

Biogeography

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Biogeography is the study of how organisms are distributed across the world. Living primates are broadly distributed throughout the tropics in continental Africa, Madagascar, Asia, and South and Central America. In the past, their distributions were even wider, with primate fossils also found in Europe and North America, including at very high latitudes. Modern primate distributions are influenced by several factors, including climate, habitat, competition with other species, historical biogeography and evolution, and anthropogenic impacts (Kamilar and Beaudrot 2013; Reed and Bidner 2004). Primates can be best described as forest-dwelling species, though some modern species in Africa and Asia live in more dry, open habitats. On every continent with primates, their species richness and diversity is highest in rainforest habitats and lowest in dry regions. Rainforests provide a wealth of dietary resources and microhabitats that allow a wide array of primates to coexist. In contrast, few species are able to persist in resource-poor and environmentally harsh regions. Primates exhibit biological adaptations for an arboreal lifestyle, and these traits often limit their ability to disperse across major geographic barriers, such as the modern Sahara, that are devoid of trees. Other geographic features are critical for explaining biogeographic patterns. Large areas tend to have more species than small areas. This is likely due to more resources and a greater diversity of resources being present in larger areas. Also, areas that are in close proximity to each other are more likely to share many species in common compared to areas that are far apart. Species are better able to disperse between areas that are close rather than far from each other.

African Primates

Sub-Saharan Africa is the home to all but one species of African primate (the exception being the Barbary macaque in Algeria and Morocco). Africa contains both haplorrhine and strepsirrhine primates, with the highest levels of species richness and diversity being found in central Africa, specifically in the forests of the Congo Basin. Many primate species are endemic to (i.e., found exclusively in) this biodiversity hotspot, including one of our closest living relatives, the bonobo. Cyclical patterns of forest expansion and contraction in equatorial Africa throughout the last 10 million years have resulted in multiple speciation events, especially in the guenons (Kamilar, Martin, and Tosi 2009; Tosi, Detwiler, and Disotell 2005). There are more than 20 recognized guenon species and most have relatively small geographic ranges throughout the Congo rainforests and adjacent regions. Red colobus monkeys, although not quite as speciose, are another radiation with a complex taxonomy that similarly reflects African forest history.

Eastern and southern Africa contain many relatively dry and open habitats that have relatively low levels of species richness, with the primate fauna in southern Africa being less speciose than in eastern Africa. The low levels of rainfall in these regions make riverine forests, and their associated water and vegetation, especially important resources for primates and other mammals. Notwithstanding the lower levels of species richness in eastern Africa compared to the Equatorial forest belt, endemism does occur, such as in the Udzungwa Mountains of Tanzania. This area is small in geographic size but has a high level of endemic species, including red colobus, mangabeys, and galagos (Dinesen et al. 2001). The mountains in this region likely act as islands, with populations evolving in isolation for enough time to result in noticeably different traits from closely related taxa in adjacent lowland areas.

Africa contains a number of ecologically flexible and geographically wide-ranging taxa,

exemplified by the terrestrial or semiterrestrial baboons and vervet monkeys, but also including some galagos, and arboreal black-and-white colobus monkeys (*guerezas*). Common (*Papio*) baboons provide a good example of how complex modern and historical biogeography can play an important role in taxonomic diversity. Found in most nonrainforest habitats in Africa (as well as forest in some parts of central Africa), their tolerance of varied environmental conditions facilitates their extremely broad geographic distribution. Determining the number of baboon species living today has been an interesting challenge. Six forms tend to be recognized, with hybrid zones where different forms meet. Interbreeding between forms is common and results in hybrid offspring that can successfully reproduce (Alberts and Altmann 2001). This suggests a single species that varies across geographic and environmental gradients and is likely in some intermediate stage of speciation. However, relatively recent molecular studies indicate an alternative (or additional) pattern, with a deep split between “northern” and “southern” baboon clades, showing that there is still much to be discovered about baboon biogeography and dispersal patterns in the past and how that influences phenotypic, behavioral, and hence taxonomic diversity.

Malagasy Primates

Lemurs, the primates of Madagascar, are found nowhere else in the world. The high level of diversity and endemism on the island is largely a product of isolation from mainland Africa and the presence of a wide array of habitat types. The geographic distribution of lemur taxa varies greatly. Some genera, such as *Eulemur*, *Microcebus*, and *Propithecus*, have species that are distributed in most habitats and regions where lemurs exist. Other genera, such as *Lemur* and *Varecia*, contain species that have very restricted geographic ranges.

Several factors likely influence modern lemur distributions on Madagascar. Lemurs are distributed in most habitats on the island, except for the central plateau, which is devoid of lemurs. In addition to this large geographic barrier in the center of the island, Madagascar contains

many rivers that act as barriers to numerous lemur species. Some of the smaller lemurs, such as mouse lemurs, have their geographic distributions bounded by rivers.

In addition to geographic barriers, lemur distributions are influenced by the substantial amount of climatic and habitat variation found on the island (Kamilar, Blanco, and Muldoon 2016). In eastern Madagascar, rainforests are distributed in longitudinally narrow yet latitudinally wide strips. This is where the highest level of lemur species richness and diversity is found. The western portion of the island contains many dry forests, which also exhibit an interesting and rich diversity of lemurs. Inhabiting the northern montane region are some highly endangered lemur species, including the silky sifaka. Southern Madagascar is quite dry and desert-like and only a few lemur species, including the ring-tailed lemur and mouse lemurs, can survive successfully under these conditions.

