ORIGINAL ARTICLE

Capuchin monkey biogeography: understanding *Sapajus* Pleistocene range expansion and the current sympatry between *Cebus* and *Sapajus*

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ABSTRACT

Aim

Our aim was to examine gracile capuchin (*Cebus*) and robust capuchin monkey (*Sapajus*) diversification, with a focus on recent *Sapajus* expansion within Amazonia. We wanted to reconstruct the biogeographical history of the clade using statistical methods that model lineages' occupation of different regions over time, to evaluate recently proposed "Out of Amazonia" and "Reinvasion of Amazonia" hypotheses as alternative explanations for the extensive geographic overlap between reciprocally monophyletic gracile (*Cebus*) and robust (*Sapajus*) capuchin monkeys.

Location

Central and South America.

Methods

We reconstructed a time-calibrated molecular phylogeny for capuchins under Bayesian inference from three mitochondrial genes. We then categorized 12 capuchin clades across four Neotropical centres of endemism and reconstructed the biogeographic history of the capuchin radiation using six models implemented in ‘BioGeoBEARS’. We performed a phylogeographic analysis for a robust capuchin clade that spans the Atlantic Forest, Cerrado, Caatinga and Amazonia.

Results

We find support for a late Miocene vicariant *Cebus*-*Sapajus* divergence and a Pleistocene *Sapajus* invasion of Amazonia from the Atlantic Forest. Our new analyses confirm *Sapajus* diversified first in the Atlantic Forest, with subsequent range expansion into widespread sympatry with *Cebus* in Amazonia, as well as multiple expansions into drier savanna-like habitats. We do not find mitochondrial molecular congruence with morphological species distinctions for *Sapajus flavius*, *S. cay*, *S. macrocephalus*, *S. libidinosus* and *S. apella*; instead, these five morphological types together form a single widespread clade (Bayesian posterior probability = 1) with geographic substructure and shared ancestry during the Pleistocene.

Main conclusions

Our results support vicariance dividing ancestral capuchin populations in Amazonia versus the Atlantic Forest, and a Pleistocene “Amazonian invasion” by *Sapajus* to explain the present day sympatry of *Cebus* and *Sapajus*.

Keywords Amazonia, Atlantic Forest, BEAST, phylogeography, Caatinga, *Cebus kaapori*, Cerrado, RASP Biogeography, range expansion, *Sapajus flavius*

INTRODUCTION

Neotropical primates are the major diurnal mammalian radiation in the Neotropics, and include over 140 species found across Amazonia, the Andes, the Atlantic Forest, and even habitats such as the Llanos, Caatinga, Cerrado and Central Grasslands that are too hot and dry to support many types of mammals. Neotropical primate diversity is highest within the tropical rainforest habitat in Amazonia. Major questions include whether Neotropical primates diversified first in Amazonia, and how and when they spread throughout the various biomes they now inhabit.

The wide distribution of capuchin monkeys, with species ranging from Central America to northern Argentina, makes them a potential model system for addressing questions of Neotropical primate biogeography. Capuchins comprise two major forms, the more lightly built gracile capuchin, *Cebus*, and the robust capuchin, *Sapajus*. Although recent studies have confirmed the genetic distinctiveness of these two lineages (Lynch Alfaro *et al.*, 2012a; Martins Jr. *et al.*, 2014), key questions remain regarding their present day distribution, including the extensive sympatry between Amazonian *Cebus* and *Sapajus* species.

Two competing hypotheses have been posited to explain current capuchin distributions (Lynch Alfaro *et al.*, 2012a). The “Out of Amazonia” (OOA) hypothesis places the ancestral range for all capuchins in Amazonia, an initial diversification of both crown robust and crown gracile capuchins within Amazonia, and subsequent independent and recent invasions of non-Amazonian regions by both gracile and robust capuchins (Lynch Alfaro *et al.*, 2012a). The “Reinvasion of Amazonia” (ROA) hypothesis proposes that gracile capuchins, *Cebus*, diverged from robust capuchins, *Sapajus* early in capuchin evolutionary history; crown *Cebus* originated in Amazonia and crown *Sapajus* in the Atlantic Forest; and the presence of *Sapajus* in the Amazonia today reflects a recent invasion from the Atlantic Forest into *Cebus*-occupied territory (Lynch Alfaro *et al.*, 2012a).

