

Annual Review of Anthropology

The Monkeying of the Americas: Primate Biogeography in the Neotropics*

Jessica Lynch Alfaro

Institute for Society and Genetics and Department of Anthropology, University of California, Los Angeles, California 90095; email: jlynchalfaro@g.ucla.edu

**ANNUAL REVIEWS Further**

Click here to view this article's online features:

- Download figures as PPT slides
- Navigate linked references
- Download citations
- Explore related articles
- Search keywords

Annu. Rev. Anthropol. 2017. 46:317–36

First published as a Review in Advance on July 28, 2017

The *Annual Review of Anthropology* is online at anthro.annualreviews.org<https://doi.org/10.1146/annurev-anthro-102116-041510>Copyright © 2017 by Annual Reviews.
All rights reserved*This article is part of a special theme on Human–Animal Interaction. For a list of other articles in this theme, see <http://www.annualreviews.org/doi/full/10.1146/annurev-an-46-themes>**Keywords**

Amazonia, Atlantic Forest, biodiversity, climate change, human–animal interactions, Platyrrhini

Abstract

Monkeys first arrived in the Neotropics about 36 Ma, and the ancestry of all living Neotropical primates (Platyrrhini) traces to a single common ancestral population from 24 to 19 Ma. The availability of lush Amazonian habitat, the rise of the Andes, the transition from the lacustrine to riverine system in the Amazon Basin, and the intermittent connection between the Amazon and the Atlantic tropical forests have all shaped how primates spread and diversified. Primates outcompeted native South American mammals but faced an influx of North American fauna with the closing of the Isthmus of Panama. Humans, extreme newcomers in the Neotropics, have influenced primate habitat and ecology over the last 13,000 years, with radical transformations in the last 500 years as a result of European colonization and land use change. Neotropical primate biogeography informs taxonomic work and conservation efforts, with a mind toward mitigating effects of direct human impact and human-mediated climate change.

INTRODUCTION

Biogeography: the study of species and ecosystem distribution in geographic space and geological time

Pleistocene: geological epoch from 2.59 Ma to 11.7 Ka, characterized by repeated glaciations of Ice Ages

The last decade has vitalized the field of Neotropical primate biogeography, coupling new statistical modeling methods with coordinate-based population-level sampling for genomic data sets. This review focuses on how new models and methods have (a) changed our understanding of evolutionary processes that have led to the current distribution of primate communities and (b) improved our capacity to assess and prioritize future conservation actions in light of predicted biogeographic impacts of both human land use and human-mediated climate change. This article reviews the dynamic interaction between geologic and faunal history in the Neotropics, with an emphasis on the diversification and spread of Neotropical primates.

Neotropical primates are a dominant mammalian radiation, with 21 genera (Byrne et al. 2016, Mittermeier et al. 2013, Rylands et al. 2016) and 171 extant species (Estrada et al. 2017), comprising one-third of all primate species diversity around the world (Mittermeier et al. 2013) and more than 10% of the extant mammal species found in South America. Primate diversity reaches 31 species within some cells in a 1° grid of Brazilian Amazonia (Pinto et al. 2014).

Extant platyrrhine species range from the ~100-g pygmy marmoset to ateline males that exceed 10 kg (Mittermeier et al. 2013; **Figure 1**), with fossil evidence for even larger taxa, such as ~25-kg Pleistocene *Protopithecus* (Hartwig & Cartelle 1996). Platyrrhine social organization can be pair-bonded; single-male, multifemale groups; or gregarious multimale, multifemale groups

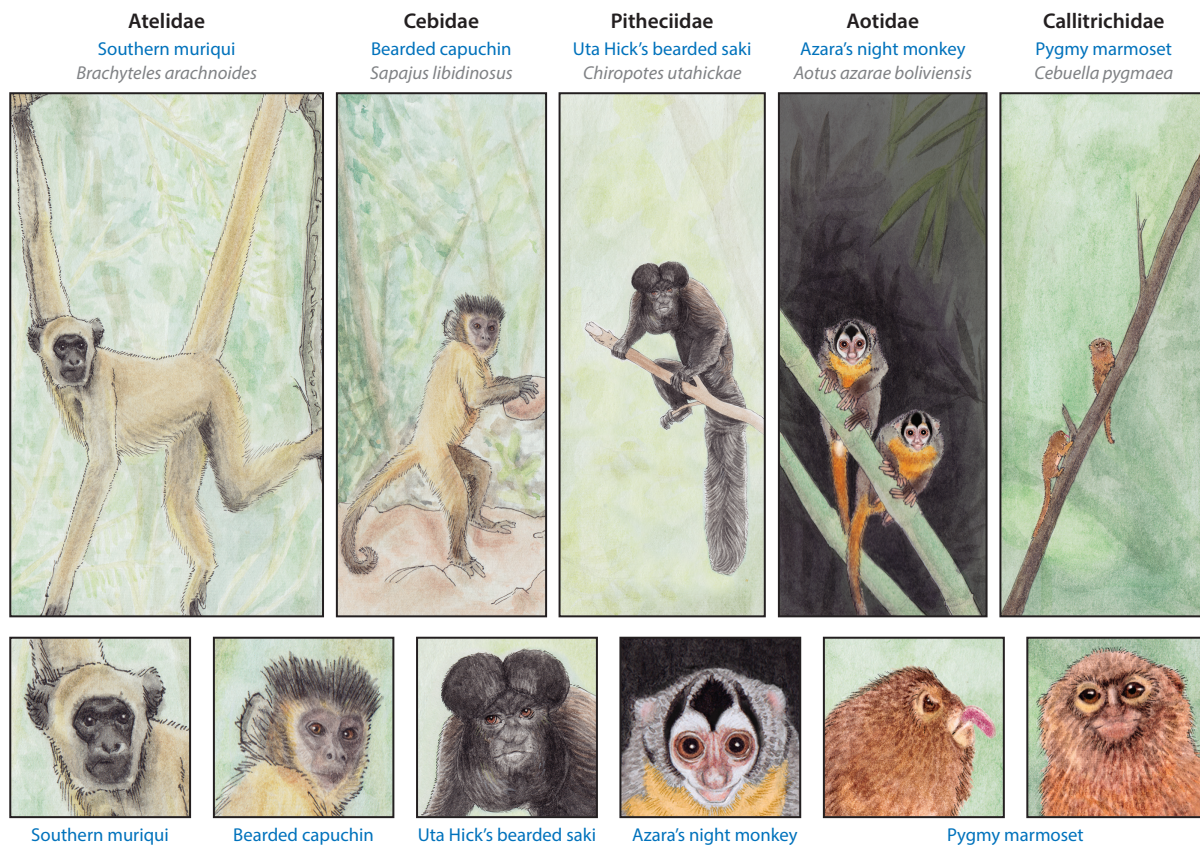


Figure 1

Neotropical primate diversity, with representatives from the five extant Neotropical primate families. Illustration by Amisha Gadani.

of 50–100 individuals. The five families of extant Neotropical primates include Atelidae (spider monkeys, woolly monkeys, and howlers), Pitheciidae (titi monkeys, uakaris, and sakis), Cebidae (capuchin monkeys, squirrel monkeys), Aotidae (owl monkeys), and Callitrichidae (marmosets and tamarins) (Mittermeier et al. 2013; **Figure 1**). All families are widely distributed in Amazonia and have representatives in diverse habitats outside Amazonia.

The combined range of extant Neotropical primates spans from southern Mexico to northern Argentina, from the Tropic of Cancer to about 10° south of the Tropic of Capricorn (Hirsch et al. 2002; **Figure 2**). Within platyrrhine distribution, key ecosystems include the Amazon and Guianan tropical rainforests as well as subtropical rainforests in Mesoamerica and Brazil's Atlantic coast. Primates have invaded drier habitats such as savannah-like Cerrado, Caatinga, the Gran Chaco region, Costa Rica's dry forest, and the Venezuelan Llanos. Other extremes of primate ecosystem diversity include the montane Andes region and Brazil's Pantanal, South America's largest wetlands. Through dramatic range expansion mediated by cultural adaptation, in the recent past, a new primate has entered and spread even more widely across the Americas to inhabit the entirety of the monkeys' distribution. This review explores the biogeographic history of primates' populating of the Americas, as well as the interaction dynamics among monkeys in the Americas with our own recently invasive species. How has arrival in the Americas changed primates, and how have primates changed the Americas?

THE MONKEYING OF THE NEOTROPICS

Lucky Landing and Early Radiations

South America separated from Africa in the breakup of Gondwanaland before 80 Ma and lost connection to Antarctica by the late Eocene, remaining an isolated island continent until ~3.5 Ma (Goin et al. 2012). The highly endemic South American mammalian fauna included marsupials, xenarthrans, and nontherian mammals, as well as megafaunal radiations of southern ungulates and marsupial-like saber-toothed carnivores (Goin et al. 2012).

