



Review

Special issue: Comparative biogeography of Neotropical primates

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ABSTRACT

New research presented in this special issue of *Molecular Phylogenetics and Evolution* on the “Phylogeny and Biogeography of Neotropical Primates” greatly improves our understanding of the evolutionary history of the New World monkeys and provides insights into the multiple platyrrhine radiations, diversifications, extinctions, and recolonizations that have taken place over time and over space in the Neotropics. Here, we synthesize genetic and biogeographic research from the past several years to construct an overarching hypothesis for platyrrhine evolution. We also highlight continuing controversies in Neotropical primate biogeography, such as whether the location of origin of platyrrhines was Africa or Asia; whether Patagonian fossil primates are stem or crown platyrrhines; and whether cis- and trans-Andean Neotropical primates were subject to vicariance through Andes mountain building, or instead diversified through isolation in mountain valleys after skirting around the Andes on the northwestern coast of South America. We also consider the role of the Amazon River and its major tributaries in shaping platyrrhine biodiversity, and how and when primates from the Amazon reached the Atlantic Forest. A key focus is on primate colonizations and extirpations in Central America, the Andes, and the seasonally dry tropical forests and savannas (such as the Llanos, Caatinga, and Cerrado habitats), all ecosystems that have been understudied up until now for primates. We suggest that most primates currently inhabiting drier open habitats are relatively recent arrivals, having expanded from rainforest habitats in the Pleistocene. We point to the Pitheciidae as the taxonomic group most in need of further phylogenetic and biogeographic research. Additionally, genomic studies on the Platyrrhini are deeply needed and are expected to bring new surprises and insights to the field of Neotropical primate biogeography.

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1. Introduction

This special issue of *Molecular Phylogenetics and Evolution* on the “Phylogeny and Biogeography of Neotropical Primates” marks a watershed moment in our understanding of the evolutionary history of the New World monkeys, or suborder Platyrrhini. Schneider and Sampaio’s (2015) comprehensive review article on the history of research on platyrrhine systematics ends with a look toward the future of Neotropical primate biogeography. But the future is now, and with the new research presented in this issue we begin to form a comprehensive picture of the multiple New World monkey radiations, diversifications, extinctions, and recolonizations that have taken place over time and over space in the Neotropics. Here, we synthesize genetic and biogeographic research – both new research from this special issue and results from other key papers published over the past several years – to construct a comprehensive hypothesis for platyrrhine evolution. We also highlight continuing controversies in Neotropical primate biogeography, such as the location of origin of platyrrhines, the relationship of Patagonian fossil primates to living platyrrhines, and the influence of the formation of the Amazon River and its major tributaries in shaping platyrrhine biodiversity. We also identify the taxonomic groups most in need of further research, most pressing the Pitheciidae. Nuclear – and especially genome-wide – studies at the species and population levels are deeply needed and are expected to bring new surprises and insights to the field of Neotropical primate biogeography.

2. Overview and synthesis of Neotropical primate biogeography

2.1. Arrival and spread of primates in the neotropics

Platyrrhines form a monophyletic clade of non-human primates found in Mexico, Central America, and South America. Their origin has been contentious, because the timing of their arrival to South America based on the fossil record is believed to have occurred since 34 Ma, in a time interval after the breakup of Gondwanaland, when South America was isolated by water from all other continents. Kay (2015) supports the long-standing and prevailing view of an African origin for platyrrhines, based on his phylogenetic analyses of molecular and morphological data on living platyrrhines, combined with morphological data from fossil platyrrhines, stem anthropoids, and parapathecids. Kay’s analysis suggests that the cranial and dental anatomy of Late Eocene African primate taxa is quite similar to what would be expected in the last common ancestor of catarrhines and platyrrhines. In his phylogenetic tree, fossil and extant catarrhines (including *Aegyptopithecus*, *Hylobates*, *Miopithecus*, *Presbytis*, *Apidium*, and *Simonsius*) form a monophyletic sister clade to living and fossil Platyrrhini. He also argues against the late Middle Eocene Amphipitheciidae of South Asia as belonging to the Catarrhini, and thus does not include Asian fossil primates in his comparative dataset (see also Kay, 2012).

In contrast to the African dispersal hypothesis (Kay, 2015; Oliveira et al., 2009; Poux et al., 2006), as well as the less favored North American dispersal through Central America hypothesis (Simpson, 1945) or the Antarctic migration hypothesis (Houle,

1999), Jameson Kiesling et al. (2015) propose an intriguing novel hypothesis that South America may have been colonized through waif or sweepstakes dispersal from proto-platyrrhines in Asia that dispersed across the Pacific Ocean. Several recent studies have suggested an Asian origin for anthropoid primates (Beard et al., 2009; Chaimanee et al., 2012; but see Kay, 2012), and Jameson Kiesling et al. (2015) reconstruct a western Amazonian ancestor to all living platyrrhines. Fossil evidence congruent with the Asian origin hypothesis includes the earliest known fossil primate in the Neotropics, *Branisella*, from Bolivia in the western Amazon, dating to ~26 Ma. Although great progress in our understanding of platyrrhine evolution has been achieved by combining information from morphological and molecular data, and from fossil and living primates, we still require further evidence that will allow for testing among the distinct hypotheses on platyrrhine origin.

2.2. Relationship of fossil primates to living Platyrrhini

2.2.1. Patagonian fossils

The taxonomic position of *Branisella* and of many Miocene primates from the Southern Cone are subjects of debate among primate paleontologists. In his recent phylogenetic reconstruction, Kay (2015) concludes that neither *Branisella* from Bolivia nor any of the Miocene primate fossils from Chile or Argentina (except *Proteropithecina*) belong within crown platyrrhines. Rather, he argues that all of these forms represent stem platyrrhines that branched off before the last common ancestor of extant New World primates. In fact, Kay (2015) argues that Eocene platyrrhines evolved first in tropical regions of South America and then later, in the Early Miocene, expanded (perhaps several times independently) into Patagonia through the Paraná Portal, and that all taxa in Patagonia subsequently were extirpated during the Middle Miocene due to climatic and geological changes. By contrast, Rosenberger and colleagues (e.g., Rosenberger, 2002; Rosenberger et al., 2009) argue that many of the Patagonian primates can be accommodated as old forms within the radiation of extant platyrrhines, specifically within the Pitheciidae. The conflicting inferences about platyrrhine evolutionary history keep us waiting for new fossil evidence to resolve the relationship of the Patagonian fossils to modern primates. One point of commonality is the inferred time of origin of modern Platyrrhini. Kay’s scenario suggests modern platyrrhines originated after ~21 Ma, which coincides roughly with the estimates obtained by Jameson Kiesling et al. (2015) without using a *Branisella* calibration point (16.5 Ma, with 15.8–18.0 95% CI), as well as with those of other recent molecular studies (e.g., Hodgson et al., 2009; Pozzi et al., 2014; Di Fiore et al., 2015).

2.2.2. Antilles fossils

The relationships of fossil primates from the Greater Antilles to living platyrrhines are also discussed in this special issue. Kay’s (2015) phylogenetic reconstruction places all of the Antillean fossils as stem primates, nested between the Patagonian forms and the extant radiation. Kay (2015) also considers Jamaican *Xenothrix* as the sister taxon to living platyrrhines, and the Cuban *Paralouatta* and Hispaniolan *Antillothrix* as sister species, together forming a

sister clade to *Xenothrix* + modern platyrrhines. Notably, this view contrasts with that of [Rosenberger et al. \(2014\)](#), who argue that, from a functional-morphological perspective, *Paralouatta* has a closer phylogenetic affinity to *Alouatta*, and that both *Xenothrix* and *Antillothrix* are accommodated within the Pitheciidae ([Rosenberger, 2002](#)). In another contrasting view, MacPhee and colleagues ([MacPhee et al., 1995](#); [Horovitz, 1999](#); [Horovitz and MacPhee, 1999](#)) have suggested that all of the Antillean primates, including *Paralouatta*, are part of a monophyletic clade with pitheciid affinities. [Kay \(2015\)](#) argues that primates reached the Greater Antilles via South America through overwater dispersal by the Early Miocene, but were extirpated there in recent times, along with about 90% of the terrestrial mammal species.