Phylogeographic analyses using pure dispersal models strongly support the “Reinvasion of Amazonia” hypothesis (Lynch Alfaro *et al.*, 2012a), and as such have transformed the interpretation of capuchin taxonomy, conservation biology, morphology and ecology (see Lynch Alfaro *et al.*, 2012b, 2014, 2015b; Matthews, 2012; Rylands *et al.*, 2013; Martins Jr. *et al.*, 2014; Oliveira *et al.*, 2014; Boubli *et al.*, 2015; Schneider & Sampaio, 2015; Wright *et al.*, 2015). However, limitations of these studies have left key predictions of the OOA hypothesis untested. For example, Lynch Alfaro *et al.* (2012a) and Nascimento *et al.* (2015) provided limited sampling of eastern Amazonia and Cerrado/Caatinga localities, which have the potential to strongly corroborate the OOA scenarios. In addition, capuchin monkey biogeography has yet to be interpreted in light of models that integrate processes beyond pure dispersal (Ronquist, 1997; Ree *et. al.*, 2005; Ree & Smith, 2008; Landis *et. al.*, 2013).

Here we assemble an expanded sampling of capuchin monkeys across their range and conduct new biogeographic analyses using recently developed statistical approaches. Our overall goal is to test hypotheses explaining capuchin biogeography (Boubli *et al.*, 2012; Lynch Alfaro *et al.*, 2012a; Nascimento *et al.*, 2015; Ruiz-Garcia *et al.*, 2016). We thus assemble a new cytochrome *b* + D-loop + cytochrome oxidase I matrix with three times the samples and more comprehensive spatial and taxonomic sampling compared to Lynch Alfaro *et al.* (2012a). We produce a detailed phylogeny for capuchin monkeys, with all major lineages represented, to confirm the monophyly of *Cebus* and *Sapajus* and to recover major clades within the capuchin radiation. We compare alternative biogeographical scenarios using a flexible framework for inferring spatial histories that allows for a number of different mechanisms causing range expansion or contraction. We assess whether the employment of a more complete genetic dataset and statistical methods with expanded models increase support for previous conclusions about capuchin biogeographical evolution or support new scenarios altogether. Our sampling allows us to address two new biogeographic hypotheses for this clade. The first hypothesis postulates vicariance between Amazonia and the Atlantic Forest. Divergence between *Sapajus* and *Cebus* is caused by isolation of ancestral capuchin populations in the Atlantic Forest versus Amazonian habitats, respectively, with subsequent expansion of *Sapajus* into sympatry with Amazonian *Cebus* ("Reinvasion of Amazonia" hypothesis). The second, opposite, hypothesis postulates vicariance within Amazonia due to the formation of the Amazon River. Capuchins arise in Amazonia, and subsequently *Cebus* is isolated north of the Amazon River, with *Sapajus* isolated south of the Amazon River and expanding into the Atlantic Forest. Sympatry occurs with subsequent crossing of Amazon River in both directions ("Out of Amazonia" hypothesis).

MATERIALS AND METHODS

DNA extraction, amplification, sequencing and alignment

We sequenced three mitochondrial genes, cytochrome *b* (*Cyt b*, 1133 bp), D-loop (1244 bp) and cytochrome oxidase I (COI, 673 bp), for 108 capuchin samples from poorly known or previously unsampled localities and species (see Table S1 in Appendix S1). For *Cyt b* and D-loop we used primers and PCR protocols from Lynch Alfaro *et al.* (2012a) and Boubli *et al.* (2012). We adapted COI primers and protocols from Ward *et al.* (2005) (see Appendix S2). We combined the 108 new samples with 40 samples analysed previously by Lynch Alfaro *et al*. (2012a) and 13 new samples with reliable species identification extracted from GenBank, totaling 161 capuchin samples. Note that samples from Ruiz-Garcia *et al.* (2016) were not available for use in this study. We used only sequences over 500 bp long to improve clade support (Nascimento *et al.*, 2015). We used the most recent comprehensive taxonomic review for capuchins (Rylands *et al.*, 2013), in relation to specimen morphology and collection locality, to assign species names to samples (locality data in Figure 1 and Table S1 in Appendix S1). Although the limitations of mitochondrial DNA studies are well understood, *Cyt b*, D-loop and COI have performed well in capturing phylogeny and biogeographical history in a wide range of species (Tobe *et al*., 2010; Zhang *et al.*, 2011; Robins *et al.*, 2014). In addition, mtDNA sequence can be reliably generated from museum “crusties” and skins using now standard protocols (e.g., Lynch Alfaro *et al.*, 2012a, 2015a; Mercês *et al*., 2015).

