

# Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region

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**The impact of climate change and anthropogenic deforestation on biodiversity is of growing concern worldwide. Disentangling how past anthropogenic and natural factors contributed to current biome distribution is thus a crucial issue to understand their complex interactions on wider time scales and to improve predictions and conservation strategies. This is particularly important in biodiversity hotspots, such as Madagascar, dominated by large open habitats whose origins are increasingly debated. Although a dominant narrative argues that Madagascar was originally entirely covered by woodlands, which were destroyed by humans, a number of recent studies have suggested that past climatic fluctuations played a major role in shaping current biome distributions well before humans arrived. Here, we address the question of the origin of open habitats in the Daraina region in northern Madagascar, using a multiproxy approach combining population genetics modeling and remote-sensing analyses. We show that (i) contrary to most regions of Madagascar, the forest cover in Daraina remained remarkably stable over the past 60 y, and (ii) the golden-crowned sifaka (*Propithecus tattersalli*), a forest-dwelling lemur, underwent a strong population contraction before the arrival of the first humans, hence excluding an anthropogenic cause. Prehuman Holocene droughts may have led to a significant increase of grasslands and a reduction in the species' habitat. This contradicts the prevailing narrative that land cover changes are necessarily anthropogenic in Madagascar but does not preclude the later role played by humans in other regions in which recent lemur bottlenecks have been observed.**

habitat loss | primate | population bottleneck | coalescent

Over the past decades, loss and fragmentation of tropical forests have greatly increased at a global scale. Their impact on climate and biodiversity are of growing concern worldwide (1–4). Deforestation alone has been estimated to be the third most important source of carbon emissions, accounting for some 18–20% of global emissions (5). Madagascar is considered as one of the “hottest” biodiversity hotspots because of its high level of endemism and species richness (3, 6). The island is also reputed to be one of the most degraded tropical landscapes on Earth. Given that probably more than 90% of the Malagasy animal species live exclusively in forests and woodlands (7), the consequences of deforestation on biodiversity will be disastrous. Indeed, a recent study estimated that deforestation alone caused the loss of 9% of Malagasy species between 1950 and 2000 (8).

Human pauperization, economic activities, and population growth are thought to be the main causes for the degradation of natural habitats in Madagascar. In particular, the supposed great increase in deforestation rates over the past century is thought to have resulted from both the rapid population growth, from less than 3 million in 1900 (9) to 20.7 million in 2011 (10), and the use of fire for slash and burn cultivation (*tavy*) and cattle raising (11, 12). For instance, it has been estimated that during the past 50 y, 50–53% of the evergreen forests from eastern Madagascar

(13, 14) and 40% of the western deciduous forests have been cut down (14). Today, open habitats dominate vast areas in the center, west, and north of Madagascar, covering 80–84% of the island surface (14, 15). Colonial botanists (16, 17) who described Malagasy flora thought that Madagascar was a land entirely covered by woodlands when humans arrived and that the first humans were responsible for most of the deforestation across the island. However, earlier naturalists and travelers, such as Grandidier (18) or Gautier (19), defended a different view, namely, that the lack of forest in some regions was natural. Despite this early controversy, the “island-wide forest” hypothesis assuming the anthropogenic origin of grassy biomes remained pervasive during the 20th century (20–23) and continues to be largely used to justify conservation fundraising and management actions (24).

However, in the past few years, the question of the antiquity of these grassy biomes has become the center of a renewed controversy (15, 24–27). Indeed, a number of palynological and biogeographical records from various bioclimatic zones in Madagascar (27–32) have provided a mounting body of evidence suggesting that significant parts of the island may have been covered by a mosaic of forests, scrublands, and grasslands well before the earliest human settlements started to be demographically significant (i.e., 1,000 y ago) (11) and even before the earliest evidence of human arrival 2300 calibrated calendar years before present (Cal. YBP) (29). Directly related to this controversy, there is a hot debate over climatic vs. human causation (or both) of giant lemur and associated megafaunal extinction. Indeed, an increasing body of data has shown that intense hunting probably played a major role in the final demise of large-bodied mammals in Madagascar and elsewhere (29, 33–35). The elimination or reduction of this megafauna then contributed to major changes in fire regime (30) and the impoverishment of habitat diversity previously maintained by large seed dispersers (36–38). This “prehistoric overkill” scenario is well supported in regions like tropical Australia (39) or New Zealand (40), where megafaunal extinction occurred at a time of only slight climate and vegetation change. However, in Madagascar, the situation is less clear because most major climatic events of the late quaternary (i.e., droughts lasting millennia) (27, 31) predated human arrival. Also, the peopling of Madagascar was very uneven from the start, and different regions may thus exhibit different patterns and histories (11). We cannot therefore exclude that prehuman climate change triggered the shrinkage of forest habitats and the collapse of associated fauna as has been shown in other parts of the world (41–43). One way of addressing these issues is to determine whether species from different regions have been

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submitted to different demographic histories with different time depths. Indeed, the genome retains the specific signature of major events, such as recent contractions (44, 45) or ancient expansions (46). Reconstructing the demographic history of extant species may thus help to investigate how climate change and anthropogenic impact affected the dynamic of their habitat (42, 47).