These native fauna evolved for tens of millions of years in relative isolation, but the occasional chance event gave rise to important competitors. Caviomorph rodents arrived through waif dispersal from Africa ~40 Ma; this group diversified into modern-day capybaras, chinchillas, viscachas, and New World porcupines (Bond et al. 2015). Primates rafted through waif dispersal from Africa by ~36 Ma (Bond et al. 2015). The earliest fossil primates yet found in South America include *Perupithecus* and two unnamed species from eastern Peru; *Perupithecus* teeth are most similar to Eocene African anthropoid *Talabpithecus* (Bond et al. 2015). A ten-million-year gap separates the next primate fossil evidence in the Neotropics: *Branisella* in Salla, Bolivia, at 26 Ma (Hoffstetter 1969). South America was closer, then, to coastal Africa, and ocean currents favored dispersal from West Africa to the eastern coast of South America (de Oliveira et al. 2009). Evidence also suggests rafting from Africa to South America for amphisbaenian and gekkotan lizards, and the Neotropical bird group hoatzins, which are notoriously bad fliers (Bond et al. 2015).

Comparative genomic analyses point to divergence at 43.5 Ma between Platyrrhini and Catarrhini (Perelman et al. 2011) and suggest that all living platyrrhines share a most recent common ancestor from about 19 to 24 Ma (Hodgson et al. 2009, Perelman et al. 2011, Springer et al. 2012). Disagreement continues over morphological stasis versus successive radiations in terms of how rapidly platyrrhines diversified into their current ecological niches; *Dolichocebus*, *Tremacebus*, and *Chilecebus* may be too old to be crown platyrrhines and are more likely part of an extinct earlier radiation, with parallel evolution creating a similar range of morphologies to many of the extant New World monkeys (Hodgson et al. 2009, but see Aristide et al. 2015; see the sidebar titled Stem Platyrrhine Fossil Diversity).

Eocene: geologic epoch from 56 Ma to 33.9 Ma; during this period some early anthropoids rafted to the Neotropics through waif dispersal

Xenarthrans: armadillos, sloths, and anteaters, including the now-extinct radiations of giant armadillos and ground sloths

Nontherian: mammals that evolved before the split of eutherian and marsupial mammals; in South America, they include monotremes, meridiolestidans, and gondwanotheres



Figure 2

Present-day distribution map of Neotropical primates with depiction of pre-Anthropocene biomes from Olson et al. (2001). Fossil sites and primate distribution modified from Kay (2015), Bond et al. (2015), and Bloch et al. (2016). Biome map adapted from Wikimedia Commons (https://commons.wikimedia.org/wiki/File%3ANeotropic_biomes.svg).

STEM PLATYRRHINE FOSSIL DIVERSITY

Kay (2015) describes three distinct geographic-geologic clusters for the stem platyrrhines: Eocene to Late Oligocene midlatitude (Amazonian) taxa, including *Branisella*, and now the recently discovered *Perupithecus* (Bond et al. 2015); Early Miocene far-southern taxa, including Chilean *Chilecebus* and Argentinean *Mazzonicebus*, *Tremacebus*, *Dolichocebus*, *Homunculus*, *Soriacebus*, and *Carlocebus*; and Early Miocene to Holocene taxa from the Greater Antilles in the Caribbean, such as *Paralouatta*, *Xenobrix*, and *Antillobrix*. The most newly discovered addition to the last group is the Central American fossil *Panamacebus* from ~20 Ma (Bloch et al. 2016). In the past, with lower sea levels, the chain of Caribbean islands was connected together and to South America (Kay 2015). Whereas Kay (2015) argues that primates dispersing into the Caribbean were caught in the “Antilles trap” and went extinct, Rosenberger and colleagues (2009) argue that these taxa were closely related to living genera.

Primates may have radiated into the Neotropics so successfully because they did not have strong mammalian competitors for their preadapted niche. Early catarrhine primates displayed functional morphology of arboreal quadrupeds specializing in fruit and insect eating, with grasping hands and forward-facing eyes, and were likely diurnal and gregarious. In the New World, many birds are gregarious arboreal fruit eaters, but mammals have tended to be solitary, nocturnal, and/or ground dwelling. Bats are frugivorous and gregarious, but strictly nocturnal in the Neotropics. Native arboreal mammals in the Neotropics were smaller in size (marsupials) or had adaptations to leaf eating (sloths) or ant eating (anteaters). The new caviomorph rodent group did evolve arboreal radiations, but these tended to remain solitary and nocturnal. Primates in the trees could get to the fruit before the ground-dwelling frugivores. However, now-extinct forest megafauna may have eaten fruit by standing at the base of trees and browsing (Barlow 2000). In a reconstruction of Neotropical primate diversification, the ancestral condition is an arboreal quadruped frugivore insectivore, with subsequent evolution of a variety of adaptations, including semibrachiation, unripe fruit specialization, gummivory, omnivory, and tool use (**Supplemental Figure 1**).

Primates may have directly displaced birds, may have gotten to fruit resources more quickly, and/or may have specialized on different fruit types compared to birds; primates strengthened their own niches through seed dispersal, creating increasingly primate-friendly forests (Stevenson 2005; Terborgh 1983, 1986). Open questions include how much fruit or leaves were incorporated into notoungulate, liptotern, or other megafauna diets and how extensively these taxa overlapped with the primate range in the Neotropics. Barlow (2000) suggests that large-seeded fruit trees in the Neotropics are a result of past history of megafauna as seed dispersers. If large generalists were using tropical forest habitats and acting as competitors for primates, competitive release and expansion of primate abundance occurred in the Holocene after the megafauna extinction, in which 50 large-bodied South American genera were lost (Barnosky et al. 2004). A major challenge to reconstructing the potential competitors and predators for early Amazonian primates is that the tropical rainforest habitat is notoriously poor for fossil preservation, owing to hot and humid climatic conditions, a thin soil layer, and intensive faunal recycling of detritus.

La Venta: The Gang’s All Here

La Venta, Colombia, is the key fossil primate site representing mid-Miocene tropical diversity; it is also the only high-yield site for South American primate fossils. Located in the foothills of the Andes, it represented a habitat with Amazonian fauna at the time of fossilization (Kay 2015). Platyrrhine evolution may include stasis after the La Venta fauna at 12.5 Ma—that is, ecological

Notoungulate: an extinct order of hoofed mammals from South America, from the Paleocene to the Pleistocene, with a diversity of body types, from rabbit-like to rhino-like

Liptotern: a once diverse but now extinct order of hoofed mammals from South America and Antarctica, some species of which persisted into the Pleistocene

Holocene: the recent geological epoch, from 11.7 Ka to ~1950 CE; this epoch began around the time when humans first colonized the Neotropics

Miocene: geological epoch spanning 23 Ma to 5.33 Ma; this time period encompasses the extant Neotropical primates’ radiation and major diversification period

Vicariance: the process by which the geographical range of a taxon is split into discontinuous regions owing to new biotic or physical barriers that interrupt gene flow

niches occupied by present-day platyrrhine taxa were already divided similarly by the mid to late Miocene (Hodgson et al. 2009). Fossil evidence is present at La Venta for all five currently recognized living platyrrhine families (**Supplemental Table 1**).

Fossil-calibrated phylogenetic reconstructions concur that primate diversification had already occurred at the subfamily level by 12 Ma (**Supplemental Table 2**). Jameson Kiesling et al. (2015) point to genus-level diversification for the Platyrrhini happening practically in sympatry in the proto-Amazon Basin; such a rich habitat with a relative paucity of mid-size arboreal competitors offered a smorgasbord of ecological niches. Subsequent diversification and specialization among primates may have been driven by primate–primate competition and niche displacement. From Amazonia, primates expanded repeatedly to more temperate, open, xeric, and high-altitude habitats.

The Rise of the Andes, the Rush of the Amazon

What is currently known as the Amazon biome included a larger region prior to 10 Ma, encompassing the Orinoco and Magdalena drainage basins (Hoorn et al. 2010). Primate fauna diversified across a relatively unrestricted continental expanse, until Andean mountain building peaked in intensity during the late middle Miocene (~12 Ma) (Hoorn et al. 2010). The uplift transformed a relatively flat continent into one with lowlands and a range of habitats along the slopes of the mountains, from foothills to ice-covered summits (Bush et al. 2011a). The intense Andean uplift in the Miocene led to both the isolation of *cis*- and *trans*-Andean taxa and the creation of an enormous freshwater wetlands area of lakes and swamps, the Pebas System, in western Amazonia (Hoorn et al. 2010). The expansive wetlands effectively cut off the tropical rainforest along the eastern foot of the Andes from the eastern Amazonian rainforest (Hoorn et al. 2010). Together these changes may have led to vicariance for several primate populations around 11–9 Ma. At that time, the western river drainage systems led into the Pebas Lake and drained north to the Caribbean, but a separate proto-Amazonian system in the eastern part of the continent drained east to the Atlantic. Dispersal pathways along forested landscapes were still available from the Guiana Shield to the Brazilian Shield and as far as what is today the Atlantic Forest. The final rise of the Andes and subsequent lowering of sea level (due to ice cap expansion) led to the current riverine system of the Amazon River flowing east, powered by Andes' runoff. The timing of the conversion of the Pebas Lake to the current Amazonian river system is a major controversy in the paleogeologic and biogeographic literature today (see the sidebar titled Old or New Amazon River?).