Phylogenetic Reconstruction

We used MRBAYES 3.2.6 (Ronquist *et al.*, 2012) to reconstruct the phylogenetic relationships among capuchins, using *Saimiri* as an outgroup. We partitioned *Cyt b* and COI by codon for the analysis and ran the Markov Chain Monte Carlo (MCMC) for 50 million generations. We used ‘sumt’ to calculate the Bayesian consensus tree. We then used BEAST 1.8.1 (Drummond *et al.*, 2012) to reconstruct a time tree appropriate for our biogeographical analyses by pruning the alignment to a single exemplar taxon for each recovered well-supported clade. We considered branch lengths and recovered polytomies in addition to posterior probabilities at nodes when distinguishing clades. This resulted in a new, pruned alignment with 13 tips, representing 12 capuchin clades and one outgroup. We specified a HKY + G model of nucleotide substitution and partitioned by codon, using *Cyt b* only to avoid branch length bias due to missing data in the other genes. We used *Saimiri* as an outgroup and the fossil *Neosaimiri* (Kay, 2015) to calibrate the split at 12.5 Ma (lognormal prior, offset=12.5, mean=0, SD=1) between capuchins and squirrel monkeys for the time tree. We ran the MCMC analysis for 100 million generations, sampling states every 10,000 generations with a Yule prior on the diversification rate, and an uncorrelated, lognormal relaxed molecular clock.

Biogeographical modelling

Biogeographical scenarios In addition to testing for evidence for “Out of Amazonia” versus “Reinvasion of Amazonia” hypotheses (see Introduction), we tested for reciprocal monophyly for *Sapajus* in Amazonia (*S. macrocephalus* + *S. apella*); the Cerrado + Caatinga + Central Grasslands (*S. cay* + *S. libidinosus*); and the Atlantic Forest (*S. flavius* + *S. xanthosternos* + *S. robustus* + *S. nigritus*). Lack of reciprocal monophyly across habitats would suggest multiple independent invasions and convergent adaptations to habitat types by independent *Sapajus* lineages.

Historical biogeography To test alternative hypotheses of capuchin origins and radiation we used the R-package 'BioGeoBEARS', a recently developed flexible maximum likelihood framework for inferring spatial histories (Matzke, 2013, 2014; see Buckner *et al.*, 2015 and Lynch Alfaro *et al.*, 2015a for its recent application to primate taxa). 'BioGeoBEARS' software allows for a statistical comparison of a suite of models that include alternative biogeographic processes related to cladogenesis and that allow for species distributions across multiple regions (Matzke, 2014).

Our tree was pruned to include one representative tip for each 'species' recovered in the MRBAYES analysis. We lumped *Sapajus flavius*, *S. cay*, *S. libidinosus*, *S. apella*, and *S. macrocephalus* (*Sapajus* clade 4, see below) as one species. This resulted in a new, pruned alignment with 12 tips. We coded presence/absence in four major geographic regions for each tip based on known species distribution using Rylands *et al.* (2013): Atlantic Forest (AF), Cerrado/Caatinga/Central Grasslands (CC), Amazonia (AM), and Central America/Andes (CA). We used the pruned, time-calibrated tree with regional coding in 'BioGeoBEARS' (Matzke, 2013; Matzke, 2014). Our candidate pool consisted of six models: DEC, DEC-J, DIVA, DIVA-J, BAYAREA-LIKE, BAYAREALIKE-J and we used model weights calculated from corrected Akaike information criterion (AICc) to identify the best model or set of models for our data (Matzke, 2014). 'BioGeoBEARS'script is available in Appendix S2**.**