In this study, we address one of the long-lasting and controversial questions of conservation biology, namely, the relative contributions of past anthropogenic and natural factors on the degradation of tropical ecosystems. We use an innovative multiproxy approach combining genetic, paleoclimatic, and remote-sensing data to question the origin and age of large open habitats in the region of Daraina in the north of Madagascar (Sava region). Forest habitat in this area corresponds to highly diversified forest fragments surrounded by a matrix of large grasslands and savannas. To assess the importance and dynamics of deforestation in the Daraina region, we combined aerial photography and satellite imagery to examine trends in forest cover change in the past 50 y, and thus to assess the importance of recent anthropogenic deforestation in Daraina compared with other regions (i.e., during the period of highest human density and impact). The genetic data were used to reconstruct the demographic history of the golden-crowned sifaka (*Propithecus tattersalli*), an endangered species of forest-dwelling lemur now restricted to the small region of Daraina, as a proxy for major changes in forest cover. Specifically, we tested the four following hypotheses: (H1) Open habitats in Daraina are recent and attributable to deforestation and human demographic growth since the first contact with Europeans (time period 1500–2000 A.D.), (H2) these open habitats are anthropogenic and dated from the first centuries of human settlement in the Daraina region (1000–1500 A.D.), (H3) open habitats were human-induced and dated from the first millennium of human presence on the island (2300–1000 Cal. YBP), and (H4) open habitats are mainly natural and expanded in relation to Holocene climatic fluctuations in prehuman times (10,000–2300 Cal. YBP).

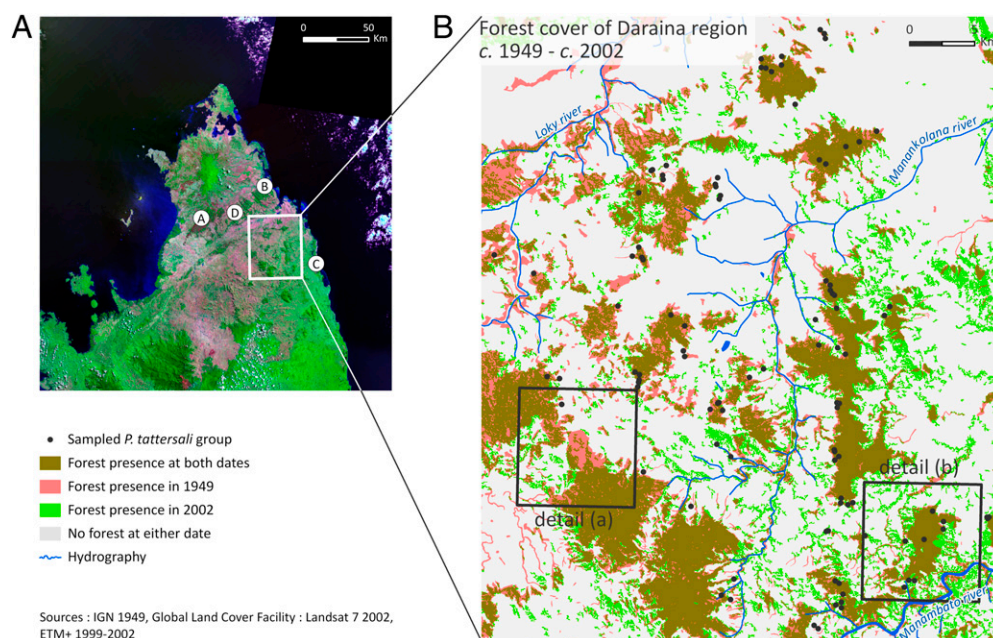
Our results show that (i) the forest cover in the Daraina region has remained remarkably stable over the past 50 y, exhibiting very low rates of deforestation in comparison to other regions; (ii) the golden-crowned sifaka genetic data exhibit a clear and robust signal of a population contraction; (iii) the dating of this collapse is anterior to the arrival of the first humans, thus excluding an anthropogenic cause (hypothesis H1, H2, or H3); (iv) the population contraction was most likely induced by climatic events, such as late prehuman Holocene droughts leading to significant shifts in

vegetation in northern Madagascar and modification in *P. tattersalli*'s habitat and resource availability; and (v) in this region, most present-day open habitats are not attributable to recent human activities but most likely originated from climate changes occurring several millennia ago. These results suggest that a reappraisal of the representation of the impact of local communities on their environment may be necessary among conservation biologists.

## Results

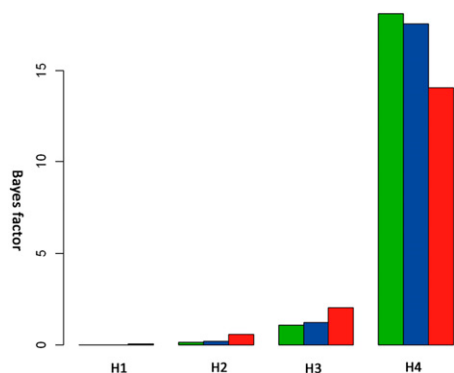
**Trends in Forest Cover Change in the Daraina Region.** For the recent period (1949–2002), diachronic analyses of different image sources and maps (Landsat images taken in 1972, 1994, and 2002; 1/100,000 topographical map, 1960; aerial photography, 1949) show a relative global stability of the forest cover surface in the distribution area of *P. tattersalli* (Fig. 1). In most cases, the main forest blocks have kept their integrity, and even seem to have grown, but the situation is locally contrasted. Deforestation dominates on the western part of the area, whereas forest progressed on wide sections of the east and southeast. Because of these opposite dynamics and the differences in the spatial and spectral resolutions of the sensors and data sources, quantifying the global forest evolution of the region or a fragmentation index would be hazardous. However, field investigations (i.e., interviews of old farmers) and a focus on two zones (Fig. S1) confirm this two-way evolution. The driest semideciduous forest of the northwestern part of the region has been affected by a progressive deforestation, particularly on the western hillsides, whereas the eastern massifs not only appear intact but significantly progressed during the period.