Neotropical Primates

The Neotropical forests of Central and South America are home to a wide array of monkeys, but no apes or lemurs. Living primates are found as far north as southern Mexico and as far south as northern Argentina. New World monkey distributions were broader in the past, including species being found on several Caribbean islands and the southern regions of Argentina and Chile (Fleagle 1990). The highest level of primate species richness and diversity is found in the rainforests of the Amazon Basin. The Amazon River and its main tributaries likely acted as a geographic barrier to some of the smaller Neotropical primates, which probably resulted in increased speciation for these taxa. For example, the high species diversity of titi monkeys and tamarins was probably generated by allopatric speciation due to riverine barriers, as different species are found on opposite sides of many rivers in the Amazon Basin (Ayres and Clutton-Brock 1992). In contrast, other species, such as howler monkeys and capuchins, appear to have a better ability to disperse across these barriers, with species exhibiting relatively large geographic ranges.

Although most primates are found in the Amazon, other regions in the Neotropics contain primates. Capuchin and howler monkey species are usually found in areas of southern Mexico, Costa Rica, and eastern Brazil that tend to be more seasonally dry and contain only a small number of primate species. This suggests that these species are more ecologically flexible than other New World primates and can persist in a wide variety of habitats. In contrast to the pattern in Africa and Asia, no primates inhabit the driest, nonforested regions of the Neotropics. This coincides with the fact that there are no habitually terrestrial Neotropical primates. The lack of terrestrial adaptations in Neotropical primates may be related to their inability to successfully colonize open habitats, though this idea has not been well tested.

Asian Primates

Primates are found throughout central and southeast Asia, including the many islands of the Sunda Shelf. Asia is the only other continent except for Africa to contain both haplorrhine and strepsirrhine primates. In addition to the large geographic area, primates can be found in a diverse array of habitat types, from the rainforests of Borneo, to the cold, mountainous areas of southern China, to the cities of India.

Macaques are easily the most widely distributed primate group in Asia. The semiterrestrial nature of many species and ability to consume a variety of food types allows macaques to live in tropical regions with high species diversity, such as Thailand and Borneo, as well as harsher, more temperate environments, of northern India for example. In addition, macaques are one of the few primate taxa to successfully persist in anthropogenically modified areas, including urban spaces. Most other Asian primates require more natural habitats. Orangutans are one of these species, being found in small geographic ranges throughout the rainforests of Sumatra and Borneo. As the only great ape outside of Africa, orangutans are large primates that typically require large home ranges to find enough dietary resources. These pristine home ranges are

becoming increasingly fragmented by human-induced forest destruction, usually to clear land for palm-oil plantations (Wich et al. 2008).

Asia contains the coldest regions where primates are found in the world. The Japanese macaque is found at the most northerly latitude of any extant nonhuman primate, which unsurprisingly is an environment associated with snowfall for several months during the year. One population of Japanese macaque, living in the Chūbu region, often uses natural hot springs to maintain their body temperatures during the coldest time of the year. Another cold-weather Asian monkey is the Yunnan snub-nosed monkey. These highly endangered primates have a highly restricted geographic range bordering the Himalayan Mountains in southern China. As opposed to the macaques, the snub-nosed monkeys are a colobine monkey, having adaptations for folivory. The combination of dietary adaptations for consuming low-quality foods such as leaves and their large body size has probably contributed to their ability to survive in their harsh mountain habitats. Food is limited for long stretches of the year, with these primates subsisting primarily on lichen and tree bark.

The Sunda Shelf, comprising the islands of Indonesia and peninsula Malaysia, exhibits a diverse set of primates. Much of this diversity may be due to the historical cycles of rising and falling sea levels, which, in turn, influences the degree of connectivity among the islands (Kamilar 2009). Times of high sea levels result in increasing separation of islands and likelihood of allopatric speciation, especially for forest-dwelling primates such as gibbons and colobine monkeys. In contrast, when sea levels are low, islands can be connected, allowing species such as macaques to disperse and colonize new regions.

Conclusions

Primate distributions are a product of multiple factors, including environmental conditions and historical patterns of climate and geographic change. Besides these natural phenomena, there is an increasing need to understand how humans influence primate biogeography. This may be best illustrated in Madagascar. Anthropogenic

impacts on Madagascar are stark and have resulted in substantial loss of primate habitats since the 1960s and the extinction of numerous species in the last couple of thousand years (Godfrey et al. 1997). Humans played a critical role in the extinction of numerous “subfossil lemur” species, many of which were substantially larger in body size compared to living species. There is evidence that these large extinct lemurs were hunted by humans, which surely contributed to their eventual demise. Large species tend to reproduce slowly and require more resources than smaller species; therefore they are often more likely to go extinct. Thus understanding modern Malagasy primate diversity and biogeography is intimately tied to understanding human impacts and historical patterns and processes. This underscores the need to take an integrative approach to biogeographic research, incorporating theory, methods, and data from multiple disciplines.

SEE ALSO: Adaptive Radiation; African Colobines; Allopatry; Asian Colobines; Extinction; GPS/GIS; Guenons, Arboreal; Habitat Fragmentation; Hybridization and Hybrid Zones; Madagascar; Colonizing the Neotropics; Paleoenvironmental and Sea-Level Change; Protected Areas; Refugia; Speciation; Subfossil Lemurs; Sympatry

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