*Phylogeographical reconstruction of widespread Sapajus*To examine phylogeographic patterns for a widespread robust capuchin group recovered in the MRBAYES tree, we performed both symmetric and asymmetric discrete states phylogeographic analyses in BEAST under a constant size coalescent prior. These analyses allowed us to take into consideration the uncertainty in the relationships by simultaneously estimating the topology and the distribution history. To compare the asymmetric and symmetric analyses for their fit to our data, we performed marginal likelihood estimation (MLE) using path sampling (PS) and stepping stone (SS) sampling (Beale, 2012, 2013). We used the default priors for the MLE. We categorized the locality of each tip for the widespread *Sapajus* clade in the Bayesian consensus tree as occurring in one biogeographical 'region' (Figure 2). We divided Amazonia into four regions using the Amazon River and two major tributaries, Negro and Madeira, as described by Wallace (1852) and later Cracraft (1985): Guianas (GU), Negro (NE), Inambari (IN), Rôndonia (RO). We also separated the drier open ecosystems Central Grasslands, Cerrado and Caatinga (CC), from the Atlantic Forest (AF). These regions were modified from Jameson Kiesling *et al.* (2015) and Cracraft (1985). As mtDNA is inherited maternally, it tracks the movement of female lineages over time. Capuchin monkeys are female philopatric with male-biased dispersal (Lynch Alfaro *et al.*, 2014), so tracing female lineage was a conservative test for the amount of movement over time in this taxon.

Within Amazonia, we tested for isolation by river barriers for widespread *Sapajus*. If gene flow within Amazonian capuchin populations was restricted to major interfluves, we expected a pattern of closely related subclades within, not across, four major Amazonian regions delineated by the Amazon River and its major tributaries. Evidence for the river barrier hypothesis was found for the sister group to capuchins, the Amazonian squirrel monkeys (Lynch Alfaro *et al.*, 2015a), as well as for marmosets and tamarins (Buckner *et al*., 2015). Robust capuchin lineages with clades spanning multiple interfluves would provide evidence against rivers as significant isolating mechanisms.

RESULTS

Capuchin Phylogenetics

We find strong support for reciprocally monophyletic clades of gracile and robust capuchins in the phylogenetic reconstruction from MrBayes (Figure 3a). Our truncated species time tree from BEAST (Figure S1 in Appendix S3) estimates the mean divergence time between *Sapajus* and *Cebus* at 5.8 Ma [95% higher posterior density (HPD) = 2.24 - 10.94] (late Miocene).

For robust capuchins we recover strong support for the clades *S. xanthosternos* (posterial probability [pp] = 1) and *S. nigritus* (pp = 1), but little evidence for reciprocally monophyletic 'species' clades for the rest of *Sapajus.* Two *S. robustus* samples form a weakly supported clade (pp = 0.74). All other robust capuchins form one large widely distributed clade ('*Sapajus* CLADE 4,' pp = 1), comprising *S. apella*, *S. macrocephalus*, *S. cay*, *S. libidinosus*, and *S. flavius*. Subclades within this group are not always congruent with morphological hypotheses about robust capuchin species, a result concordant with the mitochondrial results from Ruiz-García and colleagues (2012, 2016). Most strikingly we find *S. apella sensu stricto* to be extensively paraphyletic with respect to other *Sapajus* species. Within the widespread clade, we recover several geographical subclades: (1) *S. flavius* (pp = 0.95); (2) *S. libidinosus* together with eastern *S. apella* (pp =0.80); (3) *S. cay* from Paraguay and Rondônia/Mato Grosso plus *S. apella* from Guaporé and Apuí (pp = 0.81); (4) *S. cay* from Chapada dos Guimarães and *S. apella* from Alta Floresta, both in Mato Grosso, Brazil (pp = 1); (5) *S. apella/macrocephalus* (pp = 1) from north of the Amazon and Solimões rivers, as well as from regions just south of the Amazon River near the Xingu and Tapajos rivers, and just south of Manaus, together reaching all four Amazonian quadrants, as far northwest as Colombia; (6) *S. apella/macrocephalus* (pp = 0.95) from Brazil and Peru. Minimum clade ranges for each of the six subclades of the widespread *Sapajus* clade are geographically coherent though several do not match current morphological hypotheses about robust capuchin taxonomy (Figure 3c).

