

Baobab trees' evolutionary history could inform conservation efforts

The genomes of all eight living species of baobab tree (*Adansonia* sp.) reveal the group's origin and diversification history. Ecological analyses were incorporated to characterize the baobabs' past population dynamics and were used to propose protection measures for these iconic species, including the reassessment of their conservation status and the close monitoring of several of Madagascar's baobab species.

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The problem

Nobody travelling through the regions where baobab trees (*Adansonia*) grow can ignore the enormous and grotesque trees that dominate the landscape. These trees are known as 'the mother of the forest' for their intimate connections with various animal species¹. Of the eight living species, six are found on the island of Madagascar, one on the African continent and one in northwestern Australia (Fig. 1a). Typically, taxa distributed across continents and islands are thought to have continental origins². However, the much higher diversification of baobabs on Madagascar suggests that they might have originated there. According to an alternative, 'vicariance' hypothesis³, baobabs originated on the ancient supercontinent Gondwana, and evolved separately after it broke up. Thus, understanding where baobabs originated and how they diversified is of fundamental interest. All the baobabs on Madagascar are threatened by habitat loss and climate change, and these Malagasy species are declining continuously. An improved understanding of baobab genetics could help to inform conservation strategies.

The discovery

We generated whole-genome data for all eight baobab species, using samples from wild trees in Madagascar, Senegal and Australia. Using these data, we reconstructed the trees' evolutionary relationships. We found and dated historical periods during which genetic material was shared between species – a process known as interspecific hybridization. We conducted ecological analyses in which palaeogeographical events, such as volcanic activity and local sea-level fluctuations, had been integrated to establish the baobabs' past and current demography and distribution patterns.

We infer that the *Adansonia* genus diverged into *Adansonia digitata* (found in Africa), *Adansonia gregorii* (found in Australia) and an ancestral Malagasy lineage around 21.6 million years ago (Ma), and that the Malagasy baobabs diversified later, about 20.1 Ma. These timings are long after the break-up of Gondwana, which occurred about 160 Ma (ref. 3), thus challenging the vicariance hypothesis. Several DNA fragments showed distinct evolutionary patterns between species, suggesting that interspecific hybridization has occurred in the past, ancestral variants have been retained or both. Indeed, we saw evidence of several instances of such gene exchange between Malagasy baobabs

and *A. gregorii* or *A. digitata*, indicating that the three lineages coexisted at some point. We also detected extensive flow of genetic material between Malagasy species. The past population dynamics of Malagasy baobabs were influenced mainly by competition between species and by the geological conditions, especially local sea levels. The two endangered species, *Adansonia suarezensis* and *Adansonia grandidieri*, are characterized by distinctive ecological niches, high levels of inbreeding, a low tolerance for environmental change and a continuous decline in the number of reproductive individuals. We also found evidence that the hybridization of *Adansonia za* with *Adansonia perrieri* increases the latter species' risk of extinction.

The implications

The sharing of genetic material between the three main lineages suggests that extant baobabs originated on Madagascar. According to our reconstruction of baobab history, the progenitor of *A. digitata* dispersed from Madagascar to Africa, and *A. gregorii* arrived in Australia across the ocean (Fig. 1b). The Malagasy baobabs diversified through interspecific hybridization and competition, in the face of extreme geographical events. We propose reconsidering the conservation status of *A. suarezensis* and *A. grandidieri* and we raise concerns about the negative effects of *A. za* on populations of other Malagasy baobabs.

It remains unclear how *Adansonia*'s ancestor arrived on Madagascar, given that all its closest living relatives are found in South and Central America⁴. Reliable fossils of the Adansonieae tribe would help to resolve this question. Moreover, broad sampling would help researchers to understand how the African species *A. digitata*, which has four sets of chromosomes, replaced its progenitors with two sets of chromosomes and conquered the continent.

We aim to focus on the population genetics of baobabs that overlap in distribution and flowering time with *A. za*, to evaluate this species' potential negative effects on the others. Further studies on the genetic consequences of local geographical isolation and interspecific hybridization of Malagasy baobabs could help to highlight their diversity, as well as the extraordinary biodiversity of Madagascar⁵.