**Demographic History of Endemic Golden-Crowned Sifakas.** We found evidence of a population collapse for all *P. tattersalli* samples across all forest fragments (Fig. S2A and B). The signal was robust to the sampling strategies and subpopulations considered (Fig. S3). Across the different analyses, we found that the effective population size of *P. tattersalli* decreased by one to two orders of magnitude (Fig. S2B) from an ancestral population  $N_I$  with a median ranging from 21,715–30,915 to a present-day effective population size  $N_0$  with a median between 430 and 795 (depending on the genetic unit analyzed:  $K_A$ ,  $K_B$ , or the global sample). The posterior distribution of  $T$ , the time when the population started to decrease, exhibited median values that were older than the arrival of humans in Madagascar, with medians ranging from 7,183 to 7,567 Cal. YBP among samples (assuming a generation time of 6 y) (Fig. S2C). The Bayesian



**Fig. 1.** Trends in forest cover change in the Daraina region between 1949 and 2002. (A) Circled letters on the satellite imagery of the north of Madagascar indicate the locations of the four places named in the main text and in Fig. 4: Ankarana massif (A), Irodo (B), Vohémar (C), and Andavakoera (D). (B) Black dots on the map of the Daraina region show the sampling locations of the 105 *P. tattersalli* social groups genotyped. This figure shows that trends in forest cover change radically in the northwestern (deforestation) and southeastern (forest regeneration) parts of the region as exemplified by the two focus zones [detail (a) and detail (b)] for the periods 1949–1972, 1972–1994, and 1994–2002. The two focus zones are detailed in [Fig. S1](#).





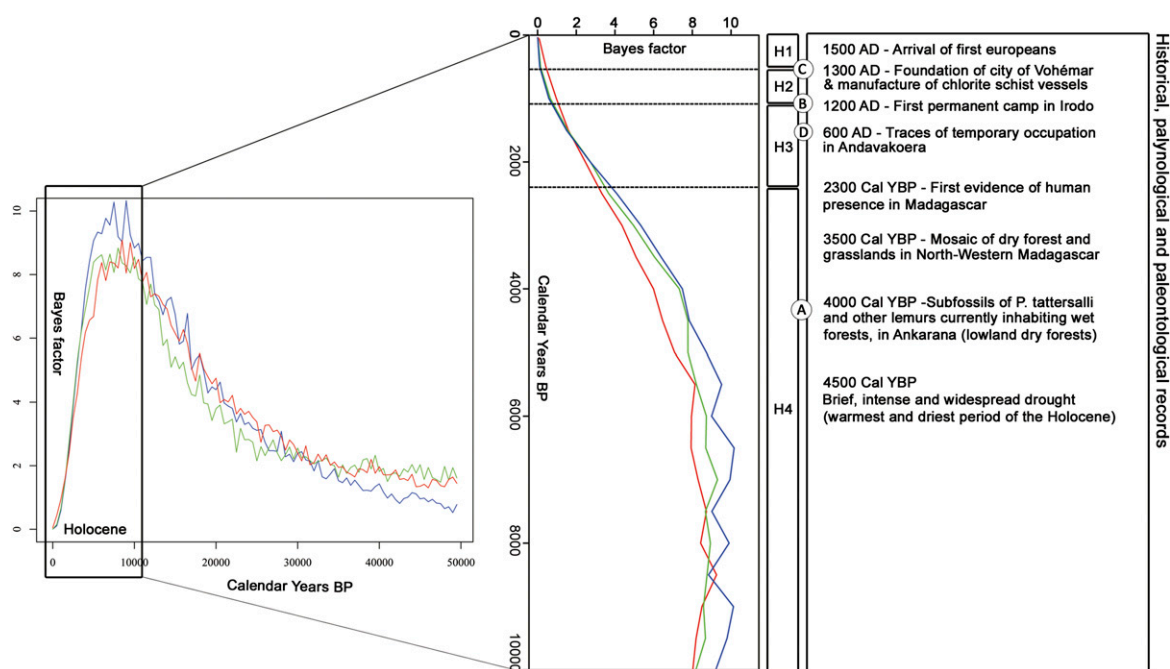
**Fig. 2.** BF values for the four tested scenarios under the different sampling schemes. H1 corresponds to a contraction attributable to anthropogenic effects following the arrival of Europeans (0–500 Cal. YBP); H2 (500–1,000 Cal. YBP) corresponds to a contraction attributable to anthropogenic effects during the period for which first cities appeared in far northern Madagascar; H3 (1,000–2,000 Cal. YBP) corresponds to the first millennium of human presence, during which human densities were probably very low; and H4 (2,000–10,000 Cal. YBP) corresponds to a contraction caused by environmental factors before the arrival of humans in Madagascar. In the “global sample” analyses (green), samples were taken across the whole sampled area, ignoring any substructure identified in a previous study. In the  $K_A$  (red) and  $K_B$  (blue) analyses, the samples were taken only considering the  $K_A$  and  $K_B$  genetic clusters identified in a previous study (details are provided in *Materials and Methods*).

method that we utilized uses lognormal priors for  $T$ , which may favor recent over ancient times. The Bayes factor (BF) analysis, which uses ratios of posteriors over priors for comparing competing hypotheses, allows one to circumvent this potential problem. The BF analysis (Fig. 2) clearly favored the fourth scenario with extremely high values (H4,  $BF > 14$ –19) over the

other scenarios that assumed an anthropogenic cause for the contraction of *P. tattersalli* populations ( $1 < BF < 3$ ). The BF analysis was robust to changes in generation length, even when we used an unrealistically low value of 3 y (H4,  $BF > 18$ ) (Table S1), hence indicating that golden-crowned sifaka populations contracted before humans arrived on the island. Furthermore, the same pattern of results was obtained when we computed BFs for equal length time periods of 500 y between the present and 50,000 y ago (Fig. 3A) or 10,000 y ago (Fig. 3B). The highest BF values ( $BF > 9$ ) correspond to a time period ranging from 5,500–10,000 y ago, whereas the lowest values were observed for the last couple of millennia ( $BF < 2$ ).

