Effects of Pleistocene glaciations and rivers on the population structure of Bornean orangutans (*Pongo pygmaeus*)

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Sundaland, a tropical hotspot of biodiversity comprising Borneo and Sumatra among other islands, the Malay Peninsula, and a shallow sea, has been subject to dramatic environmental processes. Thus, it presents an ideal opportunity to investigate the role of environmental mechanisms in shaping species distribution and diversity. We investigated the population structure and underlying mechanisms of an insular endemic, the Bornean orangutan (*Pongo pygmaeus*). Phylogenetic reconstructions based on mtDNA sequences from 211 wild orangutans covering the entire range of the species indicate an unexpectedly recent common ancestor of Bornean orangutans 176 ka (95% highest posterior density, 72–322 ka), pointing to a Pleistocene refugium. High mtDNA differentiation among populations and rare haplotype sharing is consistent with a pattern of strong female philopatry. This is corroborated by isolation by distance tests, which show a significant correlation between mtDNA divergence and distance and a strong effect of rivers as barriers for female movement. Both frequency-based and Bayesian clustering analyses using as many as 25 nuclear microsatellite loci revealed a significant separation among all populations, as well as a small degree of male-mediated gene flow. This study highlights the unique effects of environmental and biological features on the evolutionary history of Bornean orangutans, a highly endangered species particularly vulnerable to future climate and anthropogenic change as an insular endemic.

Asian great ape | genetic structure | radiation | geographical barriers | sociobehavioral barriers

Environmental mechanisms are some of the most important forces affecting the evolutionary history and current distribution of species. Such mechanisms have been invoked to explain genetic structure in many temperate European and North American species but with little focus on hotspots of biodiversity and endemism in the tropics (1), where the forces underlying patterns of genetic diversity and differentiation are especially intriguing.

The tropical Asian hotspot of Sundaland is remarkable in that it has been subject to dramatic geological and environmental changes (2, 3). This now partly submerged continental shelf encompasses the Malaysian peninsula, the islands of Borneo, Sumatra, Java, and possibly Palawan (2). It is a historically dynamic tectonic area that underwent notable landmass configuration changes (3). More recently, it has been severely affected by the Pleistocene climatic oscillations (4) of the Quaternary. Changes in sea levels resulted in the cyclical exposure of the continental shelf and the formation of land bridges between the islands (4, 5), allowing for species interchange with subsequent isolation (6). Moreover, climatic fluctuations were accompanied by vegetation changes (2, 7, 8), with shifts in the range and elevational distribution of rainforests. Thus, these changes led to habitat expansions or contractions, leading to new openings or barriers to gene flow. The Pleistocene was further punctuated by intense regional climatic and habitat changes through extraordinary volcanic eruptions, especially of Mount Toba (9, 10). Finally, Sundaland contains many interesting topographical features, including rivers, lakes, and mountains (5, 11, 12), that may have acted as barriers to dispersal for a number of species, adding yet another potential allopatric force.

The roles of these environmental forces in driving biotic diversity and endemism remain underexplored, particularly in Borneo, the world's second largest tropical island as well as the easternmost Sunda region abutting the Wallace line (13, 14). Its unusually high species endemism (14–16) suggests a combination of specialized ecological niches, refugia formation, and long periods of isolation.

Among the species endemic to the island are the Bornean orangutans (*Pongo pygmaeus*). This rainforest canopy-bound species with an unusually slow life history is characterized by a rich spectrum of genetic, morphological, and cultural variation (17–19). Fossils indicate a much wider distribution of orangutans during the Pleistocene extending from Southern China and Vietnam to Java (11, 18), but orangutans are currently only found, as distinct species, in Borneo (*P. pygmaeus*) and Sumatra (*Pongo abelii*). The ancestors of orangutans therefore probably migrated from the mainland to Sumatra and from there to Borneo (12), yet it remains unclear when and how these colonization events took place.

It is also unclear how the exceptional environmental features of Sundaland, combined with the characteristic behavioral and ecological traits of orangutans, have shaped their phylogeography. For instance, isolation in refugia or through riverine barriers have been described as important forces underlying the genetic structure of some of the African great apes (20–22), yet the evolutionary history of orangutans remains unresolved. First, the high genetic differentiation between Bornean and Sumatran orangutans (17, 23) is intriguing given recurrent land bridge formation between the islands during the Pleistocene glacial periods (5). Second, within Borneo, arguments for a stable distribution since colonization (24) clash with that of a bottleneck possibly associated

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