Within *Cebus*, we recover eight strongly supported clades: *Cebus versicolor* forms a clade (pp = 1) with *C. cesarae* within the Magdalena river valley in the Colombian Andes, as part of a larger clade including *C. capucinus* in Panama and Colombia (pp = 1), and *C. imitator* in Central America (pp = 1). In the eastern Andes, *C. brunneus* (pp = 1) is sister to *C. leucocephalus* (pp = 1). Within Amazonia, there is strong support for a *C. unicolor* + *C. albifrons* clade (pp = 1). *C. yuracus* forms a clade with one *C. unicolor* sample (pp = 1) in western Brazil and Ecuador, and *C. o. olivaceus* + *C. o. castaneus* + *C. kaapori* form a strongly supported clade (pp = 1). Our *C. kaapori* sample is from the holotype, collected by Queiroz (1992), from the type locality Chega-Tudo, in Carutapera Municipality, Maranhão State, Brazil. Here we provide a correction to the original Queiroz (1992) for the coordinates of that locality, 02°20'S 46°05'W (Table S1 in Appendix S1).

Reconstruction of Capuchin Biogeographical History

Model weights based on AICc favoured the DEC model (Table 1, Figure 4). Under this scenario the ancestral capuchin population is inferred to have had a wide range that included both Amazonia and the Atlantic Forest. The divergence between *Sapajus* and *Cebus* is a vicariance event, where *Sapajus* is isolated in the Atlantic Forest, while the lineage leading to gracile *Cebus* is isolated in Amazonia. Crown

Sapajus is recovered with a distribution restricted to the Atlantic Forest, with subsequent rapid expansion to the Caatinga/Cerrado/Central Grasslands and Amazonia regions at about 500 ka. This means that *Cebus*, established in Amazonia at approximately 2.4 Ma, diversified for about 2 million years before the appearance of any *Sapajus* clade in that region.

For crown *Cebus*, a single expansion event to the Central America/Andes region occurred at ~2.2 Ma, with subsequent range contractions to just Central America/Andes for the lineage leading to *C. capucinus*, *C. imitator* and *C. versicolor*, and to Amazonia only for both the lineage leading to *C. brunneus* (note that the "Amazonia" region extends to the northern Venezuelan coast; see Figure 4), and for the lineage leading to *C. unicolor*.

Reconstruction of widespread Sapajus radiation

We do not find any statistical difference in support for the symmetric versus the asymmetric analyses (K≈0). Both the phylogeographical reconstructions detail the explosive Pleistocene range expansion throughout Amazonia, Cerrado, Caatinga and southern grasslands for *Sapajus* (Figure 2 and Figure S2 in Appendix S3). In the asymmetric reconstruction, robust capuchins enter Amazonia by a single expansion from AF to RO at around 300-500 ka, with a second unique expansion across the Amazon River to GU at 200 ka, and at least two independent expansions across the Madeira River from RO to IN. There is also evidence for expansion from GU to IN, and IN to GU, as well as back-crossing from both IN and GU to RO. No strong geographical pattern demarcates rivers as firm barriers separating the four Amazonian regions; instead, there has been significant and recurrent recent movement by *Sapajus* across the Amazon, Solimões, Madeira and Negro rivers. *Sapajus* also spread from RO three times into the Cerrado/Caatinga (CC) region, all within the last 200 ka.

The addition of a distribution partition to our BEAST analysis provides support for the monophyly of *Sapajus robustus* (0.93) and its position as the sister group to a widespread Amazonian-Grasslands-Atlantic Forest clade (pp = 1.0). *Sapajus robustus* is restricted to the Atlantic Forest, making it clear that the explosive radiation of robust capuchin monkeys began with a recent migration into Amazonia and grasslands.

A significant difference between our asymmetric and symmetric BEAST analyses is related to *S. flavius*. In the symmetric BEAST phylogeography analysis, *S. flavius* is recovered as the sister group to *Sapajus* CLADE 4 (Figure S2 in Appendix S3). On the other hand, *S. flavius* is embedded within the widespread clade in the asymmetric analysis (Figure 2), suggesting an expansion back into the Atlantic Forest from the Amazonia/Grasslands regions.