## Discussion

During the past centuries, industrialized agriculture, forestry, and rapid urban and rural population growth have led to the global homogenization of landscapes at the continent scale and to the mass extinction of thousands of species worldwide (1, 48). The suddenness and extent of these changes have led several authors to identify this extremely short period as the Anthropocene. We cannot ignore the major impacts of humans on natural ecosystems (39, 49, 50). Indeed, there is an ample fossil record illustrating the preponderant role of human hunting on the extinction of native megafauna in Madagascar (30, 33) and other parts of the world (51). Furthermore, it is now generally accepted that megafaunal extinction triggered a large change in fire regime, affecting the structure, composition, and dynamics of plant communities and favoring more dense, uniform, and impoverished formations (30, 38, 39). However, the millennia preceding the Anthropocene should not be neglected either. Indeed, increasing data are pointing to the late Pleistocene and the Holocene as major “reshuffling” periods during which many species saw their ranges contract or shift, whereas others conquered new territories (52–54). Late Quaternary climate changes thus contributed to the extinction of large-bodied species (42, 55) both in temperate (56, 57) and tropical regions, including Madagascar (58–60).



**Fig. 3.** Most likely period for the start of the population decrease. This figure shows the value of the BF for fixed-length intervals of 500 y between 0 and 50,000 y ago and between 0 and 10,000 y ago (i.e., the Holocene period). The BF measures the weight of evidence for the hypothesis that the population started to decrease in a given interval ( $H_A$ ) vs. any other time period ( $H_B$ ). The different solid lines correspond to different sampling strategies described in *Materials and Methods*: red (genetic unit  $K_A$ ), blue (genetic unit  $K_B$ ), and green (global sample).  $BF = 1$  indicates that  $H_A$  and  $H_B$  are equally likely. BF values greater (or smaller) than 1 support  $H_A$  (or  $H_B$ ). We considered BF values  $> 7$  as significant evidence for  $H_A$ . We indicated, along the time frame, the intervals corresponding to the four tested scenarios (H1–H4) and the historical, palynological, and paleontological evidence discussed in the main text.

In this study, we add several independent pieces to the puzzle of the present location and paleodistribution of *P. tattersalli* and shed light on the origin of their habitat loss and fragmentation. Our genetic data and corresponding Bayesian analyses suggest that the golden-crowned sifaka underwent a drastic contraction during the Holocene, most likely between 5,500 and 10,000 y ago. This event certainly took place well before the earliest evidence of human presence in Madagascar (2300 Cal. YBP), which is itself earlier than the first traces left by humans on their environment, around 1,000 y ago (11). The reduction of *P. tattersalli*'s range and population size is most likely attributable to climatic fluctuations (31, 61–63). Several widespread and pronounced droughts have been documented during the Holocene in Madagascar (27) and in eastern Africa (54, 64). For instance Virah-Sawmy et al. (27) documented how an open woodland transformed into a grassland between 5,800 and 5,200 y ago in southern Madagascar. The same drought probably caused similar shifts from humid and continuous woodland forests to savanna-type habitats in many regions of the island, including the Daraina region. MacPhee et al. (63) and Matsumoto and Burney (32) also suggested that grasslands were already common in the “dry deciduous forest” ecoregion of the western coast well before any evidence of anthropogenic deforestation. Several recent studies have also argued for the relative antiquity of western grasslands on the basis of the large diversity of  $C_4$  grass lineages and the presence of plant and animal species endemic to Malagasy grassy biomes (15, 65).

Our remote-sensing analyses showed that in the Daraina region, the forest cover remained remarkably stable during the past 60 y, exhibiting a very low rate of deforestation in comparison to other regions (66). Indeed, deforestation has been only observed at very local scales and was counterbalanced by the numerous areas where regrowth occurred. This may appear surprising compared with common narratives and most scientific papers (13, 14), but a wide majority of studies on the evolution of Madagascar forests only considered the disappearance of a supposed pristine and static forest. This one-way analysis omits to consider the possible forest regeneration and the forest as a living and complex ecosystem that is not necessarily destroyed by human activities (24, 25). This is not an isolated case in Madagascar, and some recent studies also point to a possible forest resilience to (human or natural) disturbances and even forest regeneration (67, 68). This unexpected small change in forest cover during the period of highest population density is yet another argument suggesting that human impact was probably limited during the period of human occupation and that present-day open habitats are, in some regions at least, the result of ancient climatic changes. Nevertheless conservation management seems to find it hard to accept or even take into account this point of view, even though evidence of the ancientness of Madagascar's grassy and savannah lands is increasingly well-documented (15, 28, 32, 69).

As a result of differences in preservation potential across regions and research efforts, the paleontological data are not equally distributed across Madagascar (70). Subfossil localities are rare in the north of the island and provide limited information on the past distribution of extant species. However, subfossils of *Haplemur simus* (dated to  $4,560 \pm 70$  Cal. YBP) (71) and *Indri indri* (dated to  $4,400 \pm 60$  Cal. YBP) (72), two lemur species currently living exclusively in limited areas of the eastern evergreen humid forests of Madagascar, have been found in the Ankarana massif cave system, just northwest of the Daraina region (Fig. 1A). This suggests that the paleodistribution of these two species extended considerably beyond their present range. On the basis of these data alone, we cannot establish the timing and cause of their range contraction; however, we can assume a role of climate aridification because the Ankarana massif is now classified among the driest regions of the island (71–73). Interestingly, despite a poor fossil record, bones attributed to *P. tattersalli* were also found in the Ankarana cave system (72, 73), suggesting that the paleodistribution of the golden-crowned sifaka was also much wider than today. The hypothesis that *P. tattersalli* saw its distribution contract as a result of climatic rather than anthropogenic changes is also supported by phylogeographic data. Indeed, *P. tattersalli* has

a disjunct and restricted distribution in the northeastern part of the island far removed from the northern limit of its sister species, *Propithecus coquereli*. Unlike *P. tattersalli*, *P. coquereli*, like the other related species *Propithecus deckeni*, *Propithecus coronatus*, and *Propithecus verreauxi*, present wide, parapatric, and contiguous ranges along the west coast (74) (Fig. S4). An ancient contraction of *P. tattersalli* would thus explain both fossil and present-day distribution data.

