



Early Human Colonization, Climate Change and Megafaunal Extinction in Madagascar: The Contribution of Genetics in a Framework of Reciprocal Causations

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INTRODUCTION

The extinction of the megafauna in Madagascar and surrounding archipelagos (Seychelles, Comoro, and Mascarene islands) has been associated with evidence of ecological transformations, explained either by the increase of human activities (Hixon et al., 2018, 2021; Douglass et al., 2019; Godfrey et al., 2019; Railsback et al., 2020) or hydroclimatic shifts (Virah-Sawmy et al., 2009; Quéméré et al., 2012) or a combination of both (Salmona et al., 2017; Li et al., 2020; Teixeira et al., 2021). Whereas the Mascarenes lost their large-bodied endemic species within two centuries, in close association with human arrival (1638–1691 CE), in Madagascar the process has been estimated to be far slower, over a period of two millennia from 2,400 to 500 cal yBP (Godfrey et al., 2019). The temporal overlap of climate- and human-induced impact makes it challenging to discern primary from secondary causes (Burney et al., 2004; Crowley, 2010). Thus, any ultimate assessment would need an understanding of the phases of human occupation coupled with a finer temporal resolution of regional climate and ecological variability.

Over the last few years, the question has been addressed by contributions from a wide spectrum of disciplines, of which genetics and genomics are among the most promising (e.g., Quéméré et al., 2012; Williams et al., 2020). The results show a complex web of relationships between possible causal factors. These findings offer the opportunity to reconsider both human and climatic factors as agents that can trigger ecological outcomes through processes of direct and indirect causal chains.

THE DIALECTIC HUMAN/CLIMATIC FACTORS

The earliest dates for human activities in Madagascar span from >10,500 to 1,350 cal yBP (radiocarbon calibrated years before present) (Burney et al., 2004; Muldoon, 2010; Dewar and Richard, 2012; Anderson et al., 2018; Hansford et al., 2018; Douglass et al., 2019). There is uncertainty about the oldest evidence (bone remains of elephant birds and pygmy hippos), variously

interpreted as either butchery cutmarks or post-mortem artifacts (see Mitchell, 2019). Nonetheless, early sporadic presence of hunter/foragers in north-western and southern Madagascar cannot be definitively excluded. Artifacts more clearly associated with human activities appeared about 2,000 cal yBP (Burney et al., 2003, but see also Douglass et al., 2019; Mitchell, 2019), pointing to a more stable presence. However, the scarcity of extensive human-faunal interplay (hunting sites, butchery tools, and abundant cutmarks) and the limited number of non-native species introduced suggest a negligible ecological impact of these earlier incomers (Gommery et al., 2011).

Unambiguous evidence of a human demographic transition, driven by a massive immigration of Austronesian-speaking people from island Southeast Asia (Adelaar, 2009; Tofanelli et al., 2009; Tofanelli and Bertoincini, 2010; Cox et al., 2012; Crowther et al., 2016; Pierron et al., 2017; Anderson et al., 2018), can be reconstructed from post-1,300 cal yBP archeological remains, distributed in all the Malagasy ecoregions and the Comoros (Cox et al., 2012; Crowther et al., 2016; Anderson et al., 2018; Godfrey et al., 2019). The transition likely represented a cut-off between a regime of minimal ecological impact and a phase of intensive exploitation of natural resources due to the inclusion of Madagascar and the surrounding islands in the maritime trade network around the Indian Ocean rim.

Reconstructions of climate shifts based on speleothem and sediment analyses are consistent with these dates. The time when $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope trends decoupled is used as a proxy to disentangle anthropogenic and climate effects. Investigations of stalagmites at Anjohibe Cave in northwestern Madagascar are eloquent (Burns et al., 2016; Wang et al., 2019; Railsback et al., 2020). They suggest a rapid increase in $\delta^{13}\text{C}$ values not correlated to a simultaneous growth in $\delta^{18}\text{O}$ values from by 1,300 cal yBP. This is interpreted as a replacement of C3 forests with C4 grasslands and soil erosion possibly related to the practice of “burning horticulture,” under steady humidity conditions. In certain regional contexts, reductions in forest coverage correlate temporally with mutually related variables, such as the pace of megafauna demographic decline (Godfrey et al., 2019; Hixon et al., 2021), human population growth and the introduction of domesticated species (Joseph and Seymour, 2020).