2.2.3. La Venta fossils

The rich fossil record of La Venta, Colombia includes representatives of crown pitheciids (*Cebupithecia*, *Nuciruptor*), crown atelids (*Stirtonia*), and crown cebids (e.g., *Neosaimiri*, *Patasola*) – in short, it includes members of the crown groups for all of the major clades of living Platyrrhini. This implies that the radiation and diversification of forms that characterize the modern platyrrhine fauna were already well underway by the Middle Miocene (13.5–12.2 Ma). Although today the La Venta site is located within the Andes Mountains at ~400–500 m.a.s.l., prior to the eastern Andean range uplift in the Middle Miocene, this area (and the Magdalena Valley as a whole) was contiguous with the tropical lowlands. [Kay \(2015\)](#) argues that the La Venta fauna were living in habitat that was in contact with the Amazon and Orinoco Basins, and that La Venta itself was probably seasonally dry forest ([Kay and Madden, 1997](#)). [Jameson Kiesling et al. \(2015\)](#) – see Section 2.3.1) point more broadly to the Amazon rainforest as the generator of all genus-level diversity in platyrrhines.

2.2.4. Tempo and mode of platyrrhine evolution

[Aristide et al. \(2015\)](#) suggest that the best model for platyrrhine evolution is one of rapid initial diversification of taxa along a multidimensional niche based on diet composition and locomotion ([Rosenberger, 1992](#)), rather than other, more simple models based on diet or on locomotion only, or a neutral model. These authors argue that platyrrhine taxa separated relatively quickly following colonization of South America into discrete body size niches corresponding to the three major clades, after which there was a relative slowdown in platyrrhine evolution as each clade stayed mostly within those body size niches. This finding is in contrast to [Hodgson et al. \(2009\)](#), who performed a phylogenetic study using mitochondrial genomes and found not stasis but dynamic evolution among platyrrhines, at least until 12 Ma. One important difference in the two studies is that [Hodgson et al. \(2009\)](#) argue that lineages associated with early platyrrhine fossils from Patagonia such as *Tremacebus*, *Dolichocebus*, and *Chilecebus* went extinct. [Aristide et al. \(2015\)](#) point to the early Patagonian fossil platyrrhines as having similar body size evolution patterns to the modern platyrrhine clades with which they have been associated as crown taxa. In other words, in their view, including the early fossils as crown taxa within the set of modern clades is consistent with long-term stasis in body size evolution. Still, similarity in niches between Patagonian fossil taxa and modern taxa could be a result of either shared ancestry or parallel evolution in successive neotropical radiations along dietary, locomotor, and size axes. In fact, when [Aristide et al. \(2015\)](#) did not incorporate fossils in their analysis, their best fit to the molecular data was a ‘pure birth’ model with no evidence for decelerating lineage accumulation, consistent with most molecular studies of platyrrhine phylogenetic history. Nonetheless, [Aristide et al. \(2015\)](#) suggest that high extinction rates could erase the signal of a decrease in lineage diversification rates when fossils are not taken into account, and their fossil line-

age origination curve suggests there was an early rapid increase of species followed by a relative slowdown in diversification. These contrasting ideas point to the significant contribution that discovery of additional fossil taxa could bring to our understanding of platyrrhine evolutionary history, particularly of taxa that shed better light on the relationship between Early Miocene Patagonian forms and Middle Miocene forms from La Venta, Colombia and Acre, Brazil.

2.3. Biogeography of extant Neotropical primate radiations

2.3.1. The Amazon: Generator of primate diversity

[Jameson Kiesling et al. \(2015\)](#) use a statistical dispersal–vicariance analysis (S-DIVA) with a genomic data set including 36 species of Neotropical primates to reconstruct a biogeographic scenario for extant platyrrhines. Their analysis places the origin and initial diversification of the common ancestor to the extant platyrrhine primates in the Amazon, probably to the east of the large wetland area known as the Pebas system that existed in western Amazonia in the Early Miocene (but see [Sacek, 2014](#) for controversy over the timing and presence of the Pebas Lake). These initial populations would have extended their ranges in parallel with the expansion and changing landscape of Amazonian tropical rainforest. These authors suggest that rather than diversification through vicariance, the Neotropics provided such a rich and complex new ecosystem that diversification of the major platyrrhine clades could have happened ‘practically in sympatry’. [Jameson Kiesling et al.’s \(2015\)](#) reconstruction suggests that many genus- and species-level divergences within each of the families Atelidae, Pitheciidae, and Cebidae all took place first in the Amazon and that members of some genera (e.g., *Brachyteles*, *Callithrix* sensu lato, *Cebus* sensu lato) later spread into the Atlantic Forest, Cerrado, Caatinga, and Central Grasslands ([Jameson Kiesling et al., 2015](#)). Such a scenario is broadly consistent with the findings of [Lynch Alfaro et al. \(2012\)](#), [Buckner et al. \(2015\)](#) and [Morales Jimenez et al. \(2015, B\)](#) for phylogenetic histories of capuchins, marmosets, and spider monkeys, respectively. [Kay \(2015\)](#) concurs that the cladogenesis among the early crown platyrrhines was tropical.

Additionally, in their analysis of Neotropical primates’ biogeographic spread across Central and South America, [Jameson Kiesling et al. \(2015\)](#) found no evidence to support the claim that waterways form an important barrier to Neotropical primates, at least when focusing on genus-level diversity. *Alouatta*, *Cebus* (sensu lato, including *Sapajus*) and *Callicebus* are the most cosmopolitan genera, each having spread across all ecogeographic zones inhabitable by non-human primates in the Neotropics ([Jameson Kiesling et al., 2015](#)). However, it should be noted that changes in the features of river drainages throughout the period of platyrrhine evolution might have produced intermittent or permanent barriers that isolated or limited the dispersal of particular populations, serving as generators of species diversity within lineages. In other words, river barriers likely have played a more important role in the diversification of species within genera. [Boubli et al. \(2015\)](#) performed a comparative analysis to assess evidence for the Rio Negro and Rio Branco in the Amazon Basin as either barriers to dispersal or as forces of vicariance (during river formation) for several genera of Neotropical primates. They examined the concordance in divergence times between congeneric primate species pairs along the two banks of the Rio Negro and Rio Branco and concluded that the rivers indeed served as barriers promoting vicariance or limiting dispersal, with a general concordance of divergence in species pairs (within *Callicebus*, *Cebus*, and *Cacajao*) across both sides of the upper Rio Negro between 0.8 and 1.7 Ma. Their analyses suggest that formation of the Rio Negro may have occurred around that time, which is consistent with several similar

studies investigating the role of this river in the diversification of birds (d’Horta et al., 2013; Fernandes et al., 2012, 2013; Sousa-Neves et al., 2013; Ribas et al., 2012).

By contrast, Morales Jimenez et al. (B, 2015) inferred that Amazonian *Ateles* splits occurred between 6.7 and 4 Ma, and they argue that Amazonian river barriers cannot be responsible for most species-level divergences within spider monkeys as these predate the formation of the modern Amazon drainage, following Ribas et al. (2012). On the other hand, based on data from whole mitochondrial genomes and from more extensive sampling of mtDNA control region sequences in several populations from Ecuador and Colombia, modern woolly monkeys (*Lagothrix*) are recovered as being a much more recent radiation (Di Fiore et al., 2015). After a split between the yellow tailed woolly monkey, *Lagothrix flavicauda*, and the common ancestor of all other forms ~2.1 Ma (Di Fiore et al., 2015), woolly monkeys spread into the lowlands and diversified rapidly within the western Amazon and northeast Andes within the last 800 kyr (Di Fiore et al., 2015; Botero et al., 2015). The current distribution of Amazonian *Lagothrix* is limited by the Andes to the west, the Andes and Amazon River to the north, and the Tapajós River to the east, suggesting all these barriers already may have been in place during the *Lagothrix* radiation, and as such limited further expansion of this genus. More studies on comparative biogeography across the Amazon River and its major tributaries (e.g., the Negro, Branco, Madeira, Juruá, Purus, Tapajós, and Xingu rivers) are needed to fully understand their role in Neotropical primate dispersal and evolution.