Another set of arguments against a major human impact on *P. tattersalli*'s forest habitat comes from the available data on human occupation records in northern Madagascar. These data indicate that until the late 19th century, human populations were sparsely distributed in the north, with primarily fishermen and pastoralists occupying small coastal villages (11). Clear evidence of permanent occupation was detected only in the 12th century in Irodo (11, 75) (Fig. 1A). Furthermore, the largest city of the region, Vohémar (Fig. 1A), only appeared around 1350 A.D. (75). It was known to Europeans in the 16th century but was largely abandoned by the late 1700s (11). At the end of the 19th century, the total population was less than 1,800 (76). Today, the area remains poorly inhabited, with fewer than 30,000 people and a density of less than 12 individuals per square kilometer ( $\text{ind}/\text{km}^2$ ) (77) compared with an average of 33  $\text{ind}/\text{km}^2$  across Madagascar and above 60  $\text{ind}/\text{km}^2$  in the central highlands (78), where forests are absent to a large extent. Local Daraina populations primarily depend on subsistence economy dominated by shifting and irrigated agriculture, cattle raising, extraction of forest products, and fishing (77, 79).

## Conclusion

There is no doubt that deforestation has been a major phenomenon during the past century in many regions of Madagascar (14, 66) and that humans played a major role in driving numerous species to extinction since they arrived in Madagascar. This is particularly true for the megafauna. However, our work contradicts the prevailing narrative that land cover changes are necessarily anthropogenically induced and negative across the whole island. Indeed, even if *P. tattersalli*'s population size and range were decreasing today, the genetic data appear to keep memory of a much older event or series of events, in which humans cannot have played a role. This result does not necessarily hold across all of Madagascar. For instance, one of us (L.C.) has contributed to the demonstration that severe and very recent population declines affected mouse lemurs [*Microcebus* spp. (45)] and sportive lemurs [*Lepilemur* spp. (44)] from the northwest of Madagascar, where habitat loss has been massive in the past century (32). Similarly Lawler (80) concluded that *P. verreauxi* also suffered from a bottleneck less than 2,000 y ago in the southwest of Madagascar, again, a region where human impact and deforestation are more serious than in Daraina (14). Similar results have also been suggested for other primates [orangutans (81) and howler monkeys (82)]. In all these species [detection of a more ancient population size change is discussed elsewhere (46, 47)], the population bottleneck has been reasonably attributed to recent human-driven changes.

Overall, the patterns of extinction of the world's terrestrial megafauna are best explained by models combining human arrival and climatic variables (35, 41–43). However, the relative contribution of both factors appears to vary strongly among regions (53, 83–85) in relation to the velocity of climate changes (55, 86) and the pattern of human settlement and activities (35, 39). Furthermore, each species appears to respond differently to the effects of climate change, habitat redistribution, and human encroachment (42, 87) in relation to their taxonomic group (85) as well as their body size and ecological traits (53, 83). In the case of *P. tattersalli*, we did not detect recent population collapse, probably because this species is protected by a local taboo (*fady*) and is not normally hunted. However, our aim here is not to be overly optimistic. The species range is among the most restricted of any lemurs (74), and the recent political crisis that began in 2009 has led to the increase of poaching by people originating from other regions that do not have the same *fady*s. The whole Daraina region may also be strongly affected in the near future by the pending tarring of the main road bisecting the

species range. However, it is important that conservation actions, particularly from international institutions that cannot always account for regional differences, should not consider human proximity only as a threat and should not base their action on diagnoses pointing to environmental degradation by traditional land management because we saw that forest regeneration occurred in a context of human occupation. It seems risky to alienate the local communities by excluding them from their territories (88), whereas they can be precious allies to help conservationists find adapted local answers for sustainable natural resources management.

Our study calls for more regional and comparative studies that will help reconcile paleontological, genetic, and potentially geological data. More work is also needed to apprehend the history of regions that have experienced various composite histories in term of landscape transformation, human activities, and cultural attitudes toward their environment (11, 84). Multidisciplinary approaches that integrate information from genetic, paleoclimatic, biogeographic, and remote-sensing data, together with contributions from anthropology, sociology, and political sciences to clarify the relative contributions of human and natural factors on the past and ongoing environmental changes, are urgently needed in the face of major changes to come.

## Materials and Methods

A short version of the materials and methods used in this study is provided in this section. Details are provided in *SI Materials and Methods*.

**Golden-Crowned Sifaka (*P. tattersalli*).** The golden-crowned sifaka (89) is a medium-sized endangered lemur species only found in the Daraina region, located between the Loky and the Manambato Rivers on the northeastern coast of the SAVA region. Its geographic range is highly fragmented and one of the most restricted of any lemurs (74, 90).

**Analysis of Forest Cover Changes in the Daraina Region During the Period 1949–2002.** To analyze the recent trends in forest changes in the Daraina region, we first used three Landsat images taken in 1972 (November 9), 1994 (September 2), and 2002 (May 27). Supervised classification was performed on three bands (Normalized Difference Vegetation Index, Green, and Near Infra-Red) on each scene using the ENVI algorithm Support Vector Machine (ITT). Classifications were validated using field knowledge and very high-resolution data for part of the area (SPOT imagery, QuickBird Imagery from GoogleEarth). Additionally, we used the topographical maps from Foiben-Taosarintanin'i Madagasikara (FTM, Malagasy Geographical Institute) based on aerial images from 1949 to analyze the trends in forest cover changes for the period 1949–1972. These maps were georeferenced, and their forest zones were manually digitized. No information was available on the methods used by the FTM to create topographical maps from aerial images. We thus interpret the results of this latter analysis with caution and by considering the global patterns of change across these two dates qualitatively rather than quantitatively.

