

REVIEW SUMMARY

BIODIVERSITY

Madagascar's extraordinary biodiversity: Evolution, distribution, and use

Alexandre Antonelli* *et al.*

BACKGROUND: The Republic of Madagascar is home to a unique assemblage of taxa and a diverse set of ecosystems. These high levels of diversity have arisen over millions of years through complex processes of speciation and extinction. Understanding this extraordinary diversity is crucial for highlighting its global importance and guiding urgent conservation efforts. However, despite the detailed knowledge that exists on some taxonomic groups, there are large knowledge gaps that remain to be filled.

ADVANCES: Our comprehensive analysis of major taxonomic groups in Madagascar summarizes information on the origin and evolution of terrestrial and freshwater biota, current species richness and endemism, and the utilization of this biodiversity by humans. The depth and breadth of Madagascar's biodiversity—the product of millions of years of evolution in relative isolation—is still being uncovered. We report a recent acceleration in the scientific description of species but many

remain relatively unknown, particularly fungi and most invertebrates.

DIGITIZATION: Digitization efforts are already increasing the resolution of species richness patterns and we highlight the crucial role of field- and collections-based research for advancing biodiversity knowledge in Madagascar. Phylogenetic diversity patterns mirror that of species richness and endemism in most of the analyzed groups. Among the new data presented, our update on plant numbers estimates 11,516 described vascular plant species native to Madagascar, of which 82% are endemic, in addition to 1215 bryophyte species, of which 28% are endemic. Humid forests are highlighted as centers of diversity because of their role as refugia and centers of recent and rapid radiations, but the distinct endemism of other areas such as the grassland-woodland mosaic of the Central Highlands and the spiny forest of the southwest is also important despite lower species richness. Endemism in Malagasy fungi remains poorly known given the lack of data on the total diversity and global distribution of species. However, our analysis has shown that ~75% of the fungal species detected by environmental sequencing have not been reported as occurring outside of Madagascar.

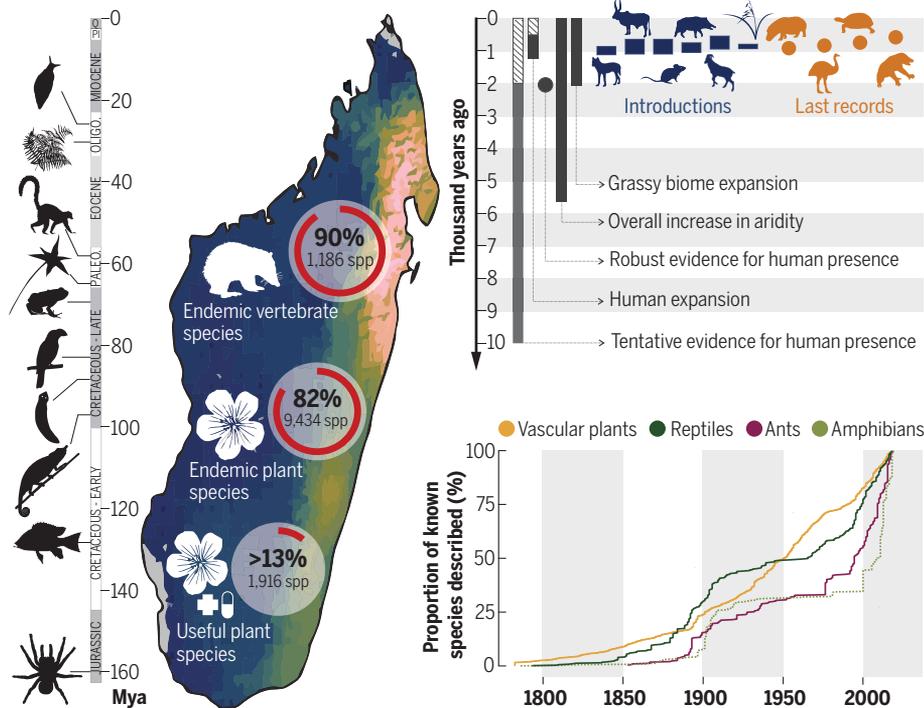
Among the 1314 species of native terrestrial and freshwater vertebrates, levels of endemism are extremely high (90% overall)—all native nonflying terrestrial mammals and native amphibians are found nowhere else on Earth; further, 56% of the island's birds, 81% of freshwater fishes, 95% of mammals, and 98% of reptile species are endemic. Little is known about endemism in insects, but data from the few well-studied groups on the island suggest that it is similarly high. The uses of Malagasy species are many, with much potential for the uncovering of useful traits for food, medicine, and climate mitigation.