Amazonian squirrel monkeys show strong geographic structure in *cyt b* and mitochondrial control region haplotypes, with individuals sampled within major interfluvia more similar to each other than those sampled across major rivers (Lynch Alfaro et al., 2015). Mercês et al. (2015) show that the Amazon River has been a barrier to dispersal to squirrel monkeys, with *Saimiri sciureus* restricted to the north of the eastern Amazon River, and *S. collinsi* restricted to the south. This is in contrast to Ferrari (2004) who cited a single *Saimiri* species (*Saimiri sciureus* sensu lato) on both sides of the lower Amazon as proof that squirrel monkeys were not limited by river barriers. Previous studies have also implied the plausible role of major rivers in the diversification of Neotropical primates (e.g., Wallace, 1852; Ayres and Clutton-Brock, 1992; Cortés-Ortiz et al., 2003), but definitive testing of the models of diversification in the Amazonia are still required for most taxa.

Little is certain yet about pitheciine evolution. Various molecular studies have estimated the split between *Chiropotes* + *Cacajao* and *Pithecia* at ~15 Ma, and that between *Chiropotes* and *Cacajao* at about 8 Ma (Boubli and Ditchfield, 2001; Springer et al., 2012). The distribution of modern *Pithecia* encompasses all of southern Amazon as far east as the Tapajós River, as well as the Guianas east of the Rio Branco (Marsh, 2014). For *Pithecia*, there has been almost no genetic work, but Springer et al. (2012) place southern Amazonian *P. monachus* and *P. irrorata* as closely related sister taxa, and northern Amazonian *P. pithecia* as a sister taxon to the southern Amazon clade. This suggests that a first major division between saki monkeys may have been a result of vicariance due to formation of the Amazon River.

In contrast, the bearded sakis (*Chiropotes*) may have diversified first in the southern Amazon, and later spread north of the Amazon River. *Chiropotes albinus* was recovered as the sister group to a clade comprising *C. utahicki* + *C. israelita* (Bonvicino et al., 2003), suggesting that the southeastern Amazon taxa diversified first (*C. utahicki* and *C. albinus* are both located east of the Madeira and south of the Amazon), with *C. utahicki* later spreading across the Amazon River to the north and speciating into the northern Amazonian forms. However, this assessment is best considered preliminary because several *Chiropotes* species were not available for the analysis. *Chiropotes* also may have expanded in the late Pleisto-

cene across the Branco River into contact with *Cacajao* in Amazonian Venezuela and in Brazil in the Branco/Negro interfluvium; competitive displacement by *Chiropotes* may have isolated two *Cacajao* populations that subsequently diversified into *C. ayresi* and *C. hosomi* (Boubli et al., 2008).

Within *Cacajao* the bald uakaris to the south of the Japurá River are estimated to have diverged from the black uakaris to the north of the Japurá at ~5 Ma (Boubli and Ditchfield, 2001; Figueredo-Ready et al., 2013). The modern radiation of bald uakaris began ~3.9 Ma (Figueredo-Ready et al., 2013), while the modern radiation of black uakaris appears more recent, at ~1.1 Ma (Boubli et al., 2015). Clearly, additional genetic sampling across species in the saki, bearded saki, and uakari clades are needed to better understand the diversification times and biogeography of this group.

2.3.2. Atlantic Forest: Miocene colonizations

Within vertebrates, a common pattern in South American biogeography is to find sister taxa with disjunct distributions in the Atlantic Forest and the Amazon. For example, Pelligrino et al. (2011) show that for lizards of the genus *Leposoma*, the split between Amazon and Atlantic Forest species took place in the Early Miocene, estimated at 22 Ma (16–29 Ma 95% CI), with the diversification of modern *Leposoma* in the Atlantic Forest starting at 16 Ma (12–22 Ma 95% CI) and no subsequent interchange between Atlantic and Amazon taxa captured in their data. For spiny rats, Galewski et al. (2005) estimated Late Miocene dates for the splits of two Amazon vs. Atlantic Forest sister taxa (*Dactylomys* vs. *Kannabateomys*, 9.5 Ma, 4.4–16.4 95%CI; *Echimyus* vs. *Phylomys* 10.3 Ma, 5.2–17.1 95% CI). Among avifauna, too, one commonly seen pattern is a relatively old split between southern Atlantic Forest upland forest birds and their Amazonian sister taxa, corresponding to Middle to Late Miocene connections along the southern Cerrado in Mato Grosso or along the transition to the Bolivian and Paraguayan Chaco (Batalha-Filho et al., 2013). In addition, some bird taxa are characterized by younger Plio-Pleistocene splits between closely related forms corresponding to connections between the northeastern lowland Atlantic Forest and the far eastern Amazon via Cerrado and Caatinga habitats (Batalha-Filho et al., 2013).

Similarly, among the primates, all Atlantic Forest genera have closely related sister taxa in the Amazon, and most of these splits occurred in the Middle to Late Miocene (Table 1). The common ancestor to all marmosets and tamarins is reconstructed with a wide geographic distribution that encompassed both Amazonian and Atlantic Forests, and *Leontopithecus* was a Middle Miocene Atlantic Forest split through vicariance (13.4 Ma; Buckner et al., 2015). In a second marmoset expansion, *Callithrix* colonized the Atlantic Forest from the Amazon some time before 6 Ma (Buckner et al., 2015). The split between Amazonian *Lagothrix* and Atlantic Forest *Brachyteles* occurred somewhat earlier, in the Late Miocene (~8.6 Ma, Di Fiore et al., 2015), while the split of Atlantic Forest and Amazonian titi monkeys (*Callicebus*) is estimated at 6.7 Ma (Springer et al., 2012). Lynch Alfaro et al. (2012) found a Late Miocene split at about 6.2 Ma for Amazonian *Cebus* and Atlantic Forest *Sapajus*, with a later Pleistocene expansion of *Sapajus* back into the Amazon around 1 Ma–400 kyr. The divergence of the Atlantic Forest howler monkey *Alouatta guariba* from the mostly Amazonian *Alouatta belzebul* has been estimated at 4 Ma (Cortés-Ortiz et al., 2003). However, it seems that the presence of these two species in the Atlantic Forest is due to multiple colonizations of this area by *Alouatta* (see below). Together these data on primates suggest that there may have been intermittent intervals of continuity across the Atlantic Forest and Amazonian biomes, at approximately 14–13 Ma and 9–4 Ma, punctuating longer intervals of discontinuity between these biomes.

Table 1
Divergence time estimates for sister taxa splits for Atlantic Forest vs. Amazonian primate clades.