OLD OR NEW AMAZON RIVER?

Hoorn et al. (2010) point to a transition from megawetlands to a more forested habitat in western Amazonia between 7 and 5 Ma, in conjunction with a transition to the modern riverine system. In contrast, the “Dynamic Young Amazon” model infers a more recent origin, with the complete formation of the cross-continental Amazon River at 3–2 Ma and new major tributary formation up through 1 Ma (Campbell et al. 2006, Latrubesse et al. 2010, Ribas et al. 2012, Rossetti et al. 2005). Biogeographic evidence has corroborated the more recent establishment of the modern Amazon River (e.g., d’Horta et al. 2013, Boubli et al. 2015, Buckner et al. 2015, Byrne et al. 2016, Fernandes et al. 2012). However, different studies’ estimates for divergence times of owl monkeys north and south of the Amazon River—8 Ma (Babb et al. 2011) versus 3.6–4.7 Ma (Ashley & Vaughn 1995, Plautz et al. 2009)—show how different assumptions, markers, and model choices in creating a time-calibrated phylogeny can result in evidence supporting either the Old Amazon or Dynamic Young Amazon models. A more rigorous and coordinated effort could evaluate these hypotheses using comparative Neotropical primate data.


All Across America: From Amazonia to the Atlantic

Each Neotropical primate genus represented in the Atlantic Forest has a sister taxa in Amazonia (**Supplemental Figure 2**). Biogeographic analyses that allow for a range of diversification scenarios have tended to reconstruct ancestral primate populations as widespread across the Amazon Basin and the Atlantic Forest, with subsequent vicariance between Atlantic Forest and Amazonian taxa occurring mostly in the middle to late Miocene (Buckner et al. 2015, Byrne et al. 2017, Lima et al. 2017). Using statistical analyses in BioGeoBEARS, the most well-supported models reconstruct the common ancestor to all extant marmosets and tamarins with a wide geographic distribution across Amazonian and Atlantic Forests; Atlantic Forest lion tamarins represent a middle Miocene Atlantic Forest split through vicariance (13.4 Ma; Buckner et al. 2015). A biogeographic reconstruction of titi monkey evolutionary history using comparative genomic data found a 10.25-Ma split between ancestral Amazon versus Gran Chaco + Atlantic Forest titis, and a late Miocene (6.7-Ma) divergence of titi monkeys via fragmentation of a widespread ancestral population across the Cerrado + Gran Chaco versus Atlantic Forest [H. Byrne, J. Lynch Alfaro, I. Sampaio, I. Farias, H. Schneider, T. Hrbek & J. Boubli, manuscript in preparation, “Biogeography of the Titi Monkeys (Callicebinae)”]. Lima et al. (2017) found evidence using three mitochondrial genes for a widespread ancestral capuchin population, with late Miocene vicariance at ~6.2 Ma resulting in the evolution of Amazonian gracile capuchins and Atlantic Forest robust capuchins. Both DIVA-J and DEC-J reconstructions in a BioGeoBEARS analysis place the marmoset ancestor as widespread from the western Amazon to the Atlantic Forest before a vicariance event separated Atlantic and Amazonian marmosets at 5 Ma (Buckner et al. 2015). These primate data corroborate evidence from Neotropical birds that suggests intermittent continuity across the Atlantic Forest and Amazonian biomes at ~14–13 Ma and 9–4 Ma, punctuating longer intervals of discontinuity (Batalha-Filho et al. 2013). The divergence of several Amazonian–Atlantic Forest primate genus pairs at 8–4 Ma coincides with floral assembly of the Cerrado, as indicated by the diversification of many Cerrado plant lineages at that time (Simon et al. 2009). Biome change from rainforest to seasonally dry forest may have caused the extirpation of regional primate lineages and vicariance between Atlantic Forest and Amazonian populations [H. Byrne, J. Lynch Alfaro, I. Sampaio, I. Farias, H. Schneider, T. Hrbek & J. Boubli, manuscript in preparation, “Biogeography of the Titi Monkeys (Callicebinae)”]; Lima et al. 2017, Lynch Alfaro et al. 2015b].

The Role of Rivers in Amazonian Species Diversification

Observations that Amazonian primate community composition could change from one river bank to the other led Wallace (1852) to hypothesize that rivers created important barriers leading to speciation. A continuing question is whether rivers are just stopping points, or if it is river formation that causes speciation through vicariance for widespread taxa (Boubli et al. 2015). Biogeographic modeling shows that even the same rivers may have different effects on different primate taxa. For example, Boubli and colleagues (2015) focused their study on the biogeography of primates along the Negro and Branco rivers in northern Amazonia. Evidence for similar divergence times for gracile capuchins, widow titis, and black uakaris on either side of the Rio Negro suggested that river formation around 2–1 Ma may have caused vicariance for each of these taxa (Boubli et al. 2015). However, squirrel monkeys have closely related populations across the upper Rio Negro, and robust capuchins are genetically indistinguishable on the two sides of the lower Rio Negro; this finding suggests that the river is not an important physical barrier or vicariant agent for these species (Boubli et al. 2015). In the same study, the Rio Branco was an important geographical “stopping point,” limiting the distribution of gracile capuchins, uakaries and widow titis to the west and sakis, large tamarins, and robust capuchins to the east (Boubli et al. 2015).

BioGeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts (BioGeoBEARS): an R package authored by Nicholas Matzke to perform inference of biogeographic history on phylogenies, including model testing

 **Supplemental Material**

BEAST**phylogeography:**

a method to reconstruct spatial dynamics of populations within a species over time and to estimate ancestral locations using a Bayesian discrete phylogeographic approach

Proboscideans:

trunked mammals in the Afrotherian order; elephant-like mammals entered South America during the GABI

Other biogeographic studies have focused on particular taxa and their diversification across the Amazon Basin. A well-resolved, time-calibrated phylogenetic reconstruction of titi monkey biogeography supports species-level diversification for both the widow titis in the north and the Amazonian titis in the south as occurring explosively from ~2.5 to 0.5 Ma. Titi monkey speciation is characterized as resulting from rare but sequential founder events across rivers, supporting the role of Amazonian tributaries as important barriers to gene flow [H. Byrne, J. Lynch Alfaro, I. Sampaio, I. Farias, H. Schneider, T. Hrbek & J. Boubli, manuscript in preparation, “Biogeography of the Titi Monkeys (Callicebinae)”. Titi monkeys were absent from the western Amazon until the Pleistocene, perhaps marking the recession of Pebas wetlands and the establishment of suitable forest habitat at that time [H. Byrne, J. Lynch Alfaro, I. Sampaio, I. Farias, H. Schneider, T. Hrbek & J. Boubli, manuscript in preparation, “Biogeography of the Titi Monkeys (Callicebinae)”].

A biogeographic analysis of marmosets and tamarins in Amazonia suggests that species diversification did not begin until 5 Ma, which may coincide with the transition to the transcontinental Amazonian river drainage system (Buckner et al. 2015). Vicariance of pygmy marmosets and Amazonian marmosets occurs across the Madeira River at 5 Ma, and the eastern Amazon River appears to have limited northern dispersal of Amazonian marmosets (Buckner et al. 2015). Species splits for Amazonian marmosets separated by other smaller Amazonian tributaries such as the Xingu and Tapajós occur during the Pleistocene, suggesting vicariance due to river formation at that time (Buckner et al. 2015). For large tamarins, speciation is reconstructed to have occurred through vicariance for the *Saguinus mystax* group at 1–2 Ma, placing river formation for the Marañón, Ucayali, and upper Amazon rivers in the Pleistocene (Buckner et al. 2015). This finding concurs with avian studies that suggest the tributary system in western Amazonia formed relatively late (Ribas et al. 2012).


Biogeographic reconstructions for robust capuchin monkeys suggest that they diversified first in the Atlantic Forest and greatly expanded their range from about 500,000 years ago, now inhabiting nearly all of Amazonia, Caatinga, Cerrado, and Gran Chaco habitats (Lima et al. 2017, Lynch Alfaro et al. 2012). A BEAST phylogeography analysis suggests that Amazonian rivers were not barriers to robust capuchins during the Late Pleistocene (Lima et al. 2017).

The modern squirrel monkey radiation, based on mtDNA (mitochondrial DNA) analysis (Lynch Alfaro et al. 2015a), including whole mitochondrial genome analysis for several species (Chiou et al. 2011), may have occurred explosively in the last 1.5 Ma. Biogeographic reconstruction suggests that squirrel monkeys were widespread in the western Amazon, possibly exploiting the Pebas lacustrine system, as they are typically found in lowlands near water (Lynch Alfaro et al. 2015a). In the last million years, squirrel monkeys have expanded their range throughout the Amazon Basin, and speciation is reconstructed as occurring through repeated dispersal events across rivers and subsequent isolation within interfluvia (Lynch Alfaro et al. 2015a).