More questionable are the possible anthropogenic causes of the faunal decline (involving among others *Palaeopropithecus*, *Archaeolemur*, *Megaladapis*, *Hadropithecus*, *Mesopropithecus*, *Pachylemur*, and *Hippopotamus* sp.) that occurred in different ecoregions a 1,000 years (2,400–1,300 yBP) before the first evidence of a stable colonization (Crowley, 2010; Anderson et al., 2018; Hansford et al., 2018; Godfrey et al., 2019; Faina et al., 2021; Hixon et al., 2021).

During the Early/Middle Holocene the Malagasy megafauna showed resilience to prolonged drought events, which changed habitats in terms of vegetation coverage and water regime (Burney et al., 2004; Quéméré et al., 2012; Wang et al., 2019). In particular, the 5,200 and 4,200 cal yBP aridity peaks are well defined in northwestern Madagascar (Wang et al., 2019). However, at no time was the entire island affected by massive natural drought, due to the antiphase between the north-west

and the central and south (Wang et al., 2019). In contrast, the Late Holocene shows the culmination of a millennial-scale drying trend with major aridity peaks between 2,000 and 500 cal yBP in different regions (Virah-Sawmy et al., 2010; Li et al., 2020). At Asafora Cave in the southwest stable carbon and oxygen isotope trends are coupled and suggest increasing CAM/C4 plant coverage and aridification between 3,320 and 880 yBP (Faina et al., 2021). Other lines of evidence support a scenario of a highly fluctuating landscape with a mosaic of grassy biomes and forested habitats at different altitudes and a diversity of endemic grass species spanning millennia (Bond et al., 2008; Vorontsova et al., 2016; Yoder et al., 2016; Samonds et al., 2019; Solofondranohatra et al., 2020; Crowley et al., 2021). This questions the dichotomy between natural and anthropogenic transformation of modern grasslands and the extent of the indirect role of humans (use of fire, introduction of domesticated species) in triggering mega-herbivore decline.

A reliable scenario should not disregard the long-standing relationships among droughts, plant communities, natural fires, and mega-herbivores (elephant birds, giant lemurs, giant tortoises, and hippopotami) that pre-dated human arrival (Samonds et al., 2019).

DISCUSSION

Speleothems and sediments are not the only source of past environmental transformations. Biological systems are intimately related to their habitats and, when investigated in appropriate contexts, they become archives of the major changes that have occurred. From this perspective, the genomes of living and subfossil animals retain signs of demographic fluctuations that may be interpreted under model-free and model-based parameters to infer either the human impact on wild fauna (Frantz et al., 2016; Pujolar et al., 2017) or the effect of climate changes on population size and structure (Kozma et al., 2018; Miller et al., 2021; Song et al., 2021).

The effective population size N_e is a key parameter in ecology and conservation biology. In one of its most widely used forms, it infers the size of an idealized population (Wright–Fisher) which, through inbreeding and/or genetic drift, underwent the same loss of genetic diversity observed in the population under study. There are many ways to genetically estimate N_e and important theoretical advances have recently been made in this field (e.g., Husemann et al., 2016; Hill and Baele, 2019). Widely used approaches test effective size declines under the statistical framework of the Coalescent Theory or the coalescent (Kingman, 1982; Wakeley, 2008). In this, the pairs of lineages of a sampled genealogy merging into an ancestral one while going backward in time (coalescence events) are compared with the expected rate of a modeled steady population: the more coalescence events, the smaller or more structured the population. Cross-disciplinary research teams have attempted to merge genetically based reconstructions of historic demography for Malagasy fauna with ecological and ethological evidence. For example, although the population size and range distribution of the extant