Amazonian taxa	Atlantic Forest taxa	Divergence time estimate	95% HPD	95% HPD	Authors
<i>Callimico/Cebuella/Mico/Callithrix</i>	<i>Leontopithecus</i>	13.6	9.9	17.3	Perelman et al. (2011)
		13.4	11.4	15.6	Buckner et al. (2015)
		13.2	10.6	16.0	Springer et al. (2012)
<i>Lagothrix</i>	<i>Brachyteles</i>	11.3	7.5	15.8	Springer et al. (2012)
		10.2	7.4	13.4	Di Fiore et al. (2015)
		9.5	6.1	13.4	(BEAST2 analysis) Perelman et al. (2011)
		8.6	6.5	11	Di Fiore et al. (2015)
					(BEAST7 analysis)
<i>Callicebus cupreus/donacophilus</i> group	<i>Callicebus personatus</i> group	9.9	6.2	14.0	Perelman et al. (2011)
		6.7	4.8	8.5	Springer et al. (2012)
<i>Cebus</i>	<i>Sapajus</i>	6.2	4.2	7.9	Lynch Alfaro et al. (2012)
		6.0	3.1	9.4	Perelman et al. (2011)
		5.7	3.6	8.3	Springer et al. (2012)
<i>Mico</i>	<i>Callithrix</i>	6.0	3.8	8.6	Perelman et al. (2011)
		5.4	4.3	6.7	Buckner et al. (2015)
		4.6	3.4	6.5	Springer et al. (2012)
					(excludes ' <i>Callithrix saterei</i> ') Cortes-Ortiz et al. (2003)
<i>Alouatta seniculus/sara/macconelli/caraya</i>	<i>Alouatta guariba + Alouatta belzebul belzebul</i>	5.1	–	–	Cortes-Ortiz et al. (2003)
		3.2	2	4.5	Springer et al. (2012)

No new primate genera appear in the Atlantic Forest after 4 Ma, although several Atlantic Forest genera expand into new habitats later in time and some species may have invaded the Atlantic Forest more recently. For example, three howler monkey species are currently found in the Atlantic Forest: *A. belzebul* in the north east; *A. guariba* in most of the Atlantic Forest from southern Bahia extending south into the state of Rio Grande do Sul, Brazil, and the extreme north of Argentina (Rylands et al., 1996; Mendes et al., 2008); and *A. caraya* on the left margin of the Rio Paraná (State of Paraná, Brazil) (Aguiar et al., 2007) and in São Francisco de Assis, State of Rio Grande do Sul, Brazil (Bicca-Marques et al., 2008). The distributions of these howler taxa seem to be the result of different processes that occurred at different times. First, a Pliocene diversification event (~4 Ma, Cortés-Ortiz et al., 2003) seem to have separated the *A. guariba* precursor population in the Atlantic Forest and *A. belzebul* ancestors in the Amazonian basin. This scenario is consistent with the proposed multiple contractions and expansions of gallery forests connecting and disconnecting the Amazon and Atlantic Forests during the Pliocene and Pleisto-

cene (see Batalha-Filho et al., 2013). However, the presence of a disjunct population of *A. belzebul* in Paraíba (northeast Atlantic Forest) with minor phylogeographic differentiation from the populations in Pará (Amazon basin) seem to be due to a more recent colonization of the northeastern Atlantic Forest, perhaps during the Holocene (Cortés-Ortiz et al., 2003). Finally, *A. caraya* occurs in some areas of the southern Atlantic Forest, mainly in syntopy and/or sympatry with *A. guariba*, and in areas considered as ecotones between the Atlantic Forest (typical habitat of *A. guariba*) and the Cerrado (considered typical habitat for *A. caraya* in Brazil by Gregorin, 2006) (e.g., Aguiar et al., 2007). Given the more widespread range of *A. caraya* outside of the Atlantic Forest it seems reasonable to assume that the presence of this howler monkey in this region is the result of expansion of this species, which must have originated elsewhere.

While some primate genera show evidence of occupation of the Atlantic Forest as early as the Middle Miocene and all extant Atlantic Forest primate genera were present in this forest by the Late Miocene or Early Pliocene, the modern species-level radiations of

Table 2
Timing of modern platyrrhine radiations within Brazil's Atlantic Forest.

North Atlantic	South Atlantic	Divergence time estimate (Ma)	95% HPD	95% HPD	Authors
<i>Alouatta belzebul belzebul</i>	<i>A. guariba</i>	4.0	–	–	Cortes-Ortiz et al. (2003)
		2.4	0.7	4.0	Springer et al. (2012)
<i>Callicebus personatus + C. coimbrai</i> <i>C. personatus</i> vs. <i>C. coimbrai</i>	<i>C. nigrifrons</i>	3.4	2.3	4.8	Springer et al. (2012)
		2.0	1.2	2.9	Springer et al. (2012)
<i>Callithrix geoffroyi + C. kuhlii + Cerrado/Caatinga marmosets</i> <i>C. geoffroyi</i> vs. <i>C. kuhlii + Cerrado/Caatinga marmosets</i>	<i>C. aurita</i>	2.5	1.6	3.5	Springer et al. (2012)
		1.0	0.5	1.7	Springer et al. (2012)
<i>Sapajus xanthosternos</i>	<i>S. nigritus + S. robustus + Amazon/Cerrado Sapajus</i>	2.4	–	–	Wright et al. (2015)
<i>S. robustus (+ Amazon/Cerrado Sapajus)</i>	<i>S. nigritus</i>	1.8	–	–	Wright et al. (2015)
<i>Brachyteles hypoxanthus</i>	<i>B. arachnoides</i>	2.0	1.3	2.9	Di Fiore et al. (2015)
<i>Leontopithecus chrysomelas</i>	<i>L. rosalia + L. chrysopygus</i>	0.5	0.2	1.1	Springer et al. (2012)
	<i>L. rosalia</i> vs. <i>L. chrysopygus</i>	0.1	0.0	0.4	Springer et al. (2012)

Table 3

Timing of arrival in and diversification within the Andes and Central America for Neotropical primates.

Trans-Andes (West)	Cis-Andes (East)	Divergence time estimate (Ma)	95% HPD	95% HPD	Authors
<i>Saguinus oedipus</i> group	<i>S. midas/bicolor</i> groups (east Amazon)	5.3 4.3 4.9	3.4	7.6	Perelman et al. (2011) Araripe et al. (2008) Buckner et al. (2015)
<i>S. leucopus</i> vs. <i>S. oedipus</i>	Crown <i>S. leucopus</i> radiation	2.0 ~ 1.6–1.1	–	–	Ruiz-García et al. (2014) Ruiz-García et al. (2014)
<i>Aotus lemurinus</i>	<i>Aotus griseimembra</i>	5.4	–	–	Babb et al. (2011)
Crown <i>Aotus lemurinus</i> radiation		3.4	0.6	6.9	Babb et al. (2011)
<i>Alouatta pigra</i> + <i>palliata</i>	All cis-Andean <i>Alouatta</i>	6.8 6.0 3.7	–	–	Cortés-Ortiz et al. (2003) Perelman et al. (2011) Springer et al. (2012)
<i>Ateles geoffroyi</i> + <i>fusciceps</i>	All cis-Andean <i>Ateles</i>	3.6	–	–	Collins and Dubach (2000)
<i>Ateles geoffroyi</i> + <i>fusciceps</i>	<i>Ateles paniscus</i>	3.5	2	5.2	Morales Jimenez et al. (B, 2015)
<i>Ateles geoffroyi</i> vs. <i>A. fusciceps</i>		2.2	1.2	3.5	Morales Jimenez et al. (B, 2015)
Central American + Andes <i>Cebus</i>	Amazonian <i>Cebus</i>	1.9	–	–	Boubli et al. (2012)
Mesoamerican <i>Saimiri</i> (<i>S. oerstedii</i>)	Amazonian <i>Saimiri</i> (<i>S. sciureus</i>)	1.0	0.5	1.5	Lynch Alfaro et al. (2015)

all primate taxa within the Atlantic Forest are relatively recent (Table 2), having occurred principally within the last 3 Ma. Some are even more recent (e.g., ~1 Ma for species-level divergences within *Leontopithecus* and within *Callithrix*; Buckner et al., 2015). This result suggests repeated cycles of expansion and contraction of genus range, with local extirpation and replacement. Recent splits between North and South Atlantic Forest taxa have also occurred, such as that between the southern and northern muriquis, estimated at ~2 Ma (Di Fiore et al., 2015), and *Alouatta guariba* and *A. g. clamitans* estimated at 1.1 Ma (de Mello Martins et al., 2011). Northern Atlantic Forest (also classified as the Bahian interior forest Ecoregion: Olson et al., 2001) differs markedly from its Southern counterpart (Serra do Mar Coastal Forests, Olson et al., 2001). Rainfall is more highly seasonal in the north, which affects forest structure, floristic composition, and, most importantly, patterns of temporal availability of edible plant parts (young leaves, fruit, flowers). Aside from differences in habitat, there is evidence for geographic barriers that later become permeable, both within the Atlantic Forest and in the adjoining Caatinga and Cerrado areas (see Section 2.3.5).