Great American Biotic Interchange: New Mouths at the Table

The separation of western and eastern South America through the final Andes uplift was followed by the closing of the Isthmus of Panama (3.5 Ma; Hoorn et al. 2010). The Great American Biotic Interchange (GABI), where North and South American fauna crossed over the Isthmus of Panama to colonize one another’s formerly exclusive ranges, was once imagined to have happened all at once. However, the newly discovered fossil *Panamacebus* at 20.9 Ma suggests that primates first crossed from South America into central Panama in the early Miocene (Bloch et al. 2016). Large Neartic herbivores such as peccaries and tapirs (as well as proboscideans and dromomerycine artiodactyls, now extinct) may have reached South America via the Baudo pathway with some island

hopping at 9–10 Ma (Campbell et al. 2010, Frailey & Campbell 2012; but see Carrillo et al. 2015). The largest wave from the north did arrive after the closing of the Isthmus of Panama; it included potential primate competitors such as raccoons, coatis, olingos, kinkajous, skunks, squirrels, and sigmodont rodents (Goin et al. 2012). An onslaught of potential predators for primates also arrived, such as felids, tayras, rattlesnakes, and pit vipers (Goin et al. 2012). Surprisingly, no carnivores or venomous snakes have shifted to a primary strategy of primate predation (Hart 2007), although they may have driven changes in primate ecology in the Neotropics. Urbani (2005) calculates that only 15% of nonhuman predation events on primates are by jaguars. Other felids occasionally do attack primates, but it is relatively uncommon, especially in comparison with data from Africa and Asia felid predation on primates (Hart 2007). Instead, raptors, including the harpy eagle, hawks, and small forest falcons, remain the most important predators on primates in the Neotropics, both from observed predation and from examination of contents of predator diet (Hart 2007). Primate vigilance and escape behavior in the Neotropics are adaptations primarily in relation to raptors; Terborgh (1983) describes three distinct raptor-avoidance strategies: crypsis, group living, and escape from predators through an increase in size (**Supplemental Figure 1**).

 [Supplemental Material](#)

During GABI, some Neotropical primates extended their range north. Species distributions and paleogeologic and geographic evidence suggest multiple waves of dispersal into Central America (Ford 2005). Divergence time data from genetic analyses reconstruct spider monkeys (Morales-Jimenez et al. 2015a,b) and howler monkeys (Cortés-Ortiz et al. 2003) entering Mesoamerica soon after the closing of the Isthmus of Panama; gracile capuchin monkeys followed at ~2 Ma (Boubli et al. 2012), and squirrel monkeys maybe not until 1 Ma or later (Chiou et al. 2011, Lynch Alfaro et al. 2015a). Despite this release into habitat unpopulated by other monkeys, Neotropical primates did not extend far into the temperate zone. The Mexican deserts formed an uncrossable barrier that limited Neotropical primate expansion. Duran et al. (2013) modeled climatic niche evolution in the Platyrrhini and found a simple structure underlying the current limits of primate distribution in the Neotropics: The average temperature in the coldest months is the most important correlate of Neotropical primate distributions, followed by rainfall. Distribution is overlapping and thoroughly explored by all the Neotropical families, although owl monkeys stand out as being able to occupy particularly dry habitats (Duran et al. 2013).

A NEW KIND OF PRIMATE

The Peopling of the Americas

Humans, like Neotropical monkeys, are primate immigrants to the Americas. Llamas et al. (2016) place the arrival of humans in the Americas at 16,000 years ago using mitochondrial genetic evidence. Archaeological evidence also supports humans in Monte Verde, Chile, at ~14,800 years ago, with more abundant archaeological material in the Americas from ~13,000 years ago (Veeramah & Hammer 2014). Humans who first reached monkey-occupied Central and South America arrived from East Asia via a land bridge across the Bering Strait and took the western coastal route from North to South America, later expanding inland from the west (Reich et al. 2012).

Genetic studies of ancient and modern human populations in Mesoamerica corroborate archaeological and cultural evidence for ancient population diversity, as well as the development of agriculture and trade, leading to regional patterns of homogeneity (Bolnick et al. 2016). In South America, continent-wide Y-chromosome genetic sampling of native South American males revealed that population genetics does not have strong geographic or linguistic structure. These results are consistent with a recent arrival of the first humans in South America and subsequent very

Anthropocene:

modern epoch in which humans are the most important force changing Earth's ecology and geology, most widely recognized as beginning in the 1950s

rapid, long-distance dispersal followed by isolation in small groups, with population expansion occurring only relatively recently before European colonization (Roewer et al. 2013). Native empire expansions contributed to relative homogeneity in Andean populations (Bolnick et al. 2016), but ancient gene flow has been documented between the Andes and Amazon regions (Barbieri et al. 2014). Together the data point to a human diaspora at the end of the last Ice Age across the entire range of Neotropical primate distribution.

Amazonian Occupation

Humans continuously occupied the Neotropics after 15–12 kya, including Amazonia by 12.9 kya (Piperno 2007). One debate is over the extent of the use of Amazonian terra firme forests by indigenous human populations—were they able to occupy and farm with high population density throughout Amazonia, or were Amazonian human populations concentrated only along rivers (Piperno 2007)? Archaeological evidence from the Amazon, including geoglyphs, Bolivian earthworks, terra preta sites, Marajó funereal pottery, muiraquitã frog pendants, Xingu settlements, and North and South Amazon petroglyph traditions, together point to indigenous Amazonian occupation, population expansion, agricultural traditions, trading and complex traditions; these findings counteract the early European claims that the Amazon Basin was “pristine forest” inhabited only by small scattered groups at the onset of European colonization (Schaan 2012). While some archaeologists have argued that the pre-Colombian Amazon was a “cultural parkland” (Heckenberger et al. 2003), highly transformed through high human population density and intensive farming and tree selection, Bush et al. (2015) suggest that monkeys and other animals actually had more agency than humans did in terms of transforming the forest through seed dispersal because of wider and longer-term occupation. Primates’ preference for forest type seems genus dependent, and evidence for human activity tends to be concentrated around floodplains, affecting the landscape only for ~15 km around occupation sites (Bush et al. 2015). Some primates, such as capuchin monkeys, may have capitalized on the availability of plants cultivated by early human occupants and continue to utilize human cultivars such as sugar cane, corn, palm nuts, and papaya, leading to frequent human–primate conflict both in Amazonia and throughout capuchins’ range.

A New Wave of Humans: European Colonization and Biotic Exchange

European colonization of the Americas at 500 years ago led to Native American disease epidemics, slavery, warfare, changes in demographics and community structure, non-Native admixture, and in many cases destruction of traditional lifestyles, decimation, or genocide (Bolnick et al. 2016). The arrival of Europeans in South America marks a significant transformation of Earth because of the resultant biotic interchange between Old World and New World as well as the subsequent population crash of indigenous human populations, and some geologists suggest this moment could be considered the onset of the Anthropocene (Lewis & Maslin 2015). The African peopling of the Americas soon followed through the transatlantic slave trade (Bolnick et al. 2016). European colonization of the Americas was driven by a desire to extract resources and to take over land for new uses. European settlers introduced a range of domesticates, including pigs, cattle, horses, and chickens, as well as various agricultural crops. Their new economies centered on these exotic species instead of local flora and fauna, and their (often unsustainable and mismatched) solution was to transform the land from forest to agriculture and ranching. One of the most complete transformations was the decimation of the Atlantic Forest biome, an early European landing site with weather similar to Mediterranean conditions, making it desirable for agriculture and settlement. Likewise, the west coast of South America has been rapidly and radically transformed.

In contrast, only ~17% of the Amazon biome to date has been deforested and converted to human use, owing in large part to its inaccessibility, high infectious disease risk, and ongoing resistance from indigenous and local communities as well as from environmentalists.

Monkeys as Sisters, Symbols, and Subsistence

In general, Europeans brought no cultural traditions that would enhance their social or symbolic relationship with monkeys or their perception of monkeys' value as living beings or communities; rather, they tended to see monkeys as pests or as meat. In contrast, primates continue to shape an important part of identity, art, and culture in indigenous groups in primate-occupied regions of the Americas (Cormier 2003, 2006). Monkeys are incorporated into Amerindian kinship systems; modern monkeys are the result of human-monkey hybrids in some cultures (Cormier 2006), whereas most cultures consider monkeys to have evolved or descended from humans (Viveiros de Castro 2004). Monkeys are kept as pets and treated as family members in many Amazonian human groups (Cormier 2006).