DISCUSSION

Our expanded sample set with comprehensive representation of capuchin species provides further support for the monophyly of robust and gracile capuchins with a split at 5.8 Ma. A late Miocene *Sapajus-Cebus* split was previously supported using combined nuclear and mitochondrial data in Perelman *et al.* (2011) (6.0 Ma, 95% confidence interval 3.13-9.35 Ma) and Springer *et al.* (2012) (5.7 Ma average, 3.55-8.33 Ma composite 95% min-max). However, these time trees did not include all capuchin species; here we add *Cebus kaapori, C. versicolor,* and *Sapajus flavius.* One exception to monophyly of *Cebus* and *Sapajus* has been recently reported in Ruiz-Garcia *et al.* (2016), where some *Cebus albifrons sensu lato* individuals from the Colombian Eastern

Llanos and Ecuadorian Amazonia displayed *Sapajus* mitochondrial haplotypes, suggesting the possibility of localized past or present introgression across these two genera. Unfortunately, neither sequences nor morphological data are publicly available for any of these individuals at this time.

Our biogeographical analyses reconstruct a widespread capuchin ancestral distribution across forested areas of South America, from Amazonia to the Atlantic Forest, supporting Amazonia versus Atlantic Forest vicariant origin for *Cebus* and *Sapajus*. The distribution of *Sapajus* exclusively in the Atlantic Forest until recently, and *Cebus* exclusively in the Amazonia and Central America/Andes regions from early on, suggests a cladogenetic event (vicariance) led to their initial diversification in isolation.

Throughout capuchin evolution, the Brazilian Shield (within AF, CC, RO Regions) and Guiana Shield (within GU) have been constant highland regions undergoing few physical changes in configuration but perhaps experiencing changes in floral assemblages related to climate (Aleixo & Rossetti, 2007). The divergence between *Sapajus* and *Cebus*, dated consistently at approximately 6 Ma, coincides with floral assembly of the Cerrado (4-8 Ma), as indicated by the onset of diversification of many Cerrado plant lineages (Simon *et al.*, 2009). The coincidence in timing of the divergence between robust and gracile capuchins and of the Cerrado assemblage suggests that the development of the Cerrado may have acted as a vicariant agent, especially given the reconstructed distributions of ancestral *Sapajus* (Atlantic Forest) and *Cebus* (Amazonia). The only extant capuchins distributed in CC belong to our widespread *Sapajus* CLADE 4 - which invaded those biomes only in the last 500 kyr, and have recent cranial and post-cranial adaptations to drier habitats (Wright *et al.*, 2015).

Combining information from our biogeographical and phylogeographical analyses, we find strong evidence that all of the Atlantic Forest robust capuchin species are monophyletic clades, with the exception perhaps of *S. flavius*, which was found as part of the widespread *Sapajus* 'clade 4' in our MRBAYES phylogeny. Major Amazonian rivers do not appear to be strong barriers for dispersal or gene flow for *Sapajus*, with up to twelve examples of dispersal across significant Amazonian rivers demonstrated through our BEAST analysis by just the sampling included in this study.

Gracile capuchin biogeography and phylogenetics

In our analysis, *Cebus* shows strong geographical divisions, suggesting a widespread ancestor diversified in Amazonia and was split by range expansion and subsequent range contraction in the Andes and Central America. The Amazonian group (*C. yuracus*, *C. unicolor*, *C. albifrons*, *C. olivaceus and C. kaapori*) is about the same age as the CA group (*C. capucinus*, *C. imitator*, *C. versicolor*, *C. cesarae*, *C. leucocephalus* and *C. brunneus*). The recently discovered *Cebus kaapori* was initially considered to be a subspecies of *C. olivaceus* (Harada & Ferrari, 1996), but other morphological taxonomists have argued that it is a unique species (Groves 2001, 2005; Silva-Júnior, 2001), with some morphological characteristics more similar to *C. albifrons sensu lato* (Masterson, 1995). In our MRBAYES analysis, *Cebus kaapori* is recovered within the strongly supported *C. olivaceus* clade. A close relationship between *C. kaapori* and *C. olivaceus* makes sense, as *C. o. castaneus* is the gracile capuchin geographically most proximate to *C. kaapori*. *Cebus versicolor* is recovered as sister to *C. cesarae.* This is concordant with geographical distribution as both species are found in isolated pockets of the Magdalena Valley in Colombia. MtDNA COII analysis of *Cebus albifrons sensu lato* by Ruiz-García *et al*. (2010) found *C. cesarae* and *C. pleei* as sister to *C. versicolor*.