2.3.3. The Andes: vicariance through mountain uplift or skirting around the edges

Several avian studies have reported splitting events for lowland wet-forest associated taxa in trans- and cis-Andean regions (trans-Andean meaning the tropical lowlands to the west of the Andes in Ecuador, Colombia, and Central America, and cis-Andean meaning east of the Andes, in the Amazon, sensu Haffer (1967)) around 3.3–3.6 Ma (*Trogon*: DaCosta and Klicka, 2008; *Ramaplastos*: Patane et al., 2009; *Dendroclina*: Weir and Price, 2011), with the uplift of the Eastern Cordillera of Colombia (estimated to have been completed at 3.5 Ma (Weir and Price, 2011), or alternately by 2 Ma (Gregory-Wodzicki, 2000)) serving as a vicariant factor. However, dispersal events postdating final Andean uplift also occur between these two regions within these same bird genera, suggesting that the Andes also function in promoting dispersal-based speciation, at least among birds (Weir and Price, 2011). Table 3 summarizes splits among trans-Andean and cis-Andean primate taxa.

Babb et al. (2011) estimated that the split between *Aotus lemurinus* and *A. griseimembra* occurred at 5.4 Ma; these two Andean taxa span the northern and central cordilleras. *A. lemurinus* has been diversifying in the Andes for about 3.4 Ma (Babb et al., 2011). Together, these data strongly suggest that *Aotus* had already

colonized the Central and Northern Andes prior to the final uplift, and that species diversification in the Andes may have been a result of vicariance due to mountain building. It is important to note that *Aotus* is well adapted to high altitude and/or cold environments; *A. lemurinus*, in particular, is a high altitude specialist in the Andes. We hypothesize that *Aotus* spanned the Northern and Central Andes prior to its completion, and that isolation between cis- and trans-Andean forms happened through niche specialization of *A. lemurinus*, whose distribution extends north to south along the highest peaks of the Andes, effectively separating the distributions of the eastern and western lowland taxa around the borders of the Andes. In the southern Andes, *A. miconax* is also restricted to high altitude forests, with its range reaching altitudes over 3000 m.a.s.l. (Shanee et al., 2014).

In the case of *Alouatta*, the genus as a whole is relatively old, with the initial cis- and trans-Andean split estimated, using different kinds of molecular markers, variously as 6.8 Ma (Cortés-Ortiz et al., 2003), 6.0 Ma (Perelman et al., 2011) or 3.7 Ma (Springer et al., 2012). This suggests that the split could have been a result of vicariance due to Andes uplift. However, what is less clear is the split between the cis- and trans-Andean populations of *A. seniculus*, which appears to be much more recent. In fact, Cortés-Ortiz et al. (2003) included both cis- and trans-Andean *A. seniculus* samples in their analyses, and the sequences were virtually identical for both mitochondrial *cyt b* and mitochondrial ATP-synthase 6 and 8 sequences, suggesting a very recent expansion in this species. This may point to initial Late Miocene colonization of the north and central Andes by *Alouatta* prior to final uplift, vicariance between ancestral *A. pigra* + *A. palliata* vs. Amazonian *Alouatta* due to high altitude barriers to dispersal in the Pliocene, and a subsequent and much more recent expansion by *A. seniculus* reaching its current distribution in northern South America from the Amazon through the lowlands in the coast of northern Venezuela and/or Colombia.

For spider monkeys, genus *Ateles*, a roughly 3.6 Ma split was estimated between the trans-Andean and Amazonian forms by Collins and Dubach (2000), using mtDNA and nuclear sequence data. In a more recent study, Morales Jimenez et al. (B, 2015) recovered the split between cis- and trans-Andean *Ateles* at ~3.5–4.5 Ma, with the sister taxon of the trans-Andean *geoffroyi* + *fusciceps* clade as either *A. paniscus* or *A. hybridus* from northeastern and northern South America. This puts the split between cis- and trans-Andean spider monkeys well within the Pliocene. While

more research is needed on *A. hybridus*, whose distribution encompasses the Magdalena Valley and the southern border of Lake Maracaibo, as well as disjunct populations east of the Andes and on the northern Venezuelan coast, the distribution of both of these species suggests that the ancestors of trans-Andean *Ateles* may have skirted around the Andes along the northern coastal route to invade the inter-Andean valleys of northern Colombia and Central America, and that *A. hybridus* has a disjunct distribution not because of vicariance through mountain-building, but instead because of fragmentation through dry forest formation in the Venezuelan Llanos region.

For gracile capuchins (*Cebus*), the best estimate from preliminary molecular and biogeographic data is that western and northern Andes + Central American capuchins form a monophyletic clade, with that radiation including *C. brunneus*, *C. leucocephalus*, *C. a. cesarae*, *C. capucinus*, and *C. imitator* (Boubli et al., 2012; Rylands et al., 2013). This Andes + Central American clade of capuchins branched off from Amazonian capuchins about 1.9 Ma (Boubli et al., 2012). However, it is unclear how *C. (albifrons) aequatorialis* reached the western side of the Andes—it is found in the trans-Andean region of western Ecuador and the very northern edge of Peru, where the Andean cordillera is the lowest in that region (Shanee et al., 2014), suggesting it may have migrated through the Marañon passage, across the Andes. However, another alternative is that *Cebus* reached that region by traveling a coastal route around the Northern Andes.

Squirrel monkeys are absent throughout the Andes, but the split between cis-Andean and trans-Andean (i.e., Mesoamerican) *Saimiri* probably occurred less than 1 Ma (Chiou et al., 2011; Lynch Alfaro et al., 2015). All modern *Saimiri* taxa, including Central American *S. oerstedii*, are found close to water bodies (Rylands and Mittermeier, 2013), and this may be an evolutionary constraint on their biology, making them less suited to colonizing Andes highlands. The squirrel monkey ancestor may have been a water-affiliated taxon, distributed in a ring around the Pebas Lake in the western Amazon (Lynch Alfaro et al., 2015). As the lake drained and river systems were formed, *Saimiri* rapidly spread throughout the Amazon and beyond, as far as the Guianas and Central America (Lynch Alfaro et al., 2015).

For both *Saimiri* and *Cebus* then, the timing of entry into the Andes and Mesoamerica post-dates the final uplift of the Eastern Cordillera of Colombia, even according to Gregory-Wodzicki's (2000) estimates. *Saimiri* is a lowland-affiliated taxon (Rylands and Mittermeier, 2013), and *Cebus* also tends to be a lowland taxon, although some species have been recorded at up to 2000 m (with the highest altitude report that of *C. (a.) yuracus* at 2425 m.a.s.l. in Ecuador east of the Andes; Harris et al., 2008). We suggest that for squirrel monkeys and capuchins, as for *Ateles* (Morales Jimenez et al., 2015), the diversification of species was not a result of vicariance through mountain uplift, but instead a result of skirting around the already fully formed Andes, by expanding westward along the northern coast, with subsequent isolation in mountain valleys and coastal areas as a result of changing sea levels during the fluctuating temperatures of the last 1 Ma that are associated with glacial maxima and warming periods. An important test of these contrasting hypotheses for *Cebus* will be to determine if *C. (a.) aequatorialis* from the western Ecuadorian and Peruvian coast is more closely related to northern Andean *Cebus* or to Amazonian *Cebus* to the east of the Andes.