Among indigenous, mixed, and European groups, monkeys can also continue to form an important part of a subsistence diet and are a preferred food for hunting. Cormier (2006) reports ethnographic evidence from Amazonia for hunting by about 50 indigenous groups, and it is safe to say that monkey hunting has been ubiquitous within the Americas. Urbani (2005) points to humans as a new kind of predator for primates, one that takes advantage of mobbing behaviors and alarm calls in order to preferentially target group-living, large-bodied primates. Human strategy differs markedly from nonhuman predators such as hawks, and Urbani (2005) argues that human predation on Neotropical primates has shaped monkey population density, group size, and population distribution. MacPhee & Horovitz (2002) suggest that primate megafauna such as the Pleistocene monkey *Xenothrix mcgregori* may have gone extinct because of humans' hunting.

The Great Acceleration

Global market demands for soybeans, sugar cane, natural rubber, cattle, and tropical hardwoods have driven deforestation in the Neotropics (Estrada et al. 2017). As a result of human encroachment on and transformation of primate habitat, hunting, and the pet trade, 36% of Neotropical primate species are threatened, and 63% have declining populations (Estrada et al. 2017). Large primates are the most vulnerable, especially the atelines, because of their specialization on primary forest ripe fruits, their preferred status as a delicacy, slow generation time, and vulnerability to hunting, especially in fragmented areas (Daily et al. 2003). Howler monkeys can often survive even intensively managed agricultural countryside because of their low-energy ecological strategy; thus, they tend to fare better than atelines but can also be locally extirpated owing to hunting (Daily et al. 2003).

THE FUTURE IS NOW: MONKEY-HUMAN RELATIONSHIPS IN THE ANTHROPOCENE

Climate Change by Biome

Human-mediated climate change is primarily a result of humans' first-world consumption and pollution patterns, which play out on a global scale. This section considers the predicted effects of climate change on key primate-inhabited biomes. Using the CMIP3 data set to model effects of climate change, along with information on primate diversity and proportion of already threatened primates in each region, Graham and colleagues (2016) highlight Amazonia, southeastern Brazil,

Coupled Model Intercomparison Project (CMIP3 or CMIP5): standard experimental protocol to study output of coupled atmosphere-ocean general circulation models for climate change diagnosis (P3 is phase 3; P5 is Phase 5)

ANDES CLIMATE CHANGE

The eastern slopes of the Andes contain high levels of biological diversity, endemism, and unique habitat types such as cloud forest. Due to steep slopes, most species occupy relatively narrow elevational ranges, making them particularly sensitive to climate change (Lutz et al. 2013). Models predicting habitat shift due over the next 100 years show a relatively high proportion of the landscape in the Andes changing across habitat types, in comparison with other biomes in South America (Bush et al. 2011a). A critically endangered primate endemic to the Andean cloud forests is the yellow-tailed woolly monkey. This primate can change its behavior in response to more extreme weather events; for example, in one study low fruit production caused the monkeys to shift their diet to more leaves and insects (Shanee & Shanee 2014). However, the combined effects of increasing pressure from farmers for land transformation, more intensive hunting of the monkeys, and more unpredictable food resources as a result of climate change may devastate this species (Shanee & Shanee 2014).

and Central America as hotspots of climate change–induced primate vulnerability in the Neotropics. Ecosystems like the Andes foothills also have endemic primates and are especially at risk for climate change effects (Lutz et al. 2013; see the sidebar titled Andes Climate Change). Effects of drought, flooding, elevated temperatures, and extreme storm events can variously affect primate populations through decreases in reproduction, decreases in offspring survival, and decreases in food supply, as well as increased enforced resting time, increased predation and infanticide, increased disease transmission and parasitic infection, and increased isolation of subpopulations (Graham et al. 2016).

Amazonia. Tropical forests exert strong influences on the global carbon cycle, and Amazonia encompasses the largest tropical forest (6.7 million km²) on Earth (World Wildl. Fund 2010). Amazonian droughts and widespread fires in the 2000s have already led to 1–2% of the carbon stock of Amazonia being committed to the atmosphere (Lewis et al. 2011; Phillips et al. 2008, 2009). Duffy et al. (2015) model future meteorological drought and wet periods within the Amazon basin using CMIP5 climate models; their results suggest that climate change may cause drought that intensifies fire activity, tree mortality, and subsequent emissions of carbon into the atmosphere from large segments of Amazonia. Climate change may produce higher rates of meteorological drought in eastern Amazonia but less change in precipitation in central Amazonia and extreme wetness in western Amazonia after 2040 (Duffy et al. 2015). Eastern Amazonia is particularly vulnerable owing to ongoing habitat fragmentation and projected decreasing precipitation; primate species at risk here include the black-bearded saki and the Ka’apor gracile capuchin, both critically endangered (IUCN 2016). In contrast, western Amazonia may become the most important ever-wet forest refuge for primates anywhere on Earth (see the sidebar titled Neotropical Ever-Wet Forests as Primate Refuges).

Atlantic forest. The Atlantic Forest is home to endemic marmosets, lion tamarins, titi monkeys, robust capuchins, howler monkeys, and muriquis, but less than 8% of the current biome remains. Colombo & Joly (2010) use GARP to model the effects of climate change on typical Atlantic Forest trees and point to a potential 25–50% reduction in area of occurrence for key species, especially in the northern Atlantic Forest. The high speed of current climate change and the present fragmentation of Atlantic Forest make it unlikely for tree species to be able to adapt to the warmer climate in the way that they adapted to climate cycling in the Pleistocene (Colombo & Joly 2010). Primate species, such as the golden-headed lion tamarin, already threatened with extinction and

Genetic algorithm for rule-set prediction (GARP)

model: determines potential distribution of particular species, modeling changes of temperature, rainfall and humidity—can be used for either future or paleo scenarios

NEOTROPICAL EVER-WET FORESTS AS PRIMATE REFUGES

Nearly one-fourth of the remaining ever-wet forests will dry out to the extent that they lose their ever-wet conditions (Underwood et al. 2014). Underwood et al. (2014) point to the tropical forests that will remain ever wet during the shifts in climate over the next decades, such as western Amazonia, as being extremely important biodiversity refuges—both to provide habitat for species that will be vulnerable in other habitats that are drying out over time and because the forests themselves help mitigate climate change impacts through carbon capture. They promote protecting “as many ever-wet tropical forests as we can, as quickly as we can” (Underwood et al. 2014, p. 741). As the largest remaining ever-wet forest, with a larger proportion already protected compared with African and Asian ever-wet forests, the Neotropics are the best place on Earth for tropical forest protection (Underwood et al. 2014). However, the southwestern edge of Amazonia and Gran Chaco may show the greatest magnitude of increasing temperature due to climate change; primates affected in this region include Amazonian titis, Rondon’s marmoset, and the Bolivian red howler (Graham et al. 2016).

living in fragmented habitats in the northern Atlantic Forest, may be most critically affected by climate change here, in particular because of a severe decrease in precipitation (Graham et al. 2016).

Cerrado and Caatinga. Cerrado is savanna vegetation with 44% endemism for plant taxa, covering about 2.5 million km² of Central Brazil (Siquiera & Peterson 2003). Siquiera & Peterson (2003) explore the consequences of climate change for Cerrado tree distribution using ecological niche modeling. By the year 2055, about 30% of species will be left without any suitable area in the Cerrado. The habitat has been assaulted since the 1960s by increasingly rapid expansion of intensive agriculture (Siquiera & Peterson 2003). Only 2.25% of the Cerrado is currently protected, and climate change models predict a shift in habitat suitability to the south and east (Siquiera & Peterson 2003).

In addition, de Oliveira et al. (2012) point to the semiarid Brazilian Caatinga biome (750,000 km²) as one of the least preserved South American habitats; at least 50% of the habitat has already been lost. Climate change is expected to increase aridity, but areas that retain natural remnants of vegetation are most likely to gain suitability for more diverse Caatinga species (de Oliveira et al. 2012). Climate change can also affect how and where agriculture and ranching move across the landscape (de Oliveira et al. 2012).

The Cerrado and Caatinga habitats already mark the most extreme hot and dry climates supporting Neotropical primates, and climate change may make these habitats unsuitable for endemics such as black-pencilled marmosets, bearded capuchins, blond titis, and Maranhão red-handed howlers (Carmignotto et al. 2012). Although these more xeric habitats do not contain high primate biodiversity per se, they do drive some of the most extreme primate adaptations, such as eating spiny cactus and using tools to dig for tubers; thus, they are important for the conservation of behavioral biodiversity (Lynch Alfaro et al. 2014, Wright et al. 2015).

Colonizing the World in Cages

Neotropical monkeys have been moved around within their native countries, used as pets, confiscated by authorities, and released back into the wild; these and other human-mediated movements have placed many species outside their historic range, actions that often end up threatening native primate species through direct competition or hybridization (Fialho et al. 2016). For example,

Ecological niche modeling: predicts species distribution in geographic space based on known limits for climate or other environmental parameters for known species occurrence data

▶ Supplemental Material

common marmosets were historically distributed in northeastern Brazil but are now found as far south as Rio de Janeiro (Malukiewicz et al. 2015). The illegal trade in Neotropical monkeys also continues, both for research and for monkeys as pets (Fialho et al. 2016, Svensson et al. 2017).