OUTLOOK: Considerable work remains to be done to fully characterize Madagascar's biodiversity and evolutionary history. The multitudes of known and potential uses of Malagasy species reported here, in conjunction with the inherent value of this unique and biodiverse region, reinforce the importance of conserving this unique biota in the face of major threats such as habitat loss and overexploitation. The gathering and analysis of data on Madagascar's remarkable biota must continue and accelerate if we are to safeguard this unique and highly threatened subset of Earth's biodiversity. ■

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Cite this article as A. Antonelli *et al.*, *Science* **378**, eabf0869 (2022). DOI: [10.1126/science.abf0869](https://doi.org/10.1126/science.abf0869)

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<https://doi.org/10.1126/science.abf0869>



Emergence and composition of Madagascar's extraordinary biodiversity. Madagascar's biota is the result of over 160 million years of evolution, mostly in geographic isolation, combined with sporadic long distance immigration events and local extinctions. (Left) We show the age of the oldest endemic Malagasy clade for major groups (from bottom to top): arthropods, bony fishes, reptiles, flatworms, birds, amphibians, flowering plants, mammals, non-flowering vascular plants, and mollusks). Humans arrived recently, some 10,000 to 2000 years (top right) and have directly or indirectly caused multiple extinctions (including hippopotamus, elephant birds, giant tortoises, and giant lemurs) and introduced many new species (such as dogs, zebu, rats, African bushpigs, goats, sheep, rice). Endemism is extremely high and unevenly distributed across the island (the heat map depicts Malagasy palm diversity, a group characteristic of the diverse humid forest). Human use of biodiversity is widespread, including 1916 plant species with reported uses. The scientific description of Malagasy biodiversity has accelerated greatly in recent years (bottom right), yet the diversity and evolution of many groups remain practically unknown, and many discoveries await.