***P. tattersalli* Sample Collection and DNA Analysis.** Fecal material from 292 putative individuals belonging to 107 social groups was collected in the nine main forest fragments of the species range during two field missions in 2006

and 2008. Extraction and genotyping procedures were performed as described by Quéméré et al. (91). DNA was amplified using a set of 13 (or 20) micro-satellite loci. We obtained reliable multilocus genotypes for 230 unique individuals (105 groups) (92). We performed the demographic history analyses detailed below by considering the whole sample (i.e., 230 individuals from the entire species range) or the individuals from  $K_A$  ( $n = 83$  individuals) and  $K_B$  ( $n = 126$  individuals) genetic units separately (*SI Materials and Methods*).

**Past Demography Analysis.** To investigate the demographic history of *P. tattersalli*, we used a full-likelihood Bayesian inferential approach designed to detect, quantify, and date changes in population effective size (93). This method was originally developed by Beaumont (94) and implemented in the program MSVAR 1.3 (93). The underlying model assumes that a population of size  $N_t$  (ancestral population size) started to decrease (or increase) exponentially  $T$  generations ago to the present-day population size ( $N_0$ ). Mutations are assumed to occur under the Stepwise Mutation Model (SMM) at a rate  $\theta = 2N_0\mu$ , where  $\mu$  is the per locus mutation rate per generation. MSVAR estimates the posterior distribution of the model parameters ( $N_0$ ,  $N_t$ ,  $t$ ,  $\mu$ ), given the allelic distribution and prior information, using Markov chain Monte Carlo simulations. For each dataset, we performed four independent runs with wide uninformative priors (Table S2) and three different values of generation length (3, 6, and 17.5 y; justification is provided in *SI Materials and Methods*). To compare alternative scenarios and identify the most likely scenario within a Bayesian framework, we performed a BF analysis (e.g., ref. 82). A BF of 1 indicates that the two hypotheses are equally probable, whereas values greater than 1 would favor H1 and values less than 1 would favor H2. BFs greater than 4 are considered as positive evidence for H1, and BFs greater than 7 are considered as significant evidence for H1 (e.g., 93). We identified four time intervals corresponding to four scenarios indirectly related to the origin of grasslands in the Daraina region. The BFs were first computed for each of the four time intervals against all other periods taken together. Given that the different scenarios corresponded to time periods of different duration, we additionally computed BFs for equal length intervals covering the whole Holocene time period (i.e., 10,000 y) and the past 50,000 y.

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1. Sala OE, et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
2. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
3. Ganzhorn JU, Lowry PP, Schatz GE, Sommer S (2001) The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx* 35:346–348.
4. Laurance WF, Peres C (2006) *Emerging Threats to Tropical Forests* (Univ of Chicago Press, Chicago).
5. IPCC (2007) *Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ Press, Cambridge, UK).
6. Ganzhorn J, Goodman S, Dehgan A (2003) Effects of forest fragmentation on small mammals and lemurs. *The Natural History of Madagascar*, eds Goodman S, Benstead J (Univ of Chicago Press, Chicago), pp 193–200.
7. Dufils J (2003) Remaining forest cover. *The Natural History of Madagascar*, eds Goodman S, Benstead J (Univ of Chicago Press, Chicago), pp 88–96.
8. Allnutt TF, et al. (2008) A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conservation Letters* 1:173–181.
9. Kent R (1970) *Early Kingdoms in Madagascar, 1500–1700* (Holt Rinehart and Winston, New York).
10. INSTAT (2008) Population et démographie de Madagascar. Available at [http://www.instat.mg/index.php?option=com\\_content&view=article&id=33&Itemid=56](http://www.instat.mg/index.php?option=com_content&view=article&id=33&Itemid=56). Accessed June 27, 2011.
11. Dewar RE, Wright HT (1993) The culture history of Madagascar. *J World Prehist* 7: 417–466.
12. Minten B, Randrianarison L, Randrianarisoa C (2003) *Agriculture, Pauvreté rurale et politiques économiques à Madagascar* (INSTAT, Antananarivo).
13. Green GM, Sussman RW (1990) Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248:212–215.
14. Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environ Conserv* 34:325–333.
15. Bond WJ, Silander JA, Ranaivonasy J, Ratsirason J (2008) The antiquity of Madagascar's grasslands and the rise of  $C_4$  grassy biomes. *J Biogeogr* 35:1743–1758.
16. Perrier de la Bâthie H (1921) La végétation Malgache. *Annales du Musée Colonial de Marseille* 9:1–266.
17. Humbert H (1927) Principaux aspects de la végétation à Madagascar. La destruction d'une flore insulaire par le feu. *Mémoires de l'Académie Malgache Fascicule V*.
18. Grandidier A (1898) Le boisement de l'Ile de Madagascar. *Bulletin du Comité de Madagascar* 4(2):83–87.
19. Gauthier E (1902) *Madagascar: Essai de géographie physique* (Challamel, Paris).