In fact, during the Anthropocene, humans have captured and transported Neotropical monkeys all over the world, setting the stage for new chance colonization events in the wild (**Supplemental Figure 3**). Between 1977 and 2013, almost 90,000 live Neotropical primates were exported legally directly from South American countries to 63 countries; the United States and Japan were involved in ~50% and 20% of the imports, respectively (Fialho et al. 2016). By far, the most mobile primate was the squirrel monkey, with more than 60,000 individuals moved across borders (Fialho et al. 2016). More than half of platyrrhine imports were listed for commercial purposes, but “scientific testing is likely to be the true driver behind the majority of the primate trade” (Fialho et al. 2016, p. 5). Neotropical primates are found around the world in zoos, sanctuaries, as pets in private homes, and even in free-ranging groups. For example, the Florida Fish and Wildlife Conservation Commission (2017) describes squirrel monkeys as nonnative species inhabiting at least 6 counties in Florida; some were released as tourist attractions, others when small zoos closed, and they have been breeding in the wild for more than 10 years in at least 3 counties. Squirrel monkeys are also free ranging in some locations in Japan, South Africa, and northeastern Brazil.

Perspectival Multinaturalism and Transspecies Engagement

People who work toward biodiversity conservation and climate change impact mitigation have recognized the importance of the multiple evidence base approach, which values indigenous and local knowledge on an equal platform with scientific knowledge for informing policy change (Tengö et al. 2014). Although multiculturalism and interdisciplinarity allow for more inclusive insights into solving today’s problems, an even more radical shift in worldview may be necessary if we hope to stem the impending primate extinction crisis (Estrada et al. 2017) or, more broadly, the defaunation in the Anthropocene (Dirzo et al. 2014). Unlike the Western perspective of multiculturalism, many indigenous Amazonian groups see the world through a lens of “perspectival multinaturalism” (Kohn 2007; Viveiros de Castro 1998, 2004). This frame recognizes that any animal aware of its environment in a predator or prey relationship has a soul and sees the world from its own perspective (Kohn 2013). We as anthropologists have been tasked to step outside of our species-centric focus and to consider an anthropology of life (Kohn 2007, 2013), to begin to assemble multispecies ethnographies (Kirksey 2014). A shift in our understanding and valuing of the viewpoints and lived experiences of other animals on our planet could guide a transition to a more inclusive cultural practice of transspecies engagement (Kohn 2007). Imagining the world as seen through wild monkeys’ eyes may help us to stop destroying their habitats, disassembling their communities, and dislocating individuals to become zoo curiosities and laboratory tools.

FUTURE ISSUES

1. Statistical modeling techniques should be employed to understand the diversification dynamics of Aotidae, Pitheciinae, and Atelidae biogeography.
2. Emphasis should be placed on amassing a better comparative nuclear genomic and mitochondrial data set to examine species-level biogeography for all Neotropical primate taxa together so that time calibrations match up across taxa and can be considered as a whole in comparison to geological events.

3. There is an urgent need to find more fossil mammal assemblages from the Amazon Basin or surrounding areas to better inform our knowledge of primate distribution and diversity in the paleo-Amazon beyond La Venta.
4. New ancient DNA techniques could capture genomic sequences from Holocene platyrrhine fossils from the Antilles and Brazil to answer questions about stem and crown forms and to better understand taxonomic relationships between fossil and living primates.
5. Models of the effect of climate change on Neotropical mammalian taxa need to incorporate the effects of landscape fragmentation, human land use changes due to climatic shifts, pollution effects, and consequences of planned human activities such as the more than 200 hydroelectric dams projected for Brazilian rivers.
6. Some whole-genome sequences are now available for Neotropical primate taxa, allowing for a new wave of functional genomic comparisons to understand the adaptive radiations within Neotropical primates from a new and complementary perspective.
7. Neotropical primate taxonomy has been revolutionized with biogeographic statistical modeling techniques, revealing hidden diversity in capuchins, titi monkeys, and tamarins. New biogeographic studies will continue to refine platyrrhine taxonomy.
8. Primate conservation occurs through data gained through science; collaboration among scientists, land owners, government officials, and local and indigenous stakeholders; and dissemination of the findings to advocate for national and international political will and attention.
9. The future of primates in the Americas depends not only on humans' ability to utilize science and technology but also on our willingness to reform our own cultural practices to better match the constraints of the Earth on which we live.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Thanks go to Amisha Gadani, Frederico Lynch Ribeiro, Michael E. Alfaro, and Doug Beckner for their invaluable help with production of figures, to Karen Strier and Don Brenneis for the invitation to produce this manuscript, and to Jennifer Mann for assistance with manuscript production. This is Amazonian Mammals Research Group publication #40.

LITERATURE CITED

- Aristide L, Rosenberger AL, Tejedor M, Perez I. 2015. Modeling lineage and phenotypic diversification in the New World monkey (Platyrrhini, Primates) radiation. *Mol. Phylogenet. Evol.* 82:375–85
- Ashley MV, Vaughn JL. 1995. Owl monkeys (*Aotus*) are highly divergent in mitochondrial cytochrome C oxidase (COII) sequences. *Int. J. Primatol.* 16:793–806
- Babb PL, Fernandez-Duque EF, Baiduc CA, Gagneux P, Evans S, Schurr TG. 2011. mtDNA diversity in Azara's owl monkeys (*Aotus azarai azarai*) of the Argentinean Chaco. *Am. J. Phys. Anthropol.* 146:209–24

- Barbieri C, Heggarty P, Yao DY, Ferri G, de Fanti S, et al. 2014. Between Andes and Amazon: The genetic profile of the Arawak-speaking Yanésa. *Am. J. Phys. Anthropol.* 155:600–9
- Barlow C. 2000. *The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms*. New York: Basic Books
- Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306:70–75
- Batalha-Filho H, Fjeldså J, Fabre P-H, Miyaki CY. 2013. Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. *J. Ornithol.* 154:41–50
- Bloch JI, Woodruff ED, Wood AR, Rincon AF, Harrington AR, et al. 2016. First North American fossil monkey and early Miocene tropical biotic interchange. *Nature* 533:243–247
- Bolnick DA, Raff JA, Springs LC, Reynolds AW, Miró-Herrans AT. 2016. Native American genomics and population histories. *Annu. Rev. Anthropol.* 45:319–40
- Bond M, Tejedor MF, Campbell KE Jr., Chornogubsky L, Novo N, Goin F. 2015. Eocene primates of South America and the African origins of New World Monkeys. *Nature* 520:538–41
- Boubli JP, Ribas C, Lynch Alfaro JW, Alfaro ME, da Silva MN, et al. 2015. Spatial and temporal patterns of diversification in the Amazon: a test of the riverine hypothesis for all diurnal primates of Rio Negro and Rio Branco in Brazil. *Mol. Phylogenet. Evol.* 82(B):400–12
- Boubli JP, Rylands AB, Farias IP, Alfaro ME, Lynch Alfaro JL. 2012. *Cebus* phylogenetic relationships: a preliminary reassessment of the diversity of the untufted capuchin monkeys. *Am. J. Primatol.* 74:381–93
- Buckner JC, Lynch Alfaro JW, Rylands AB, Alfaro ME. 2015. Biogeography of the marmosets and tamarins (Callitrichidae). *Mol. Phylogenet. Evol.* 82(B):413–25
- Bush MB, Flenley JR, Gosling WD, eds. 2011a. *Tropical Rainforest Responses to Climatic Change*. Berlin/Heidelberg, Ger.: Springer-Verlag. 2nd ed.
- Bush MB, Gosling WD, Colinvaux PA. 2011b. Climate and vegetation change in the lowlands of the Amazon Basin. See Bush et al. 2011a, pp. 61–84
- Bush MB, McMichael CH, Piperno DR, Silman MR, Barlow J, et al. 2015. Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. *J. Biogeogr.* 42:2277–88
- Byrne H, Rylands AB, Carneiro JC, Lynch Alfaro JW, Bertuol B, et al. 2016. Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. *Front. Zool.* 13:10
- Campbell KE Jr., Frailey CD, Romero-Pittman L. 2006. The Pan-Amazonian Ucayali Peneplain, late Neogene sedimentation in Amazonia, and the birth of the modern Amazon River system. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 239:166–219
- Campbell KE, Prothero DR, Romero-Pittman L, Hertel F, Rivera N. 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *J. S. Am. Earth Sci.* 29:619–26
- Carmignotto AP, Vivo M, Langguth A. 2012. Mammals of the Cerrado and Caatinga: distribution patterns of the tropical open biomes of central South America. See Patterson & Costa 2012, pp. 307–50
- Carrillo JD, Forasiepi A, Jaramillo C, Sanchez-Villagra MR. 2015. Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America's fossil record. *Front. Genet.* 5(article 451):1–11
- Chiou KL, Pozzi L, Lynch Alfaro JW, Di Fiore A. 2011. Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences. *Mol. Phylogenet. Evol.* 59:736–45
- Colombo AF, Joly CA. 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. *Braz. J. Biol.* 70:697–708
- Cormier L. 2006. A preliminary review of neotropical primates in the subsistence and symbolism of indigenous lowland South American peoples. *Ecol. Environ. Anthropol.* 2:14–32
- Cormier LA. 2003. *Kinship with Monkeys: The Guajá Foragers of Eastern Amazonia*. New York: Columbia Univ. Press
- Cortés-Ortiz L, Bermingham E, Rico C, Rodríguez-Luna E, Sampaio I, Ruiz-García M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus *Alouatta*. *Mol. Phylogenet. Evol.* 26:64–81
- d'Horta FM, Cuervo AM, Ribas CC, Brumfield RT, Miyaki CY. 2013. Phylogeny and comparative phylogeography of *Sclerurus* (Aves: Furnariidae) reveal constant and cryptic diversification in an old radiation of rain forest understorey specialists. *J. Biogeogr.* 40:37–49

- Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A. 2003. Countryside biogeography of Neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv. Biol.* 17:1814–26
- de Oliveira FB, Molina ECE, Marroig G. 2009. Paleogeography of the South Atlantic: a route for primates and rodents into the New World? See Garber et al. 2009, pp. 55–68
- de Oliveira G, Araújo MB, Rangel TF, Alagador D, Diniz-Filho JAF. 2012. Conserving the Brazilian semiarid (Caatinga) biome under climate change. *Biodivers. Conserv.* 21:2913–26
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014. Defaunation in the Anthropocene. *Science* 345:401–6
- Duffy PB, Brando P, Asner GP, Field CB. 2015. Projections of future meteorological drought and wet periods in the Amazon. *PNAS* 112:13172–77
- Duran A, Meyer ALS, Pie MR. 2013. Climatic niche evolution in New World monkeys (Platyrrhini). *PLOS ONE* 8:e83684
- Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, et al. 2017. Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* 3:e1600946
- Fernandes AM, Wink M, Aleixo A. 2012. Phylogeography of the chestnut-tailed antbird (*Myrmeciza hemimelaena*) clarifies the role of rivers in Amazonian biogeography. *J. Biogeogr.* 39:1524–35
- Fialho MS, Ludwig G, Valença-Montenegro MM. 2016. Legal international trade in live Neotropical primates originating from South America. *Primate Conserv.* 30:1–7
- Fla. Fish Wildl. Conserv. Comm. 2017. *Nonnatives - squirrel monkey*. Fla. Fish Wildl. Conserv. Comm., Tallahassee. <http://myfwc.com/wildlifehabitats/nonnatives/mammals/squirrel-monkey/>
- Ford SM. 2005. The biogeographic history of Mesoamerican primates. In *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*, ed. A Estrada, PA Garber, MSM Pavelka, L Luecke, pp. 81–114. New York: Springer
- Frailey CD, Campbell KE Jr. 2012. Two new genera of peccaries (Mammalia, Artiodactyla, Tayassuidae) from upper Miocene deposits of the Amazon Basin. *J. Paleontol.* 86:852–77
- Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, eds. 2009. *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation*. New York: Springer-Verlag
- Goin FJ, Gelfo JN, Chornogubsky L, Woodburne MO, Martin T. 2012. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. See Patterson & Costa 2012, pp. 20–50
- Graham TL, Matthews HD, Turner SE. 2016. A global-scale evaluation of primate exposure and vulnerability to climate change. *Int. J. Primatol.* 37:158–74
- Hart D. 2007. Predation on primates: a biogeographical analysis. In *Primate Anti-Predator Strategies*, ed. SL Gursky-Doyen, KAI Nekaris, pp. 27–59. New York: Springer
- Hartwig WC, Cartelle C. 1996. A complete skeleton of the giant South American primate *Protopithecus*. *Nature* 381:307–11
- Heckenberger MJ, Kuikuro A, Kuikuro UT, Russell JC, Schmidt M, et al. 2003. Amazonia 1492: pristine forest or cultural parkland? *Science* 301:1710–14
- Hirsch A, Dias LG, Martins LO, Campos RF, Landau EC, Resende NAT. 2002. BDGEOPRIM - database of georeferenced occurrence localities of neotropical primates. *Neotropical Primates* 10(2):79–83
- Hodgson JA, Sterner KN, Matthews LJ, Burrell AS, Jani RA, et al. 2009. Successive radiations, not stasis, in the South American primate fauna. *PNAS* 106:5534–39
- Hoffstetter MR. 1969. Un primate de l'Oligocène inférieur sudaméricain: *Branisella boliviana* gen. et sp. nov. *Comp. Rend. Acad. Sci. Paris* 269:434–37
- Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330:927–31
- IUCN (Int. Union for Conserv. of Nat. and Nat. Resour.). 2016. *The IUCN red list of threatened species*. Version 2016-3. IUCN, Cambridge, UK. <http://www.iucnredlist.org>
- Jameson Kiesling NM, Yi SV, Xu K, Sperone FG, Wildman DE. 2015. The tempo and mode of New World monkey evolution and biogeography in the context of phylogenomic analysis. *Mol. Phylogenet. Evol.* 82:386–99
- Kay RF. 2015. Biogeography in deep time—what do phylogenetics, geology and paleoclimate tell us about early platyrrhine evolution? *Mol. Phylogenet. Evol.* 82:358–74

- Kirksey E, ed. 2014. *The Multispecies Salon*. Durham, NC: Duke Univ. Press
- Kohn E. 2007. How dogs dream: Amazonian natures and the politics of transspecies engagement. *Am. Ethnol.* 34(1):3–24
- Kohn E. 2013. *How Forests Think: Toward an Anthropology Beyond the Human*. Berkeley: Univ. Calif. Press
- Latrubesse EM, Cozzuol M, Silva-Caminha SAF, Rigsby CA, Absy ML, Jaramillo C. 2010. The late Miocene paleogeography of the Amazon Basin and the evolution of the Amazon River system. *Earth Sci. Rev.* 99:99–124
- Lewis SL, Brando PM, Phillips OL, van der Heijden MF, Nepstad D. 2011. The 2010 Amazon drought. *Science* 331:554
- Lewis SL, Maslin MA. 2015. Defining the Anthropocene. *Nature* 519:171–80
- Lima MGM, Buckner JC, Silva-Júnior JS, Aleixo A, Martins AB, et al. 2017. Capuchin monkey biogeography: understanding *Sapajus* Pleistocene range expansion and the current sympatry between *Cebus* and *Sapajus*. *J. Biogeogr.* 44:810–20
- Llamas B, Fehren-Schmitz L, Valverde G, Soubrier J, Mallik S, et al. 2016. Ancient mitochondrial DNA provides high-resolution time scale of the peopling of the Americas. *Sci. Adv.* 2:e1501385
- Lutz DA, Rebecca LP, Miles RS. 2013. Four decades of Andean timberline migration and implications for biodiversity loss with climate change. *PLOS ONE* 8(9):e74496
- Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, et al. 2012. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. *J. Biogeogr.* 39:272–88
- Lynch Alfaro JW, Boubli JP, Paim FP, Ribas CC, Nazareth M, et al. 2015a. Biogeography of squirrel monkeys (genus *Saimiri*): south-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. *Mol. Phylogenet. Evol.* 82(B):436–54
- Lynch Alfaro JW, Cortés-Ortiz L, Di Fiore A, Boubli JP. 2015b. Special issue: Comparative biogeography of neotropical primates. *Mol. Phylogenet. Evol.* 82:518–29
- Lynch Alfaro JW, Izar P, Ferreira RG. 2014. Capuchin monkey research priorities and urgent issues. *Am. J. Primatol.* 76:705–20
- MacPhee RDE, Horowitz I. 2002. Extinct Quaternary platyrrhines of the greater Antilles and Brazil. In *The Primate Fossil Record*, ed. WC Hartwig, pp. 189–200. Cambridge, UK: Cambridge Univ. Press
- Malukiewicz J, Boere V, Fuzessy LF, Grativol AD, Silva IO, et al. 2015. Natural and anthropogenic hybridization in two species of eastern Brazilian marmosets (*Callithrix jacchus* and *C. penicillata*). *PLOS ONE* 10:e0127268
- Mittermeier RA, Rylands AB, Wilson DE, eds. 2013. *Handbook of the Mammals of the World*. Vol. 3: *Primates*. Barcelona: Lynx Ed.
- Morales-Jimenez AL, Cortes-Ortiz L, Di Fiore A. 2015. Phylogenetic relationships of Mesoamerican spider monkeys (*Ateles geoffroyi*): Molecular evidence suggests the need for a revised taxonomy. *Mol. Phylogenet. Evol.* 82(Part B):484–94
- Morales-Jimenez AL, Disotell T, Di Fiore A. 2015. Revisiting the phylogenetic relationships, biogeography, and taxonomy of spider monkeys (genus *Ateles*) in light of new molecular data. *Mol. Phylogenet. Evol.* 82:467–83
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51(11):933–38
- Patterson BD, Costa LP, eds. 2012. *Bones, Clones and Biomes: The History and Geography of Recent Neotropical Mammals*. Chicago: Univ. Chicago Press
- Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, et al. 2011. A molecular phylogeny of living primates. *PLOS Genet.* 7:e1001342
- Phillips OL, Aragão LEOC, Lewis SL, Fisher JB, Lloyd J, et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323:1344–47
- Phillips OL, Lewis SL, Baker TR, Chao K-J, Higuchi N. 2008. The changing Amazon forest. *Philos. Trans. R. Soc. B* 363:1819–27
- Pinto MP, Silva-Júnior JDSE, de Lima AA, Grelle CEV. 2014. Multi-scales analysis of primate diversity and protected areas at a megadiverse region. *PLOS ONE* 9:e105205