REVIEW

BIODIVERSITY

Madagascar's extraordinary biodiversity: Evolution, distribution, and use

Alexandre Antonelli^{1,2,3,4,*†}, Rhian J. Smith^{1,3,†}, Allison L. Perrigo^{2,3,†}, Angelica Crottini^{5,6,7}, Jan Hackel¹, Weston Testo^{8,2,3}, Harith Farooq^{2,3,9}, Maria F. Torres Jiménez^{10,2,3}, Niels Andela¹¹, Tobias Andermann^{12,13,2,3}, Andotiana M. Andriamanohera¹⁴, Sylvie Andriambololona¹⁵, Steven P. Bachman¹, Christine D. Bacon^{2,3}, William J. Baker¹, Francesco Belluardo^{5,6,7}, Chris Birkinshaw^{15,16}, James S. Borrell¹, Stuart Cable¹, Nataly A. Canales¹⁷, Juan D. Carrillo^{18,3,13,19}, Rosie Clegg^{20,1}, Colin Clubbe¹, Robert S. C. Cooke^{21,2,3}, Gabriel Damasco^{22,2}, Sonia Dhanda¹, Daniel Edler^{23,2,3}, Søren Faurby^{2,3}, Paola de Lima Ferreira^{24,2,3}, Brian L. Fisher²⁵, Félix Forest¹, Lauren M. Gardiner²⁶, Steven M. Goodman^{8,27}, Olwen M. Grace¹, Thaís B. Guedes²⁸, Marie C. Henniges^{1,29}, Rowena Hill^{1,29}, Caroline E. R. Lehmann^{30,31}, Porter P. Lowry II^{16,32}, Lovanomenjanahary Marline^{14,3,27}, Pável Matos-Maravi^{24,3}, Justin Moat¹, Beatriz Neves^{33,3}, Matheus G. C. Nogueira^{33,3}, Renske E. Onstein^{34,35}, Alexander S. T. Papadopoulos³⁶, Oscar A. Perez-Escobar¹, Leanne N. Phelps^{31,30}, Peter B. Phillipson^{16,32}, Samuel Pironon^{1,37}, Natalia A. S. Przelomska^{1,38}, Marina Rabarimanarivo¹⁵, David Rabehevitra¹⁴, Jeannie Raharimampionona¹⁵, Mamy Tiana Rajaonah¹⁴, Fano Rajaonary¹⁵, Landy R. Rajaovelona¹⁴, Mijoro Rakotoarinivo³⁹, Amédée A. Rakotoarisoa¹⁴, Solofo E. Rakotoarisoa¹⁴, Herizo N. Rakotomalala¹⁴, Franck Rakotonasolo¹⁴, Berthe A. Ralaveloarisoa¹⁴, Myriam Ramirez-Herranz^{40, 3, 41}, Jean Emmanuel N. Randriamamonjy¹⁴, Tianjanahary Randriamboavonjy¹⁴, Vonona Randrianasolo¹⁴, Andriambolantsoa Rasolohery⁴², Anitry N. Ratsifandrihamanana⁴³, Noro Ravololomanana¹⁵, Veloso Razafiniary¹⁴, Henintsoa Razanajatovo¹⁴, Estelle Razanatsoa⁴⁴, Malin Rivers⁴⁵, Ferran Sayol^{46,3}, Daniele Silvestro^{13,19,2,3}, Maria S. Vorontsova¹, Kim Walker^{1,47}, Barnaby E. Walker¹, Paul Wilkin¹, Jenny Williams¹, Thomas Ziegler^{48,49}, Alexander Zizka⁵⁰, Hélène Ralimanana^{14,*†}.

Madagascar's biota is hyperdiverse and includes exceptional levels of endemism. We review the current state of knowledge on Madagascar's past and current terrestrial and freshwater biodiversity by compiling and presenting comprehensive data on species diversity, endemism, and rates of species description and human uses, in addition to presenting an updated and simplified map of vegetation types. We report a substantial increase of records and species new to science in recent years; however, the diversity and evolution of many groups remain practically unknown (e.g., fungi and most invertebrates). Digitization efforts are increasing the resolution of species richness patterns and we highlight the crucial role of field- and collections-based research for advancing biodiversity knowledge and identifying gaps in our understanding, particularly as species richness corresponds closely to collection effort. Phylogenetic diversity patterns mirror that of species richness and endemism in most of the analyzed groups. We highlight humid forests as centers of diversity and endemism because of their role as refugia and centers of recent and rapid radiations. However, the distinct endemism of other areas, such as the grassland-woodland mosaic of the Central Highlands and the spiny forest of the southwest, is also biologically important despite lower species richness. The documented uses of Malagasy biodiversity are manifold, with much potential for the uncovering of new useful traits for food, medicine, and climate mitigation. The data presented here showcase Madagascar as a unique "living laboratory" for our understanding of evolution and the complex interactions between people and nature. The gathering and analysis of biodiversity data must continue and accelerate if we are to fully understand and safeguard this unique subset of Earth's biodiversity.

The Republic of Madagascar, an island country off the east coast of Africa, is home to a unique assemblage of taxa and a diverse set of ecosystems. The high levels of terrestrial and freshwater diversity have arisen over millions of years through complex processes of speciation and extinction. Understanding the origins, evolution, current distribution, and uses of this extraordinary diversity is crucial to highlighting its

global importance and guiding urgent conservation efforts (1, 2).

