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thesis abstract

Orang-utan genes in space and time: the impact of evolutionary processes of diversification on Bornean orang-utans

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Abstract. The evolutionary processes driving patterns of genetic diversity and differentiation, and thus speciation, are poorly understood. The aim of this thesis was to investigate the effects of environmental and biological mechanisms on gene flow and genetic diversity in the Bornean orang-utans. Specifically, I examined the effects of Pleistocene climatic changes and riverine barriers as well as sex-biased dispersal. My results suggest that current Bornean orang-utan populations are the result of a recent radiation throughout the island, following the probable confinement within a glacial refugium in the Pleistocene. Furthermore, I found evidence for an extreme pattern of female philopatry and male-biased dispersal. These processes have led to highly structured genetic diversity, rendering the orang-utans particularly vulnerable to anthropogenic effects and future climatic changes.

Keywords: glaciations, great apes, philopatry, phylogeography, population genetics

The evolutionary processes driving genetic diversity and differentiation, and thus responsible too for speciation, are not well understood and often debated (Coyne and Orr 2004). Speciation, from a genetic perspective, takes place when the genetic diversity in populations reaches fixation (Dobzhansky 1951). Various evolutionary processes operating at different levels, such as environmental and biological mechanisms, can lead to the structuring of genetic diversity among populations, and speciation. For instance, large-scale environmental factors such as climatic oscillations can result in changes that pose barriers to gene flow, or conversely, that open channels to gene flow. Biological factors characteristic of species, including generation time and breeding structure, are critical in shaping the effects of migration, selection and drift (Sugg et al. 1996, Storz 1999). Although environmental and biological factors play a major role in shaping patterns of genetic diversity and differentiation, the way they operate and interact in doing so is still an area of research requiring clarification.

A particularly exciting geographic region in which to study the impact of evolutionary processes on species diversification is Sundaland, a tropical hotspot of biodiversity and endemism.

This shallow continental shelf in Southeast Asia encompassing the Malayan peninsula and the islands of Borneo and Sumatra, Java and Palawan among others has been affected by major environmental processes including the repeated exposure and flooding of land bridges connecting the islands. These occurred through the sea level fluctuations of the Pleistocene (Bird et al. 2005). Moreover, Sundaland has a rich topography including many mountain chains, rivers and lakes. The link between the region's environmental forces and its biotic diversity and endemism is of great interest.

Some of the species endemic to Sundaland are the orang-utans (*Pongo* spp.). These endangered Asian great apes present an interesting opportunity to examine the impact of regional environmental factors, coupled with the characteristic biological traits of orang-utans, in shaping current phylogeographic and population genetic patterns. Orang-utans are characterized by slow life histories and long generation times (Delgado and Van Schaik 2000, Wich et al. 2009), as well as a strong dependence on rainforest habitat. These traits suggest high susceptibility to environmental changes. Moreover, the possible male-biased dispersal indicated by behavioural studies (Galdikas

1985, van Schaik and van Hooff 1996, Singleton and van Schaik 2002), is expected to profoundly influence population genetic structure.

My doctoral thesis addressed questions regarding the impact of evolutionary processes on orang-utans by focusing on the Bornean species. In order to first examine broad patterns of genetic diversity and differentiation throughout the island, the goal of chapter 2, I capitalized on a large genetic data set, encompassing the largest number of geographical regions and natural populations throughout the range of Bornean orang-utans investigated to date. I carried out phylogenetic and population genetic analyses based on markers with different inheritance systems: a maternally inherited mitochondrial DNA (mtDNA) marker, and up to 25 biparentally inherited nuclear microsatellite markers. The results point to a complex evolutionary history in Borneo, contesting previous suggestions of smooth continuous dispersal throughout the island (c.f. Warren et al. 2001, Arora et al. 2010). Surprisingly, the most recent common ancestor of Bornean mtDNA haplotypes was dated to 176 thousand years ago (ka; 95% highest posterior density 72-322 ka), contrasting with the circa 3 million years ago (ma) deep coalescence of Bornean and Sumatran mtDNA haplotypes. This finding indicates that Sumatran orang-utans did not contribute to Bornean mtDNA genetic diversity during the last glacial period, despite the presence of a land-bridge between the islands. In addition, the star-like topology and recent coalescence of the Bornean clade in the phylogenetic tree as well as comparisons with other rainforest species all suggest that Bornean orang-utan populations are the result of a recent expansion throughout the island from a glacial refugium. This glacial refugium was most probably a response to the contraction of their rainforest habitats, which came about through the cooling of temperatures and decrease in precipitation that occurred during the Pleistocene glaciations (Bird et al. 2005, Arora et al. 2010, Arora 2011, Chapter 1).