20. Gade DW (1996) Deforestation and its effects in highland Madagascar. *Mt Res Dev* 16(2):101–116.
21. Hannah L, et al. (2008) Climate change adaptation for conservation in Madagascar. *Biol Lett* 4:590–594.
22. Koehlin J (1993) *Grasslands of Madagascar*. Natural Grasslands. Ecosystems of the World, ed Coupland RT (Elsevier, Amsterdam), pp 291–301.
23. Lowry PI, Schatz G, Phillipson P (1997) The classification of natural and anthropogenic vegetation in Madagascar. *Natural Change and Human Impact in Madagascar*, ed Patterson GBD (Smithsonian Institution Press, Washington, DC).
24. Kull C (2000) Deforestation, erosion, and fire: Degradation myths in the environmental history of Madagascar. *Environ Hist* 6:423–450.
25. Klein J (2002) Deforestation in the Madagascar highlands, established “truth” and scientific uncertainty. *GeoJournal* 56(3):191–199.
26. Pollini J (2010) Environmental degradation narratives in Madagascar: From colonial hegemonies to humanist revisionism. *Geoforum* 41:711–722.
27. Virah-Sawmy M, Willis KJ, Gillson L (2010) Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. *J Biogeogr* 37:506–519.
28. Burney D (1999) Rates, patterns, and processes of landscape transformation and extinction in Madagascar. *Extinctions in Near Time: Causes, Contexts, and Consequences*, ed MacPhee RDE (Plenum, New York), pp 145–164.
29. Burney DA, et al. (2004) A chronology for late prehistoric Madagascar. *J Hum Evol* 47:25–63.
30. Burney DA, Robinson GS, Burney LP (2003) Sporormiella and the late Holocene extinctions in Madagascar. *Proc Natl Acad Sci USA* 100:10800–10805.
31. Gasse F, Van Campo E (2001) Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar). *Palaeogeogr Palaeoclimatol Palaeoecol* 167:287–308.
32. Matsumoto K, Burney DA (1994) *Late Holocene Environments at Lake Mitsinjo, Northwestern Madagascar* (Sage, London).
33. Perez VR, et al. (2005) Evidence of early butchery of giant lemurs in Madagascar. *J Hum Evol* 49:722–742.
34. Godfrey LR, Irwin MT (2007) The evolution of extinction risk: Past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatol (Basel)* 78:405–419.
35. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306:70–75.
36. Bond WJ, Silander JA (2007) Springs and wire plants: Anachronistic defences against Madagascar’s extinct elephant birds. *Proc Biol Sci* 274:1985–1992.
37. Godfrey LR, Jungers WL, Schwartz GT, Irwin MT (2008) *Ghosts and Orphans Elwyn Simons: A Search for Origins. Developments in Primatology: Progress and Prospects*, eds Fleagle JG, Gilbert CC (Springer, New York), pp 361–395.
38. Johnson C (2009) Paleontology. Megafaunal decline and fall. *Science* 326:1072–1073.
39. Rule S, et al. (2012) The aftermath of megafaunal extinction: Ecosystem transformation in Pleistocene Australia. *Science* 335:1483–1486.
40. McWethy DB, et al. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proc Natl Acad Sci USA* 107:21343–21348.
41. de Bruyn M, Hoelzel AR, Carvalho GR, Hofreiter M (2011) Faunal histories from Holocene ancient DNA. *Trends Ecol Evol* 26:405–413.
42. Lorenzen ED, et al. (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479:359–364.
43. Prescott GW, Williams DR, Balmford A, Green RE, Manica A (2012) Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. *Proc Natl Acad Sci USA* 109:4527–4531.
44. Craul M, et al. (2009) Influence of forest fragmentation on an endangered large-bodied lemur in northwestern Madagascar. *Biol Conserv* 142:2862–2871.
45. Olivieri GL, Sousa V, Chikhi L, Radespiel U (2008) From genetic diversity and structure to conservation: Genetic signature of recent population declines in three mouse lemur species (*Microcebus* spp.). *Biol Conserv* 141:1257–1271.
46. Schneider N, Chikhi L, Currat M, Radespiel U (2010) Signals of recent spatial expansions in the grey mouse lemur (*Microcebus murinus*). *BMC Evol Biol* 10:105.
47. Ting N, et al. (2012) Genetic signatures of a demographic collapse in a large-bodied forest dwelling primate (*Mandrillus leucophaeus*). *Ecol Evol* 2:550–561.
48. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
49. Burney DA, Flannery TF (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol Evol* 20:395–401.
50. Laurance WF, et al. (1997) Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118.
51. McGlone M (2012) Paleontology. The hunters did it. *Science* 335:1452–1453.
52. Graham RW (1986) *Response of Mammalian communities to Environmental Changes During the Late Quaternary* (Harper and Row, New York).
53. Lyons SK, Wagner PJ, Dzikiewicz K (2010) Ecological correlates of range shifts of Late Pleistocene mammals. *Philos Trans R Soc Lond B Biol Sci* 365:3681–3693.
54. Mayewski PA, et al. (2004) Holocene climate variability. *Quat Res* 62:243–255.
55. Nogués-Bravo D, Ohlemüller R, Batra P, Araújo MB (2010) Climate predictors of late quaternary extinctions. *Evolution* 64:2442–2449.
56. Hewitt GM (1996) Some genetic consequences of ice ages, and their role, in divergence and speciation. *Biol J Linn Soc Lond* 58:247–276.
57. Nogués-Bravo D, Rodríguez J, Hortal J, Batra P, Araújo MB (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol* 6:685–692.
58. Ceballos G, Arroyo-Cabrales J, Ponce E (2010) Effects of Pleistocene environmental changes on the distribution and community structure of the mammalian fauna of Mexico. *Quat Res* 73:464–473.
59. De Vivo M, Carmignotto AP (2004) Holocene vegetation change and the mammal faunas of South America and Africa. *J Biogeogr* 31:943–957.
60. Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar’s microendemic biota. *Science* 312:1063–1065.