The distribution of the *Saguinus* clade in the trans-Andes region is disjunct from its sister group, *S. midas* and *S. bicolor*, found in northeastern Amazonia. Large-bodied tamarins are generally lowland taxa, and the distribution of *S. geoffroyi* and *S. oedipus* in the Magdalena Valley in between the two major northern Andes mountain ranges, suggest that this clade is a lowland group that,

like *Ateles*, *Cebus*, and *Alouatta seniculus* probably entered this area by skirting around the mountains with subsequent isolation across the Andes due to habitat changes along the western South American coast. The timing of the arrival of tamarins west of the Andes is unclear; they diverged from the *S. midas* group at 4.7 Ma (Springer et al., 2012), but diversification within the *oedipus-geoffroyi* clade may date from only 600 kya (Springer et al., 2012). Springer et al. (2012) recover the trans-Andean tamarin group as paraphyletic, with *S. leucopus* diverging independently from cis-Andean tamarins at ~3.9 Ma, suggesting two probable invasions of the trans-Andes area. Based on morphological analyses, Ackermann and Cheverud (2002) also found *S. oedipus* and *S. geoffroyi* to form a clade together, as a sister group to *S. leucopus* + all Amazonian tamarins. However, in other molecular studies, the three trans-Andean tamarins form a clade together (Cropp et al., 1999; Buckner et al., 2015). A recent population-level mtDNA analysis of *S. leucopus* recovered the divergence between *S. leucopus* and *S. oedipus* at 2 Ma and a subsequent divergence within *S. leucopus* beginning at 1.6–1.1 Ma; this analysis, however, did not find any geographic structure within *S. leucopus* across the Colombian Andes (Ruiz-García et al., 2014).

Taken as a whole, we propose two main patterns for primate evolution in the northern and central Andes. Howler monkeys (the ancestors of *Alouatta palliata* and *A. pigra*) and owl monkeys had probably first colonized the trans-Andean region in the Late Miocene or early Pliocene, and diversified through vicariance due to mountain uplift and through the multiple connections and disconnections between South and Central America during the formation of the Panama land bridge. These taxa also would have had the time to adapt to highland habitats with the incremental rise in local altitude over millions of years of Andes occupation. By contrast, spider monkeys, tamarins, capuchins, squirrel monkeys and *A. seniculus* arrived in northern South America later in time, and never fully colonized the Andes; instead, they skirted around its edges to invade coastal regions and the inter-Andean valleys of northern Colombia, with most of them reaching Central America. Vicariance for these species was a result of changing coastlines and isolation in valleys, as well as local extirpations, possibly due to climate fluctuations during the last 1 Ma. It is likely that *Alouatta seniculus* did not colonize Central America due to the presence of *A. palliata*, already occupying the area. Interestingly, there is a known area of sympatry for *A. seniculus* and *A. palliata* in northern Colombia (Zuñiga Leal and Defler, 2013), which is consistent with secondary contact of these species.

2.3.4. Central America: primates in the great American interchange

All living primates in Mexico and Central America are closely related to extant taxa residing in northern South America (Kay, 2015). Mesoamerica is inhabited by six genera and over twenty taxa (species and subspecies) of primates (Rylands et al., 2006). It has been inferred that these species colonized Central America when the land connection between North and South America occurred, approximately 3 million years ago, as a consequence of the formation of the Panama Isthmus (Colinvaux, 1998). Nonetheless, the different primate taxa that are currently distributed in Mesoamerica seem to have different evolutionary histories in the region and probably reached their current ranges at different times (Cortés-Ortiz et al., 2003; Ford, 2006). Only recently have a few studies concentrated on the evolutionary history of primate genera that inhabit the Mesoamerican region (Cortés-Ortiz et al., 2003; Chiou et al., 2011; Ruiz-García et al., 2012; Lynch Alfaro et al., 2012; Boubli et al., 2012; Morales Jimenez et al., 2015; Lynch Alfaro et al., 2015).

New biogeographic analyses reveal a surprising pattern of relatedness between Guiana Shield and Eastern Amazonian taxa with Central American taxa. For example, the sister group to Central

American squirrel monkeys (*Saimiri oerstedii*), are Guianan squirrel monkeys (*Saimiri sciureus*) (Chiou et al., 2011; Lynch Alfaro et al., 2015), and the sister group to the Central American and north Andean clade of tamarins (*Saguinus leucopus*, *S. geoffroyi* and *S. oedipus*) is recovered as the Eastern Amazonian tamarin clade (*Saguinus martinsi*, *S. bicolor*, *S. midas*, and *S. niger*) (Buckner et al. 2015). In the spider monkeys as well, Guiana Shield + Eastern Amazonian *Ateles paniscus* was recovered as the sister taxon to Central American *A. geoffroyi* + *A. fusciceps* (Boubli et al., 2015; Morales Jimenez et al., B, 2015). Finally, for *Cebus*, there is preliminary evidence that the capuchins surrounding Lake Maracaibo in northern Venezuela and those on Trinidad together form a sister clade to the trans-Andean and Central American capuchins, although the relationships of these species to *C.(a.) aequatorialis* is yet unknown (Boubli et al., 2012). These data all suggest that there was once a continuous linked habitat, perhaps along the northern coast of South America, that allowed for species interchange between Central America and the Guianas, and that subsequently all the intervening primate populations (at least for certain genera) were extirpated due to climate change and disappearing forests. As mentioned above, the presence of *A. seniculus* in northern Colombia also supports this possible route, although phylogeographic analyses are required to evaluate the relationships of the red howler population in northern Colombia with those of southern Colombia, as well as with *A. arctoidea* and *A. macconnelli*.

A molecular time tree based on *cyt b* and HV1 data (Boubli et al., 2012) indicates that *Cebus* experienced a rapid Early Pleistocene diversification, with the crown radiation at 2.5 Ma, the split between Andes + Central American and Amazonian capuchins about 1.9 Ma, and the split between *C. c. capucinus* from western Panama and Costa Rica and *C. c. imitator* from eastern Panama and Colombia at ~1.6 Ma. Ruiz-García et al. (2012), using the mitochondrial COII gene, estimated a much earlier split between western Colombian and Central American gracile capuchins, at 3.7–4.8 Ma. Boubli et al.'s (2012) data align more closely with those of Perelman et al. (2011), who estimated from nuclear markers that the gracile *Cebus* radiation began at 2.2 Ma (1.0–3.5 Ma 95% HPD). The divergence time estimates from Boubli et al. (2012) and Perelman et al. (2011) suggest that capuchins ancestral to *C. c. imitator* may have first entered Central America around 1.6 Ma, similar to the 2 Ma suggested by Ford (2006), but that there was also a later, independent colonization of eastern Panama by *C. c. capucinus* ancestors (Boubli et al., 2012).

Using mtDNA sequence data, Morales Jimenez et al. (A, 2015) reconstructed the age of the most recent common ancestor of *Ateles geoffroyi*, from Central America, and *Ateles fusciceps*, from Panama and the Pacific Coast of Colombia and Ecuador, at roughly 2.3 Ma, suggesting that the initial invasion of spider monkeys into Central America must have predated that split, with a subsequent isolation of the populations of northern South America and Central America, and a more recent expansion of *A. fusciceps* into Central America, as was suggested by Ford (2006). The common ancestor of these two trans-Andean species was inferred to share a common ancestor with *Ateles paniscus* from the Guianas at ~3.5–4.5 Ma and with *A. hybridus* ~4.0–4.5 Ma, putting an upper bound on when the genus might have moved into Central America (Morales Jimenez et al., B, 2015).

As mentioned above, *Alouatta palliata* and *A. pigra* form a clade that is reciprocally monophyletic to all other South American howler monkeys, and their ancestor seems to have diverged from the Amazonian species through vicariance as a consequence of the final uplift of the Andes (Cortés-Ortiz et al. 2003). This divergence occurred prior to the land connection between South and Central America. The diversification of the ancestral population that eventually gave rise to *A. palliata* and *A. pigra* (3 Ma, Cortés-Ortiz et al., 2003; or 2.5 Ma, Springer et al., 2012) is coincident with the com-

plex and dynamic process of the final closure of the isthmus of Panama, in a time period that included changes in sea level and vegetation coverage due to climatic fluctuations that connected and disconnected populations between Central and South America (Cortés-Ortiz et al., 2003; Ford, 2006). Overall, it seems likely that spider monkeys and howler monkeys were indeed among the many mammalian taxa that moved from South into Central America as part of the great faunal interchange that followed the establishment of the Panamanian Isthmus.