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FIGURE

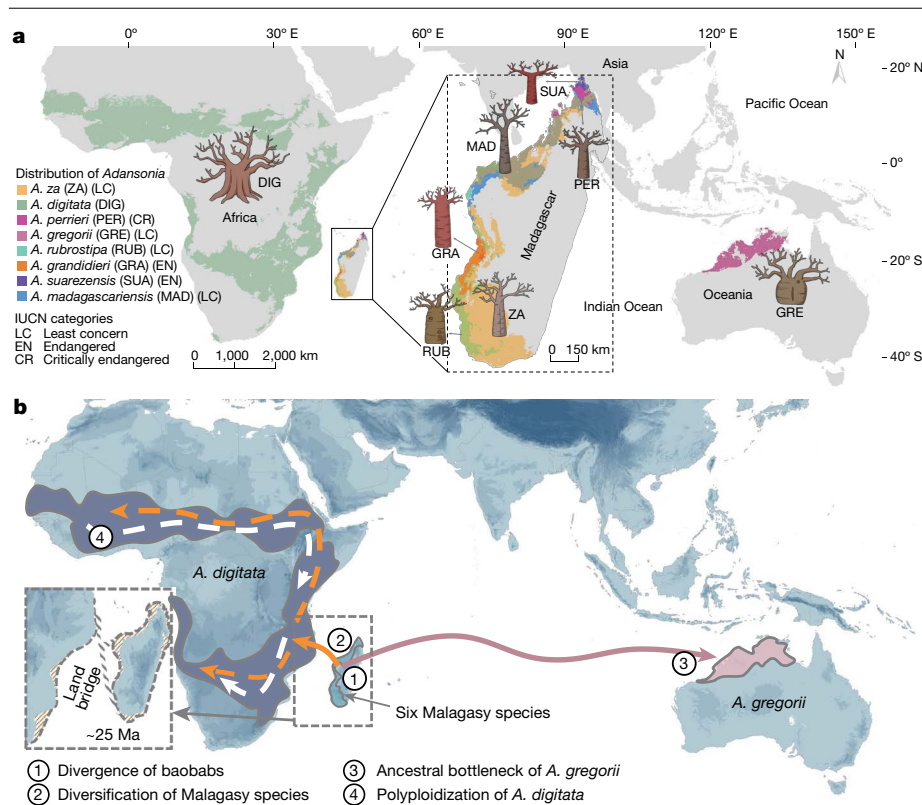


Figure 1 | The geographical distribution of baobab trees and their evolutionary history.

a, The distribution of the eight living *Adansonia* species and their conservation status according to the International Union for Conservation of Nature. Coloured areas show the occurrence of each species.

b, Key inferred evolutionary events and the proposed dispersal routes of *Adansonia digitata* and *Adansonia gregorii*. Polyploidization refers to the occurrence of more than two sets of chromosomes. Orange arrows, dispersal routes of *A. digitata* progenitors with two sets of chromosomes; white arrow, *A. digitata* migration after polyploidization; pink arrow, dispersal of *A. gregorii*. Inset, the probable land bridge that once linked Africa and Madagascar. Wan, J.-N. *et al.* *Nature* (CC BY 4.0).

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BEHIND THE PAPER

This project was initially launched with limited funds, and aimed to provide a small-scale *in situ* survey of baobab populations. After two years of field investigation and rounds of discussion with local botanists and research institutes, we realized that effective and biologically informed conservation strategies are urgently needed for baobabs, especially the Malagasy species. In 2020, our team managed to gain support from the Sino-Africa Joint Research Center at the Chinese Academy of Sciences, an international collaborative institute devoted to the conservation of African biodiversity. This

project was then able to grow into a highly collaborative effort, involving 11 institutes and more than 30 scientists, who have expertise in diverse fields, including genomics, ecology, evolutionary biology and palaeogeography. Improved conservation measures are needed to protect baobab trees, and such policies will benefit from interdisciplinary approaches and strong international collaborations. Only through such combined efforts shall we see the resurgence of Madagascar's baobab populations.

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FROM THE EDITOR

Baobabs comprise a genus of iconic trees for which high-quality reference genomes have been missing so far. In this study, the genomes of all members of the genus were assembled. In addition to answering questions about the evolutionary history of these trees, the paper also presents important data on the genetic diversity of baobabs, leading the authors to make recommendations regarding the conservation status of several baobab species.

Michelle Trenkmann, Senior Editor, *Nature*