of maintaining a good mosaic of protected areas that form protected corridors of habitat. As hypothesized from Chapter 3 findings, the Negro/Amazon interfluvium might be an important connection region, and its considerable area of legally established conservation units could be key to promoting gene flow between aquatic species between different river basins.

Building on this last point, the outcomes of this thesis also emphasize the importance of choice of conservation management units. Being top-predators, otters can be good "umbrella" species and their conservation needs might reflect and nest the needs of a broad range of freshwater species. So, over the landscape scale, I argue in favor of considering the main Amazon tributaries sub-basins as basic management units for aquatic and semi-aquatic Amazonian vertebrates. Future work should focus on assessing

connectivity and permeability of drainages for different taxonomic groups, and include considering potential anthropogenic disturbances that could affect species movements.

Regarding the focal species, several questions remain unanswered, paving way for research on further aspects of otter demography, genetics and behavioral patterns. It would be interesting to assess genetic structure over more locations, including some key sites that were not sampled in this study, such as Uatumã River downstream of Balbina dam, the Branco River, and eastern Amazonian populations (including coastal ones). If possible, long-term projects that include the method of biopsy sampling for assessing genetic patterns of giant otters would be ideal, as this would alleviate some of the issues generated by poor-quality data from scats.

One relevant point that is difficult to assess was the complete lack of signs of Neotropical otters in Trombetas, Abufari and Viruá National Park. It could be due to a seasonal issue - for example, animals could temporarily migrate to headwaters that were not accessible by boat during my field trips. However, other areas sampled in the peak of the dry season showed abundant signs of otters (Jaú and Balbina in particular). Secondly, this is not consistent with described habitat preferences of the species, for wider, deeper river channels (e.g., Muanis et al. 2011).

SDMs have also shown fragmented potential distribution of Neotropical otters. Therefore, their distribution might be more discontinuous and heterogeneous over Amazonia than previously thought. Considering this, I strongly recommend an intensification of survey efforts focused on the species in Amazonia, in order to elucidate occurrence and distribution patterns in this biome. New efforts to study its population genetics would be equally important. The possibility that its distribution is indeed fragmented warrants further investigation - if true, then more patterns of structure and cases

of isolated populations could emerge, and historical demography analyses will be useful to provide additional evidences for explanations. Studies focusing on the two otters' fine-scale interactions would also improve predictions related to species occurrence and habitat preferences, which might bring more clues to the processes behind their distribution patterns.

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