For *Saimiri*, it is difficult to determine a specific date for the entry into Central America. Central American *Saimiri oerstedii oerstedii* and *S. o. citronellus* diverged from one another approximately 100–200 kyr (Chiou et al., 2011; Lynch Alfaro et al., 2015), but these remnant populations of *S. oerstedii* are so geographically restricted that they are unlikely to encompass the genetic diversity that would allow us to estimate the timing of their arrival. We do know that modern *Saimiri* as a whole is a relatively recent radiation (~1–2 Ma), and that the split between *S. oerstedii* and *S. sciureus* occurred approximately 1 Ma, suggesting a maximum age for entry into Central America at 1–2 Ma, with a much more recent minimum age (Chiou et al., 2011). Little is known to date about the phylogenetics and timing of entry into Central America for either tamarins (*Saguinus geoffroyi*) or owl monkeys (*Aotus zonalis*).

2.3.5. Caatinga, Cerrado, Chaco, Llanos: primate expansion and extirpation in dry open habitats

Neotropical primates are broadly thought of as arboreal rainforest dwellers, but in fact there have been multiple independent radiations into drier habitats across the Neotropics, including into the Caatinga and Cerrado regions of Brazil, the Chaco region of Argentina and Paraguay, and the Llanos of Venezuela and Colombia (see Fig. 1). These radiations into drier habitats have involved members of each of the three major clades of platyrrhines: Cebidae (*Cebus*, *Sapajus*, *Saimiri*, *Callithrix*, *Mico*, *Aotus*), Pitheciidae (*Callicebus*), and Atelidae (*Alouatta*). Molecular data provide evidence that modern radiations of platyrrhines have invaded these drier regions relatively recently, and we suggest a pattern of continuous occupation of rainforest habitats and intermittent colonizations of drier habitats, with repeated extirpations from the drier environments due to climatic fluctuations.

Seasonally dry tropical forests are thought to have gone through a series of expansions and contractions during the Late Pleistocene as a result of climate change, with the largest expansions of seasonally dry forests occurring during cool-dry phases of the Glacial Maxima (Pennington et al., 2000). In fact, at the extreme of the last glacial maximum, it is hypothesized that the seasonally dry tropical forests may have formed an extensive arc through South America, linking northeastern and southeastern Brazil to southwestern Bolivia, northwestern Argentina, and northwest to dry Andean valleys of Peru (Prado and Gibbs, 1993), effectively isolating the Atlantic Coastal Forest from the Amazon Forest and also encroaching upon and fragmenting both of those biomes.

Robust capuchin monkeys (*Sapajus*) spread into the Cerrado and Caatinga from the Atlantic Forest only in the last 400 kyr, according to a study by Lynch Alfaro et al. (2012). The capuchin species currently widespread in these habitats –the bearded capuchin or *S. libidinosus*–appears to have undergone recent evolutionary change in limb proportions and tail length, perhaps in response to selection pressures in these more open and drier habitats (Wright et al., 2015). The Cerrado biome covers 2 million km² in central Brazil, and consists of a highly diverse number of savanna-like habitats that can range from open grassland to dense woodland (Felfili et al., 2005). The Cerrado is bordered on the north by Caatinga, the dominant vegetation type in semi-arid northeastern Brazil (Queiroz, 2005). Caatinga covers 850,000 km² and is likely the driest and hottest habitat that is inhabited by any Neotropical

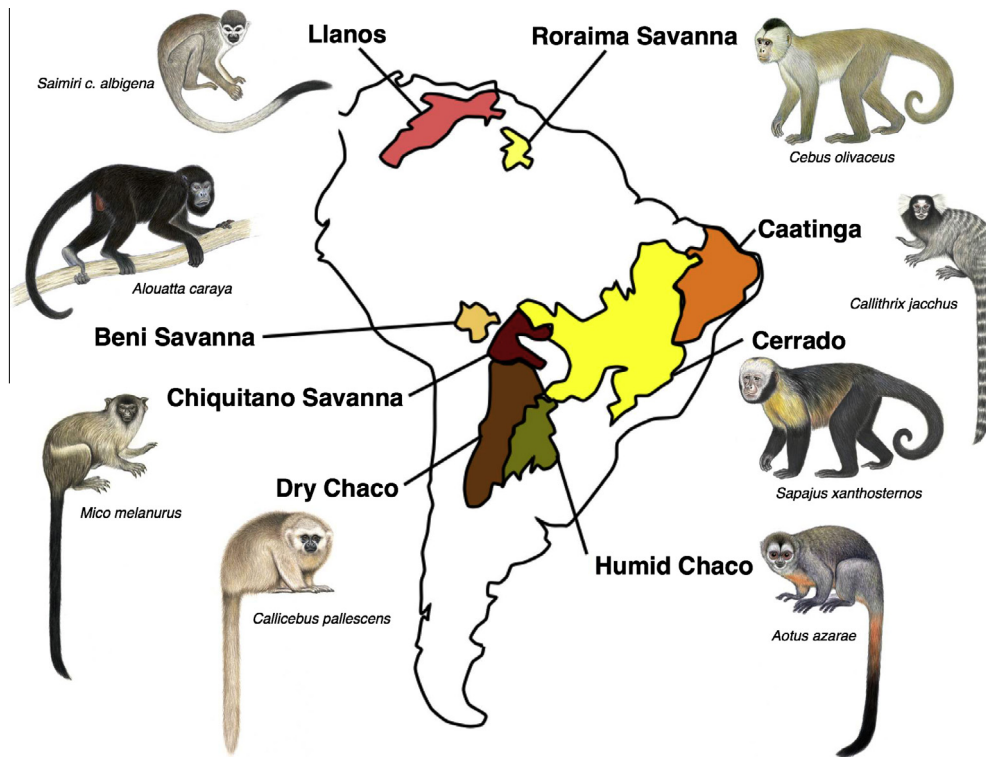


Fig. 1. Map of cis-Andean distribution of the major 'dry' ecoregions inhabited by Neotropical primates. Ecoregion boundaries redrawn from CIESIN (2012) following ecoregions from World Wildlife Fund (2014). The Chiquitano Savanna is classified as a Dry Broadleaf Forest, the Caatinga is a Xeric Shrubland, and the other ecoregions included here are classified as Tropical or Subtropical Grasslands, Savannas, and Shrublands (World Wildlife Fund, 2014). Exemplar primate species are represented for each ecoregion; illustrations by Stephen D. Nash. Primate species present in each ecoregion (based on species distribution data from IUCN, 2014) include: **Llanos:** *Alouatta arctoidea*, *A. macconnelli*, *A. seniculus*, *Callicebus ornatus*, *Cebus olivaceus*, *Saimiri cassiquiarensis albigena*, *Sapajus macrocephalus*; **Roraima Savanna:** *Alouatta macconnelli*, *Cebus olivaceus*; **Caatinga:** *Alouatta caraya*, *A. ululata*, *Callicebus barbarabrownae*, *Callithrix jacchus*, *Sapajus flavius*, *S. libidinosus*; **Cerrado:** *Alouatta caraya*, *Callithrix jacchus*, *C. penicillata*, *Sapajus cay*, *S. libidinosus*, *S. xanthosternos*; **Humid Chaco:** *Alouatta caraya*, *Aotus azarae*, *Sapajus cay*; **Dry Chaco:** *Alouatta caraya*, *Callicebus pallescens*, *Mico melanurus*; **Chiquitano Savanna:** *Alouatta caraya*, *Aotus azarae*, *Callicebus pallescens*, *Mico melanurus*, *Sapajus cay*; **Beni Savanna:** *Alouatta caraya*, *Aotus azarae*, *Callicebus donacophilus*, *Mico melanurus*. In many cases, a particular primate species only inhabits a relatively small fraction of the entire dry ecoregion range, and its range may also continue extensively into rainforest habitat. We depict the entire range of each ecoregion, even if primates may not inhabit that entire range. Note that Neotropical primates have also expanded into dry forests in the inter-Andes and trans-Andes regions, including those in Central America.

primate (Emidio and Ferreira, 2012). The marmosets *Callithrix jacchus* and *C. penicillata* also have very recently colonized the Cerrado and Caatinga from the Atlantic Forest, at about 1 Ma (Buckner et al., 2015). This mid-Pleistocene timing predates the onset of the Glacial Maxima period (900–16 kya).