Origins of Madagascar's biota

Once part of the Gondwana supercontinent, Madagascar and India split from Africa 150 to 160 million years ago (Ma), with India separating 84 to 91 Ma (3). The Malagasy fossil record shows both regional and widespread Gondwanan fauna before continental breakup

(Fig. 1A) (4) but plant remains are scarce in the record (5). The Cretaceous-Paleogene (K-Pg) mass extinction (66 Ma), when Madagascar had already become an island, is believed to have greatly reduced the ancient Malagasy fauna. This species turnover presented new opportunities for the establishment and radiation of colonizers (6, 7). Biotic history during this period is almost entirely inferred from molecular phylogenies as there is a long gap in the fossil record during the Cenozoic (8). Molecular clock estimates suggest that few extant groups date back to potential Gondwanan vicariance, including some reptile, fish, and insect lineages (6, 9, 10) and the plant genus *Takhtajania* (11) (Fig. 1A). Most of the current animal, plant, and fungal diversity originated from ancestors with mainly African and Indo-Pacific origin according to phylogenies and biogeographic reconstructions, and reached Madagascar through overseas dispersal (6, 10–12) (Fig. 1B). The presence of oceanic surface currents flowing from Africa to Madagascar during the Paleogene, which subsided in the Miocene (13), coincided with the arrival of multiple vertebrate lineages that subsequently diversified (6, 7). It has also been proposed that short-lived land bridges in the Mozambique channel during the Neogene may have aided migration (14), although the significance of this is debated (14, 15). In addition, stepping-stone islands in the Indian Ocean, now submerged, may have facilitated animal and plant dispersal from the Indo-Pacific region (16).

The current peaks and plateaus of Madagascar probably formed in the past 30 to 40 million years (My) through mantle upwelling and volcanism, and the past 10 My have seen accelerated uplift (17, 18). This suggests that rather than evolving on an old stable surface, many of the current patterns of biodiversity were shaped by environmental gradients and dispersal barriers that are relatively young, geologically speaking (17).

Regional differences

Madagascar's diverse biota and ecosystems have been categorized using many different systems (e.g., 19, 20), but data scarcity means that any inferences on the extent of native vegetation prior to major anthropogenic influences come with a very high level of uncertainty. We summarize the current vegetation types of Madagascar (dry forest, grassland-woodland mosaic, humid forest, mangrove, tapia, spiny forest, and subhumid forest) based on a simplified version of the *Atlas of the Vegetation of Madagascar* (21) (Fig. 1 and table S1) (22). Although our resulting simplified map is adequate for providing an overview of Madagascar's main vegetation types, a higher resolution map and more detailed classification is needed for in-depth analyses such as systematic conservation planning. We suggest that any

new mapping classification should build on existing mapping [including the updated classification of (23)] but follow the suggestions of the IUCN global ecosystem typology (24), which is a hierarchical classification system that at its top level defines ecosystems by ecological function and at detailed levels distinguishes ecosystems by species assemblage (25).

There is a marked longitudinal rainfall gradient created by the high eastern edge of the mountain range running from north to south, most of which exceeds 800 m above sea level. Humidity brought by easterly trade winds and summer monsoons from the Indian Ocean is captured by the edge and forms a cloud layer at ca. 900 to 1200 m. This rain-producing system sustains the patchy remains of a ca. 100-km-wide band of evergreen humid forest along the east coast, with extensions to certain portions of the north. Rainfall patterns are largely unpredictable throughout the country, and there are frequent but irregular cyclones during the rainy season. This unpredictability is suggested to have led to unique biological adaptations in Malagasy species, including extremes of very fast or slow life histories (26, 27).

The Central Highlands have a subhumid climate, which is cooler and drier during the winter. They are dominated by a grassland-woodland mosaic, where grasslands are mixed with agricultural land, shrubland, and patches of woodland. There are also areas of humid forest and tapia—woodland dominated by the tree species tapia (*Uapaca bojeri*)—from which the vegetation type takes its name. Although grasslands increased as a result of the degradation of woody vegetation types following human settlement, some are derived from the pantropical savanna expansion that started in the late Miocene (28). The extent of grasslands at the time of human arrival, especially in the Central Highlands, remains debated (29). To the southwest, the highland mosaic transitions into subhumid forests and more extensive tapia.