Robust capuchin biogeography and phylogenetics

Our phylogeographic analysis suggests robust capuchins were able to colonize an array of divergent habitat types all within a very short time period, in the last 1 Myr. Robust capuchins show evidence of multiple moves within and between all regions, except that they are absent from the Central American and Andean region. This may be explained because their arrival at the foot of the eastern Andes was so recent that the mountain range was already fully formed and impassable (Lynch Alfaro *et al*., 2012a).

Consistent with this recent explosive radiation, we find little support for the internal topology of a morphologically diverse and geographically expansive clade of robust capuchins. Morphological species contained in this group include *S. libidinosus*, *S. cay*, *S. flavius*, *S. macrocephalus*, and *S. apella*. While there is significant individual variation within *Sapajus* populations, these five morphological species each display distinct morphological patterns with clear geographic correspondence (Silva-Júnior, 2001), possibly as a consequence of repeated founder effects. While the recent divergence times among all the Amazonian and open region grasslands capuchins (all under 400 Ka) suggest there probably has not been time enough for speciation among these morphological types, our data do point to geographical clades that deserve further study for their morphological and behavioural population characteristics. For example, morphological differences between *S. macrocephalus* north and south of the Amazon River have already been described (Rylands *et al.*, 2013); our analysis here provides new hypotheses for geographic boundaries between major population centers within

Amazonian *Sapajus*, and suggests the need for new morphological and morphometric analyses for undersampled regions. We suggest nuclear genomic methods will be necessary to provide a complementary perspective to help resolve the relationships within this clade.

Rapid Pleistocene expansion throughout Amazonia has been recovered for the sister taxon to capuchin monkeys, the squirrel monkeys (Chiou *et al.*, 2011; Lynch Alfaro *et al.*, 2015a). *Sapajus* presence today in western Amazonia is explained in the BEAST phylogeography analysis as resulting from two distinct pathways: one was expanding from RO west across the Madeira River, into IN, and then spreading north into NE. The second was a move first from RO across the Amazon River into GU, then expansion west across the Negro River into NE, and from there south to IN. The exact distribution of *S. macrocephalus* in western Amazonia is contested (Groves, 2001, 2005; Silva-Junior, 2001). Rylands *et al.* (2013) depict *S. macrocephalus* morphological diversity with Brazilian, Peruvian, Bolivian and Colombian forms; one explanation for this variation congruent with our results is that western Amazonia has been colonized multiple times from different *Sapajus* seed populations from different parts of Amazonia. In contrast, most of *Sapajus* diversity in eastern Amazonia can be explained by a single founder event from AF into RO, and another single founder event from RO into GU, with some later expansions back to RO from GU.

Sapajus cay has been the subject of controversy within robust capuchin taxonomy, and two major authorities (Groves, 2001, 2005; Silva-Junior, 2001) disagree significantly about its distribution, in part due to differences in the localities of samples available in each of their studies. *Sapajus cay* (*sensu* Rylands *et al*., 2013) is recovered here as paraphyletic, with evidence for at least two distinct *Sapajus* populations moving independently into gallery forests in more open habitat types. *Sapajus cay* samples from

Paraguay, Rondônia, and Mato Grosso cluster with *S. apella* from Rondônia; while *S. cay* from northern central Mato Grosso forms a clade with nearby *S. apella* from Alta Floresta. These two populations have apparently converged morphologically to a lighter pelage phenotype in the drier, open regions. *Sapajus libidinosus* (*sensu* Rylands *et al*., 2013) marks a third expansion into CC from Amazonian *Sapajus*, with a resultant lighter pelage (Figure 2). All expansions into drier habitats appear to have occurred in the last 200-100 kyr, similar to findings for other Neotropical primates (Lynch Alfaro *et al*., 2015b).

We expected to recover *Sapajus flavius* as sister to *S. xanthosternos* because of geographical proximity or sister to *S. libidinosus* based on a gradation of morphology between the two morphotypes (Silva, 2010); or possibly sister to all other *Sapajus* species, based on its unusual morphology (Lynch Alfaro *et al.*, 2012a). In our BEAST phylogeography and MrBayes analyses, *Sapajus flavius* is recovered as part of the widespread *Sapajus* CLADE 4 (Figure 2 and 3b). However, in the symmetric BEAST phylogeography analysis, *S. flavius* is recovered as the sister group to *Sapajus* CLADE 4 (Figure S2 in Appendix S3), suggesting all four Atlantic Forest *Sapajus* taxa may have diverged from each other first prior to *Sapajus* expansion into other regions. Given the difference in topology and the range of support values among analyses, the phylogenetic placement of *S. flavius* remains uncertain, though close phylogenetic affinity to *Sapajus* CLADE 4 is clear.