- Piperno DR. 2007. Prehistoric human occupation and impacts on Neotropical forest landscapes during the Late Pleistocene and Early/Middle Holocene. See Bush et al. 2011a, pp. 185–212
- Plautz HL, Goncalves EC, Ferrari SF, Schneider MP, Silva A. 2009. Evolutionary inferences on the diversity of the genus *Aotus* (Platyrrhini, Cebidae) from mitochondrial cytochrome C oxidase subunit II gene sequences. *Mol. Phylogenet. Evol.* 51:382–87
- Reich D, Patterson N, Campbell D, Tandon A, Mazieres S, et al. 2012. Reconstructing Native American population history. *Nature* 488:370–75
- Ribas CC, Aleixo A, Nogueira ACR, Miyaki CY, Cracraft J. 2012. A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proc. Biol. Sci.* 279:681–89
- Roewer L, Nothnagel M, Gusmão L, Gomes V, González M, et al. 2013. Continent-wide decoupling of Y-chromosomal genetic variation from language and geography in native South Americans. *PLOS Genet.* 9:e1003460
- Rosenberger AL, Tejedor MF, Cooke S, Pekkar S. 2009. Platyrrhine ecophylogenetics, past and present. See Garber et al. 2009, pp. 69–116
- Rossetti DF, Toledo PM, Góes AM. 2005. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quat. Res.* 63:78–89
- Rylands AB, Heymann EW, Lynch Alfaro JW, Buckner JC, Roos C, et al. 2016. Taxonomic review of the New World tamarins (Primates: Callitrichidae). *Zool. J. Linn. Soc.* 177:1003–28
- Schaan DP. 2012. *Sacred Geographies of Ancient Amazonia*. Walnut Creek, CA: Left Coast Press
- Shanee N, Shanee S. 2014. Yellow-tailed woolly monkey (*Lagothrix flavicauda*): conservation status, anthropogenic threats, and conservation initiatives. In *The Woolly Monkey*, ed. T DeFler, P Stevenson, pp. 283–99. New York: Springer
- Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009. Recent assembly of the Cerrado, a Neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *PNAS* 106:20359–64
- Siquiera MFd, Peterson AT. 2003. Consequences of global climate change for geographic distributions of Cerrado Tree species. *Biota Neotropica* 3:1–14
- Springer MS, Meredith RW, Gatesy J, Emerling CA, Park J, et al. 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLOS ONE* 7(11):e49521
- Stevenson P. 2005. Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In *Tropical Fruits and Frugivores: The Search for Strong Interactors*, ed. JL Dew, JP Boubli, pp. 37–58. Dordrecht, Neth.: Springer
- Svensson MS, Shanee S, Shanee N, Bannister FB, Cervera L, et al. 2017. Disappearing in the night: an overview on trade and legislation of night monkeys in South and Central America. *Folia Primatol.* 87:332–48
- Tengö M, Brondizio ES, Elmquist T, Malmer P, Spierenburg M. 2014. Connecting diverse knowledge systems for enhanced ecosystem governance: the multiple evidence base approach. *Ambio* 43:579–91
- Terborgh J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton, NJ: Princeton Univ. Press
- Terborgh J. 1986. Keystone plant resources in the tropical forest. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. ME Soulé, pp. 330–44. Sunderland, MA: Sinauer
- Underwood EC, Olson D, Hollander AD, Quinn JF. 2014. Ever-wet tropical forest as biodiversity refuges. *Nat. Clim. Change* 4:740–41
- Urbani B. 2005. The targeted monkey: a re-evaluation of predation on New World primates. *J. Anthropol. Sci.* 83:89–109
- Veeramah KR, Hammer MF. 2014. The impact of whole-genome sequencing on the reconstruction of human population history. *Nat. Rev. Genet.* 15:149–62
- Viveiros de Castro E. 1998. Cosmological deixis and Amerindian perspectivism. *J. R. Anthropol. Inst.* 4(3):469–88
- Viveiros de Castro E. 2004. Exchanging perspectives: the transformation of objects into subjects in Amerindian ontologies. *Common Knowl.* 10(3):463–84

Wallace AR. 1852. On the monkeys of the Amazon. *Proc. Zool. Soc. Lond.* 20:107–10

World Wildl. Fund. 2010. *Amazon Alive! A Decade of Discovery 1999–2009*. Brasilia: World Wildl. Fund. http://wwf.panda.org/about_our_earth/all_publications/?200056/AmazonAliveAdecadeofdiscovery1999-2009

Wright KA, Wright BW, Ford SM, Fragaszy D, Izar P, et al. 2015. The effects of ecology and evolutionary history on robust capuchin morphological diversity. *Mol. Phylogenet. Evol.* 82:455–66

Contents

Perspectives

- Recovering the Body
Margaret Lock 1

Archaeology

- Rock Art and Ontology
Andrew Meirion Jones 167

- Collective Action Theory and the Dynamics of Complex Societies
Elizabeth DeMarrais and Timothy Earle 183

- Archaeologies of the Contemporary World
Rodney Harrison and Esther Breithoff 203

- The Archaeological Study of Sacrifice
Glenn M. Schwartz 223

- Archaeology and Human–Animal Relations: Thinking Through
Anthropocentrism
Brian Boyd 299

- Social Network Analysis in Archaeology
Barbara J. Mills 379

Biological Anthropology

- Late Australopiths and the Emergence of *Homo*
Darryl J. de Ruiter, S.E. Churchill, J. Hawks, and L.R. Berger 99

- Primate Positional Behavior Development and Evolution
Michelle Bezanson 279

- The Monkeying of the Americas: Primate Biogeography in the
Neotropics
Jessica Lynch Alfaro 317

- Brain Plasticity and Human Evolution
Chet C. Sherwood and Aida Gómez-Robles 399

Anthropology of Language and Communicative Practices

Language and the Newness of Media <i>Ilana Gershon</i>	15
Personal Narratives and Self-Transformation in Postindustrial Societies <i>Cynthia Dickel Dunn</i>	65
Human–Animal Communication <i>Don Kulick</i>	357

Sociocultural Anthropology

Consuming DNA: The Good Citizen in the Age of Precision Medicine <i>Sandra Soo-<i>jin</i> Lee</i>	33
Precarious Placemaking <i>Melinda Hinkson</i>	49
Marriage and Migration <i>Caroline B. Brettell</i>	81
Fluid Drugs: Revisiting the Anthropology of Pharmaceuticals <i>Anita Hardon and Emilia Sanabria</i>	117
Humans and Animals in Northern Regions <i>David G. Anderson</i>	133
What Does Catastrophe Reveal for Whom? The Anthropology of Crises and Disasters at the Onset of the Anthropocene <i>Roberto E. Barrios</i>	151
A Bundle of Relations: Collections, Collecting, and Communities <i>Joshua A. Bell</i>	241
The Datafication of Health <i>Minna Ruckenstein and Natasha Dow Schüll</i>	261
China–Africa Encounters: Historical Legacies and Contemporary Realities <i>Helen F. Siu and Mike McGovern</i>	337
Epidemics (Especially Ebola) <i>Sharon Abramowitz</i>	421

Theme: Human–Animal Interaction

Humans and Animals in Northern Regions <i>David G. Anderson</i>	133
--	-----

The Archaeological Study of Sacrifice <i>Glenn M. Schwartz</i>	223
Primate Positional Behavior Development and Evolution <i>Michelle Bezanson</i>	279
Archaeology and Human–Animal Relations: Thinking Through Anthropocentrism <i>Brian Boyd</i>	299
The Monkeying of the Americas: Primate Biogeography in the Neotropics <i>Jessica Lynch Alfaro</i>	317
Human–Animal Communication <i>Don Kulick</i>	357

Indexes

Cumulative Index of Contributing Authors, Volumes 37–46	447
Cumulative Index of Article Titles, Volumes 37–46	451

Errata

An online log of corrections to *Annual Review of Anthropology* articles may be found at <http://www.annualreviews.org/errata/anthro>