Mico melanurus is the only *Mico* species found in the Brazilian Cerrado and Paraguayan Chaco (although most of this species' distribution is within the Amazon rainforest), and as yet there are no genetic data to determine the timing of the expansion into Cerrado and Chaco. In any case, there have been at least two independent marmoset radiations into dry habitats: *Callithrix* from the Atlantic Forest to Cerrado and Caatinga, and *Mico* from the Amazon to Cerrado and Chaco. The Chaco extends from northwest Argentina to northwest Paraguay, and southeast Bolivia. The Chaco Biome is considered to be a Tertiary or Early Pleistocene relict by Spichiger et al. (2004), although Müller (1973) suggests it is much younger.

Callicebus barbarabrownae is a critically endangered primate in the Caatinga of the Brazilian State of Sergipe. It appears to have diversified from its neighboring forest-dwelling *Callicebus coimbrai* on the basis of habitat preference (Jerusalinsky et al., 2006; Printes et al., 2013). Population genetics could reveal how recently these two species have diversified; the most likely explanation is that *C. coimbrai* recently expanded into the Caatinga ecotone from the Atlantic Forest, and speciated in response to habitat differences.

Another independent radiation of *Callicebus* into dry habitat is that of *C. donacophilus* in the Guaporé grasslands (Ferrari et al., 2000) and *C. pallescens* in the Paraguayan Chaco scrublands. The

donacophilus group (*C. donacophilus*, *C. pallescens*, *C. olallae*, *C. oenanthe*, and *C. modestus*) has the most disjunct set of species distributions among all the titi monkey clades and may represent a relatively old lineage that was more successful in the past but now has been extirpated across several areas in its range due to climatic and habitat changes.

Alouatta caraya is also found in the Cerrado and Caatinga, as well as the Atlantic Forest, Pantanal, and Pampas regions. The species split from other Amazonian howler monkeys at ~4 Ma (Cortés-Ortiz et al., 2003; Perelman et al., 2011), apparently expanding its range east into drier habitats and reaching the Atlantic Forest (Bicca-Marques et al., 2008). *Alouatta belzebul* has a disjunct distribution, with most of its range in the Amazon and other isolated populations in the Atlantic Forest and perhaps the Caatinga of northeastern Brazil. This species diverged from the Atlantic Forest *A. guariba* ~4 Ma (Cortés-Ortiz et al., 2003). The coincidence in divergence dates between *A. caraya* (usually associated with drier environments) and red howlers (commonly considered to be a humid tropical forest species), and between *A. belzebul* (mostly Amazonian) and *A. guariba* (Atlantic Forest), makes it tempting to speculate on the possible role of the development of dry environments as an important force in the diversification of South American howlers, with *A. caraya* becoming more tolerant to drier habitat conditions but also surviving in humid tropical forest when available. Although another putative howler species, *Alouatta ululata*, also occupies the Caatinga of northeastern Brazil, no genetic analyses have been performed on individuals of this

species to confirm their taxonomic identity and phylogenetic distinction from *A. belzebul* (Cortés-Ortiz et al., 2014).

Aotus azarae is found in the Argentinean Chaco. Springer et al. (2012) place the *Aotus azarae/A. infulatus* split as the most recent split among owl monkeys (at least from their subsample of 8 species), occurring at about 1 Ma (or less). *A. infulatus* is a widespread eastern Amazonian taxon, and these two species were formerly considered subspecies of the same taxon (*A. azarae*). The dating suggests another relatively recent invasion of dry habitat.

Cebus olivaceus in the Venezuelan Llanos is also a recent radiation, dating only from about 500 kyr, based on an analysis of mitochondrial markers (Boubli et al., 2012). This parallels the recent timing of the spread of both capuchin monkeys and marmosets into Caatinga and Cerrado habitats in eastern Brazil (see above). Another primate that has colonized the Llanos in Colombia and Venezuela is the red howler *Alouatta arctoidea*. The inclusion of this taxon in phylogenetic reconstructions of howler monkeys as well as population-level genetic analyses of *A. arctoidea* in the tropical forest and Llanos habitats could elucidate the more recent evolutionary history of this taxon, such as whether its spread into the drier region coincided in time with that of *C. olivaceus*. The Venezuelan Llanos occupies about 240,000 km² and extends along a huge 'geosyncline' between the Guyana Shield (demarcated by the Orinoco River) and the Andes Coastal Cordillera along the Caribbean Sea (Huber et al., 2005). In the Tertiary, this area was a depression and unavailable for terrestrial colonization due to flooding from marine waters, with several prolonged marine transgressions in the later Tertiary and Quaternary (Huber et al., 2005). It has been suggested that the more recent paleoecology of the area included fluctuation between arboreal evergreen and dry forests and savanna ecosystems, although these data are mostly inferred from palynological studies in surrounding mountain regions (Huber et al., 2005). The unstable paleoclimate may help explain why extant primates colonized this region only recently as well as why there is a disjunct distribution for some primate species found on either side of this region.

3. Conclusions

This is an exciting time for the study of platyrrhine phylogenetics and evolution. Debates over the origins of New World monkeys – e.g., whether the platyrrhine ancestor arrived from Africa, North America, or Asia – have been reinvigorated by new molecular studies and by the growing diversity of newly discovered fossils from the Caribbean whose relationships to the South American fauna are still being assessed. Another ongoing controversy is whether the early Patagonian fossils represent stem or crown platyrrhines. Understanding these issues has implications for our reconstruction of the mode and tempo of primate evolution in the Neotropics. There is continuing debate about the relationship of the Antillean fossils to living platyrrhines, but agreement that the La Venta fossils are representatives of diversified lineages including Cebidae, Atelidae, and Pitheciidae.

Current evidence suggests a tropical origin for platyrrhines, and most or all of generic diversity among extant species seems to have been generated in the Amazon. We point to multiple periods during the Miocene when Amazonian radiations expanded into the Atlantic Forest, with subsequent vicariance. We also note that modern radiations within the Atlantic Forest are relatively recent, dating from Late Pliocene to the Pleistocene, suggesting contraction, isolation, and re-expansion of populations.

The data suggest that there have been two modes of trans-Andean colonization by Neotropical primates. One is the more ancient spreading across the Andes before it had reached its final uplift in the north and central regions, followed by subsequent

vicariance through mountain building. A second appears to be more recent colonization of trans-Andes habitat by skirting around the mountains along a northern coastal route. Central American primate taxa did not all cross immediately into this region from South America with the closing of the Isthmus of Panama at 3–3.5 Ma, but instead the presence of some of these taxa are the result of more recent colonizations.

While Neotropical primates are generally considered a tropical rainforest group, in fact there have been many radiations into drier, more open habitats, particularly into ecoregions such as the Llanos, Chaco, Caatinga, and Cerrado, as well as other savanna habitats. Molecular dating of splits for taxa presently inhabiting these drier areas provides a consistent pattern of invasion within the Pleistocene, about 1–2 Ma. This suggests a general pattern for platyrrhines of a history of long-term occupation of rainforest habitat, punctuated by cycles of invasion and extirpation in drier areas.

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