large lemur *Propithecus tattersalli* is decreasing today, Quéméré et al. (2012) revealed, *via* bottleneck modeling, a population collapse much older than the likely arrival of humans in their current range (northern Madagascar). Similarly, Bertoncini et al. (2017) inferred habitat shifts from the genetic diversity of a medium-sized lemur (*Eulemur collaris*) living in south-eastern Madagascar (Rakotoarisoa, 1997; Virah-Sawmy et al., 2010). Genetic estimates of N_e and mitochondrial coalescence times depict a scenario of strong demographic contraction for *Eulemur* groups now separated by extended strips of grasslands and swamps. This is in line with an original condition of mixed woodland forest and a rapid transition to an open habitat dominated by ericoid grassland driven by marine surges before 700–1,500 cal yBP (Virah-Sawmy et al., 2009, 2010). Other studies detected recent bottlenecks in species from different regions over the island with a population decrease of approximately two orders of magnitude that occurred in the last millennium both in small nocturnal lemurs (*Lepilemur edwardsi*: Craul et al., 2008; *Microcebus ravelobensis*: Olivieri et al., 2007; *Microcebus murinus* and *Microcebus ravelobensis*: Teixeira et al., 2021) and larger diurnal lemurs (*Lemur catta*: Parga et al., 2012; *Propithecus verreauxi*: Lawler, 2008; *Propithecus perrieri* and *Propithecus tattersalli*, Salmons et al., 2017). Taken together, such studies depict more complex relationships between the candidate factors of faunal demise.

Given the endangered status of the Malagasy living fauna (Schwitzer et al., 2014), which makes non-invasive sampling a common practice, and the low quality of DNA from fossil remains (e.g., Dabney et al., 2013), approaches that maximize the reconstruction of demographic profiles from few low-coverage genomes are a priority. Methods combining hidden Markovian chains and the coalescent (PSMC, Pairwise Sequentially Li and Durbin, 2011; MSMC, Multiple Sequentially Markovian Coalescent, Schiffels and Durbin, 2014) allow millennial time-series of population size/structure fluctuations to be obtained to support evidence of past ecological shifts even from a single specimen (Stoneking, 2017). Ideally, the graphs based on the Markovian coalescent approaches represent more exhaustive indicators of extinction dynamics than the extent of the skeletal record.

To date PSMC has been applied to whole genomic data from hibernating dwarf lemurs (*Cheirogaleus medius*, *C. major*, *C. crossleyi*, and *C. sibreei*, Williams et al., 2020) and mouse lemurs (*Microcebus murinus*, *M. ravelobensis*, Teixeira et al., 2021). In the former study, evidence for a slow decline in the last 50,000 years, long before the arrival of any human beings on the island, was found. Long-term reductions in N_e and low heterozygosity may have heavily affected the survival of dwarf lemurs due to inbreeding depression, namely the expression of detrimental genes or the scanty diversity across immune genes (Morris et al., 2015; Rogers and Slatkin, 2017). Interestingly, a less fluctuating N_e was estimated in the genome of *C. sibreei*, the only species adapted to high-altitude habitats, consistent with the paleoecological evidence of more stable habitats in the Central Highlands

(Wilmé et al., 2006; Samonds et al., 2019). It can be argued that climatic pulsing exerted more extreme demographic consequences on low-altitude species, which likely experienced greater levels of habitat fragmentation, vegetation shifts, cyclones, and marine transgressions/tsunami. These climatic shifts have been hypothesized to be frequent during the Quaternary and used to explain the remarkable process of speciation on the island (Wilmé et al., 2006).

CONCLUSION

Whether humans or climatic shifts are the primary source that triggered the megafaunal extinction in Madagascar is still highly questioned. There is general convergence upon the fundamental role that the demographic growth of Austronesian colonizers and their introduction of subsistence agriculture had played in the over-exploitation of natural resources by around 1,300 yBP (e.g., Crowther et al., 2016; Anderson et al., 2018; Godfrey et al., 2019). There is also growing evidence of complex climate-driven shifts in geological and biological archives that suggests a move away from the narrative of human/climate duality and toward a paradigm of mutual rather than distinct causality (Salmons et al., 2017; Li et al., 2020). To further complicate the picture, the relative contribution of multiple drivers of change appears to vary among the regions of the island depending on the local climate, the faunal/vegetational assemblages and the pattern of human settlement (e.g., Virah-Sawmy et al., 2010; Yoder et al., 2016; Wang et al., 2019; Railsback et al., 2020; Teixeira et al., 2021). We hope that an increase in cross-disciplinary research will help to clarify whether historical human colonization of Madagascar and neighboring archipelagos were facilitated by a long-term biotic stress experienced by endemic megafauna. From this perspective, genomes of both living and extinct taxa, at either individual or population level, need to be explored more extensively as repositories of past demographic trends closely associated with changing ecosystems.

AUTHOR CONTRIBUTIONS

ST wrote the manuscript. SB and GD contributed to the interpretation and the revision of the work. All authors contributed to the article and approved the submitted version.

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