The highest mountains (>2500 m) are igneous in origin and support sclerophyllous shrublands dominated by species of the plant family Ericaceae in addition to open grasslands around their summits. Humidity and rainfall decrease in the rain shadow to the west of the Central Highlands, with the dominant vegetation type transitioning to dry forest, with some deciduous plant species and succulent elements toward the western coast. Mangroves are mostly found along the Mozambique Channel coast. The southwest region is the driest part of the island, and the rainy season, when present, lasts ≤ 3 months. This climate supports the spiny forest ecosystem, which in global terms is strictly a thicket but classed as forest within the context of Madagascar (21). This ecosystem was previously thought to be Madagascar's oldest and was widespread across the island when it lay at the edge of the tropical belt before the mid-Oligocene. When continental drift moved Madagascar north and directly into the trade wind zone, the spiny forest ecosystem contracted (3). However, the humid forest has been found to contain taxa belonging to lineages that date back to the Paleocene, and further evidence from climate reconstructions suggests that Madagascar was moderately humid at the K-Pg boundary (11, 30) (Fig. 1A).

The arrival of humans

Human presence in Madagascar—from both Austronesian and African origins—dates to at least the start of the CE with some evidence pointing to the Early Holocene—8000 BCE onward (31, 32) (Fig. 3). Settlement in the interior and large-scale anthropogenic impacts likely took place after 1000 CE, with subsequent progressive population growth from initially sparse settlements from 1200 CE onward (33, 34). As in other parts of the world once human populations began to expand, their activities had substantial impacts on local biota. This process resulted in landscape transforma-

tion from ca. 300 CE onward (35, 36) and subsequent extinction of Madagascar's once rich megafauna (here defined as vertebrates >10 kg) through a combination of hunting and habitat displacement (34, 37–40). These extinctions may have accelerated as a result of a shift from hunting and foraging to herding and farming as the predominant methods of obtaining food, which brought land clearance and transformation to agricultural land (41). Drought may have further compounded these changes (42).

Since settling on the island, humans have introduced crops and livestock for agriculture and husbandry (43–45) (Fig. 3). Of these, rice and zebu cattle have had the largest impacts on the landscape (43, 44) as a result of their vital role in sustaining human populations. Rice is currently widely cultivated both in the Central Highlands (using paddy production) and in the humid east, where swidden agricultural methods are used (i.e., shifting cultivation involving clearing forest for conversion to cropland, usually by burning). With the latter practice, soils are rapidly depleted and remain fertile for only a short period, meaning that the land is abandoned for long fallow periods with further vegetation being cleared at a new location. The expansion of the Kingdom of Madagascar in the late 1700s, followed by British and French colonialism in the 1800s and 1900s, accelerated trade and landscape transformation, resulting in a substantial loss of native vegetation across the island (33). Current patterns of Madagascar's biological diversity are therefore shaped both by ancient evolution and recent anthropogenic activities.

Contemporary patterns of richness, endemism, and use

Madagascar is one of Earth's "hottest" biodiversity hotspots (46), with high species richness and exceptional levels of endemism across many taxonomic groups, combined with high rates of habitat degradation and fragmentation