Sympatry between robust and gracile capuchins

Overall, our data and analyses support the "Reinvasion of Amazonia" hypothesis (Lynch Alfaro *et al.*, 2012a) by *Sapajus* as indicated by the ancestral reconstructions of the crown *Cebus* and crown *Sapajus* clades. The two capuchin genera diversify in isolation, with *Sapajus* species only later invading a *Cebus*-occupied Amazonia at about 500 kya. The BEAST phylogeography analysis shows *Sapajus* invasion of Amazonia occurring first in Rondonia (south-western Amazon) and quickly spreading to all four quadrants of Amazonia. The recovered timing of entry into sympatry for gracile and robust capuchins indicate an event in Amazonia less than 1 Ma, as a result of *Sapajus* counter-invasion into a region already occupied by *Cebus*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of individual and GenBank accession numbers.

Appendix S2 Supplementary details of methods.
Appendix S3 Supporting results.

BIOSKETCH:

Marcela G. M. Lima is a biologist interested in biogeography, phylogenetics and population genetics, with a focus on Neotropical vertebrates. Author Contributions: M.G.M.L., J.C.B., M.E.A. and J.W.L.A. designed and ran phylogenetic and biogeographic analyses and developed the article; M.G.M.L., J.S.S.J., A.M., A.L., I.P.F., J.P.B., F.R., H.Q., M.N.S., A.D.F. and J.W.L.A. collected and curated sample material; M.G.M.L., A.M. and I.P.F. generated new genetic sequences; K.C., M.G.M.L., J.C.B. and J.L.A. designed maps and figures; and all authors contributed to the writing of the article.

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Tables

Table 1 Comparison between models estimated in 'BioGeoBEARS'. For each model implemented in the analysis are shown: values of log-likelihood (LnL), numbers of parameters and Akaike's information criteria (AIC, ΔAIC and AICc Weight).

Model	LnL	No. Parameters	AICc	ΔAICc	AICc Weight
DEC	-17.29	2	39.92	0	0.68
DIVALIKE	-18.9	2	43.14	3.22	0.14
BAYAREALIKE	-21.41	3	51.81	11.9	0
DEC+J	-17.19	3	43.38	3.46	0.12
DIVALIKE+J	-18.61	3	46.22	6.3	0.03
BAYAREALIKE+J	-18.61	3	46.22	6.3	0.03

Figure Legends

Figure 1 Maps of capuchin monkey sample provenance: (a) *Cebus*, (b) *Sapajus*.

Figure 2 Asymmetric discrete states time tree for the widespread clade of robust capuchin monkeys with ancestral state reconstruction for regions of ancestral nodes and map delineating centres of endemism used for the BEAST phylogeography analyses: GU: Guianas; NE: Negro; RO: Rondonia; IN: Inambari; CC: Caatinga, Cerrado and Central Grasslands; AF: Atlantic Forest. Branches are colour-coded to regions from inset map. Posterior probabilities are shown as asterisks for above 0.95 and as circles for between 0.70 and 0.95.

Figure 3 Bayesian consensus tree for capuchin phylogeny: (a) *Cebus* and *Sapajus* phylogeny and (b) details of *Sapajus* CLADE 4; (c) map with minimum convex polygons to show geographic distribution of major subclades within the widespread *Sapajus* clade. Subclades are presented as minimum convex polygons that connect sample localities. Branches are colour-coded to regions from polygons map. Posterior probabilities are shown as asterisks for above 0.95 and as circles for between 0.70 and 0.95. Sample species ID and number correspond to Table S1 in Appendix S1.

Figure 4 ‘BioGeoBEARS’ ancestral range reconstruction of capuchin monkeys using the DEC model. CA = Central America/Andes; AM = Amazonia; CC = Caatinga, Cerrado and Central Grasslands; AF = Atlantic Forest. Inset map for four regions of analysis.