61. Burney DA (1987) Late Holocene vegetational change in central Madagascar. *Quat Res* 28:130–143.
62. Burney DA, et al. (1997) Environmental change, extinction and human activity: Evidence from caves in NW Madagascar. *J Biogeogr* 24:755–767.
63. MacPhee RDE, Burney DA, Wells NA (1985) Early Holocene chronology and environment of Ampasambazimba, a malagasy subfossil lemur site. *Int J Primatol* 6:463–489.
64. Kiage LM, Liu K-B (2006) Late Quaternary paleoenvironmental changes in East Africa: A review of multiproxy evidence from palynology, lake sediments, and associated records. *Prog Phys Geogr* 30:633–658.
65. Willis KJ, Gillson L, Virah-Sawmy M (2008) Nature or nurture: The ambiguity of C<sub>4</sub> grasslands in Madagascar. *J Biogeogr* 35:1741–1742.
66. MEFT/USAID (2009) *Evolution de la couverture de forêts naturelles à Madagascar*, ed MEFT (Programme JARIALA, Antananarivo, Madagascar).
67. Elmqvist T, et al. (2007) Patterns of loss and regeneration of tropical dry forest in Madagascar: The social institutional context. *PLoS ONE* 2:e402.
68. Elmqvist T, Tengö M (2009) Spontaneous regeneration of tropical dry forest in Madagascar. *Forest Regeneration: Patterns and Processes*, eds Nagendra H, Southworth J (Springer, Amsterdam).
69. Morat P (1973) *Les savanes du Sud-Ouest de Madagascar* (ORSTOM-IRD, Paris).
70. Crowley BE (2010) A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat Sci Rev* 29:2591–2603.
71. Simons EL, et al. (1995) AMS <sup>14</sup>C dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quat Res* 43:249–254.
72. Jungers WL, Godfrey LR, Simons EL, Chatrath PS (1995) Subfossil Indri indri from the Ankarana Massif of northern Madagascar. *Am J Phys Anthropol* 97:357–366.
73. Godfrey LR, Jungers WL, Simons EL, Chatrath PS, Rakotosamimanana B (1999) *Past and Present Distributions of Lemurs in Madagascar* (Kluwer Academic/Plenum, New York), pp 19–53.
74. Mittermeier RA, et al. (2010) *Lemurs of Madagascar (Conservation International Tropical Field Guide Series)* (Broché), 3rd Ed.
75. Vénin P (1986) *The History of Civilization in North Madagascar* (Balkema, Rotterdam).
76. Kestell-Cornish R (1876) *Journal of a Tour of Exploration in the North of Madagascar* (The Society for the Propagation of the Gospel in Foreign Parts, London).
77. Rakotondravony H (2006) Communautés locales et gibiers dans la région de Daraina, extrême Nord-Est de Madagascar. *Madagascar Conservation and Development* 1(1):19–21.
78. FAO (2008) Country profile of human development indicators: Madagascar. Available at <http://hdrstats.undp.org/en/countries/profiles/MDG.html>. Accessed December 15, 2011.
79. Vargas A, Jimenez I, Palomares F, Palacios MJ (2002) Distribution, status, and conservation needs of the golden-crowned sifaka (*Propithecus tattersalli*). *Biol Conserv* 108:325–334.
80. Lawler R (2011) Historical demography of a wild lemur population (*Propithecus verreauxi*) in southwest Madagascar. *Popul Ecol* 53(1):229–240.
81. Goossens B, et al. (2006) Genetic signature of anthropogenic population collapse in orangutans. *PLoS Biol* 4(2):e25.
82. Milton K, Lozier J, Lacey E (2009) Genetic structure of an isolated population of mantled howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. *Conserv Genet* 10(2):347–358.
83. Fritz SA, Bininda-Emonds OR, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecol Lett* 12:538–549.
84. Muldoon KM (2010) Paleoenvironment of Ankililolo Cave (late Holocene, southwestern Madagascar): Implications for the extinction of giant lemurs. *J Hum Evol* 58:338–352.
85. Turvey ST, Fritz SA (2011) The ghosts of mammals past: Biological and geographical patterns of global mammalian extinction across the Holocene. *Philos Trans R Soc Lond B Biol Sci* 366:2564–2576.
86. Sandel B, et al. (2011) The influence of Late Quaternary climate-change velocity on species endemism. *Science* 334:660–664.
87. Stewart JR, Lister AM, Barnes I, Dalen L (2010) Refugia revisited: Individualistic responses of species in space and time. *Proc Biol Sci* 277:661–671.
88. Amelot X, Moreau S, Carrière S (2011) Des justiciers de la biodiversité aux injustices spatiales: L’exemple de l’extension du réseau d’aires protégées à Madagascar. *Justice et Injustices Environnementales*, dir Blanchon D, Gardin J, Moreau S (Presses Universitaires de Paris Ouest, Nanterre, France), pp 193–214.
89. Simons EL (1988) A new species of *Propithecus* (primates) from northeast Madagascar. *Folia Primatol (Basel)* 50(1–2):143–151.
90. Quéméré E, et al. (2010) Spatial variation in density and total size estimates in fragmented primate populations: The golden-crowned sifaka (*Propithecus tattersalli*). *Am J Primatol* 72(1):72–80.
91. Quéméré E, Louis E, Ribéron A, Chikhi L, Crouau-Roy B (2010) Non-invasive conservation genetics of the critically endangered golden-crowned sifaka (*Propithecus tattersalli*): High diversity and significant genetic differentiation over a small range. *Conserv Genet* 11:675–687.
92. Quéméré E, Crouau-Roy B, Rabarivola C, Louis EE, Jr., Chikhi L (2010) Landscape genetics of an endangered lemur (*Propithecus tattersalli*) within its entire fragmented range. *Mol Ecol* 19:1606–1621.
93. Storz JF, Beaumont MA, Alberts SC (2002) Genetic evidence for long-term population decline in a savannah-dwelling primate: Inferences from a hierarchical bayesian model. *Mol Biol Evol* 19:1981–1990.
94. Beaumont MA (1999) Detecting population expansion and decline using microsatellites. *Genetics* 153:2013–2029.