Despite the recent expansion of orang-utans throughout Borneo, current populations show high genetic differentiation, both at the mi-

tochondrial and at the nuclear level. By examining the relationship between genetic and geographical distances, I found evidence that Bornean rivers act as strong barriers to dispersal, particularly for females. The striking geographical clustering of mtDNA haplotypes, representative of female histories, point to limited female movement in the past, whereas the nuclear patterns suggests male-mediated gene flow. Further support for sex-biased dispersal is provided by two studies showing weak geographical structuring of orang-utan Y-chromosomal haplotypes (Nater et al. 2011, Nietlisbach et al. 2012). Thus, the mtDNA and Y-chromosome markers are congruent in suggesting broad-scale male-biased dispersal in orang-utans. But what about current patterns of dispersal and relatedness in extant populations?

To examine the issue of sex-biased dispersal, three studies have investigated the relatedness of individuals in different populations. All three studies were based on the conventional genetic method that relies on the comparison of average pairwise biparental relatedness (r) estimates of adult females and adult males obtained using biparentally inherited microsatellite markers. The results varied across studies, providing evidence for either female and male dispersal, female and male philopatry, or male-biased dispersal (Utami et al. 2002, Goossens et al. 2006, Morrogh-Bernard et al. 2010). This discrepancy left the question on sex-biased dispersal and the presence of kin structures within populations unresolved. Nonetheless, answering this question is critical to understand the dynamics affecting the structuring of population genetic diversity.

My thesis tackled the question of sex-biased dispersal, the goal of chapter 3, in a novel way: I focused on a model population where I could combine genetic, spatial and behavioural data from the largest longitudinal set of individuals to date. In addition, I examined different genetic approaches: looking at mtDNA variation, reconstructing a shallow pedigree using 24 autosomal microsatellite markers, and comparing the average relatedness estimates used in previous studies. My results showed that in agreement with a pattern of male-biased dispersal, males had sig-

nificantly higher mtDNA variation and more unique haplotypes compared to females, a finding that pointed to their more different maternal ancestries. Moreover, the pedigree reconstruction revealed three clusters of females broadly overlapping in their ranging patterns. Each of these comprised a number of mother-daughter pairs. By contrast, the males rarely had relatives at the study site. Importantly, my findings highlighted that in orang-utans and possibly other non-gregarious species where sampling is not group-based, comparing r estimates of males and females to infer sex-biased dispersal is extremely problematic. This is because the sampling regime frequently employed in non-gregarious species, combined with the overlapping space use of distinct matrilineal clusters, may lead to lower r estimates than expected for the philopatric sex. Thus, in non-gregarious species, correct inferences of dispersal require the combination of several genetic approaches with detailed spatial information (Arora 2011, Chapter 2, Arora et al. 2012).

In conclusion, through my doctoral thesis I was able to show that current orang-utan populations are generally characterized by extreme female philopatry and male-biased dispersal, which is important not only due to its effects on population structure but also on the social interactions of individuals (Noordwijk et al. 2012). Furthermore, the penultimate glaciation may have been responsible for a contraction of Bornean orang-utans within a refugium, which should have led to greater and faster genetic divergence from Sumatran orang-utans. The high genetic structuring and population differentiation resulting from these evolutionary processes make orang-utan genetic diversity especially vulnerable to anthropogenic habitat fragmentation and future climatic change (Arora 2011).

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