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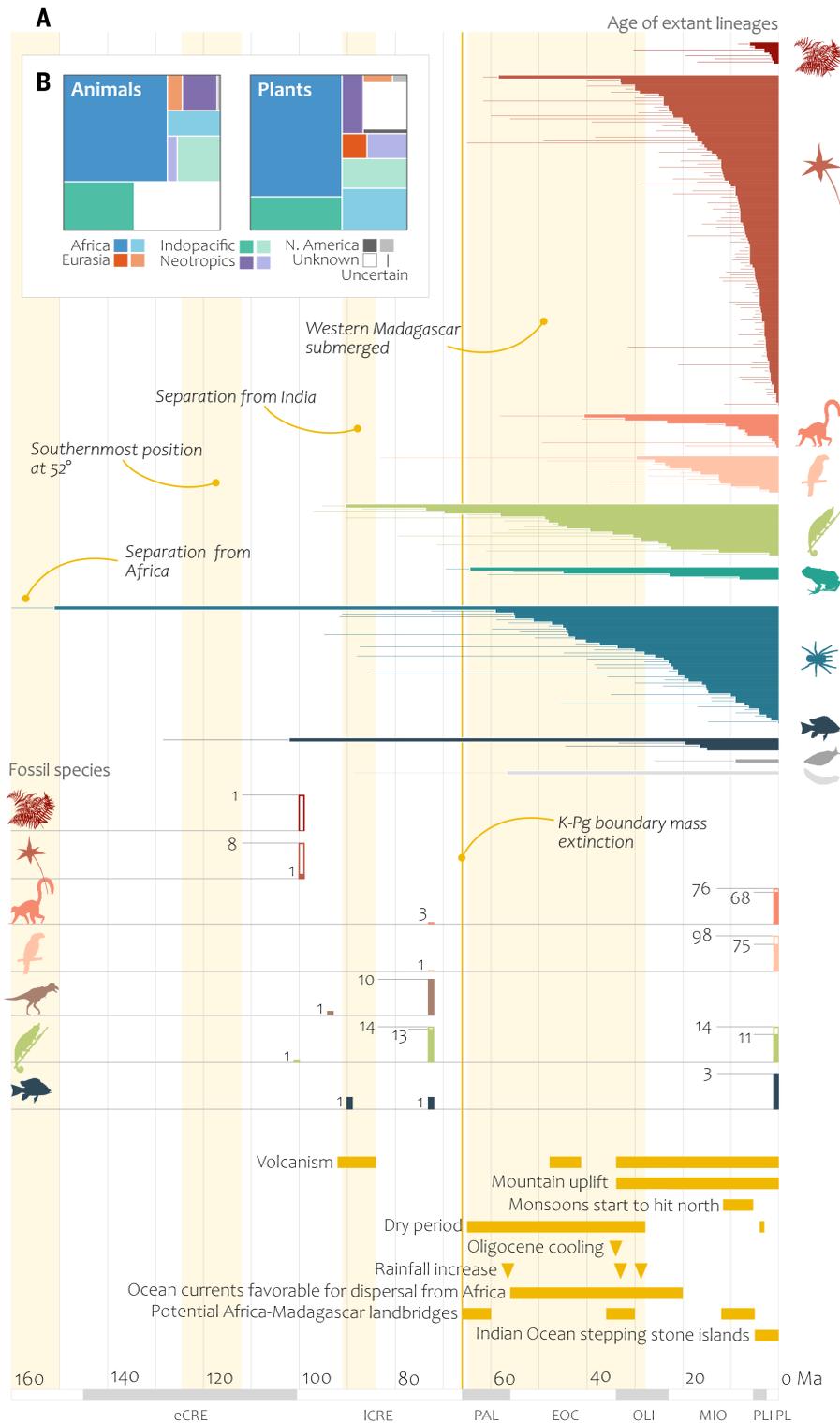


Fig. 1. Timing and origins of Madagascar's biodiversity. (A) Geological and environmental events in relation to the age of multiple organismal groups. The dark yellow horizontal bars at the bottom show the timing of landscape and climatic events. Vertical yellow shading along the panel corresponds to longer geographical events. Bars and lines show crown and stem ages of 217 lineages that each produced at least two endemic Malagasy species, estimated from molecular and fossil data. Icons correspond (from top to bottom) to nonflowering vascular plants, flowering plants, mammals, birds, dinosaurs (for fossil data), reptiles (here all Sauropsida, excluding birds), amphibians, arthropods, bony fishes,

mollusks, and flatworms. In the fossil data section, the empty bars show the number of unique species in the fossil record through time that were found in Madagascar, with filled bars showing the number of unique species endemic to Madagascar. PL, Pleistocene; PLI, Pliocene; MIO, Miocene; OLI, Oligocene; EOC, Eocene; PAL, Paleogene; ICRE, late Cretaceous; eCRE, early Cretaceous. (B) Geographical origins of Madagascar's biodiversity. These treemaps show the proportional origins of the 217 endemic lineages in (A), estimated through biogeographic reconstruction, or if unavailable, the distribution of the sister group. Unsaturated hues represent the proportion of lineages whose origin is ambiguous.

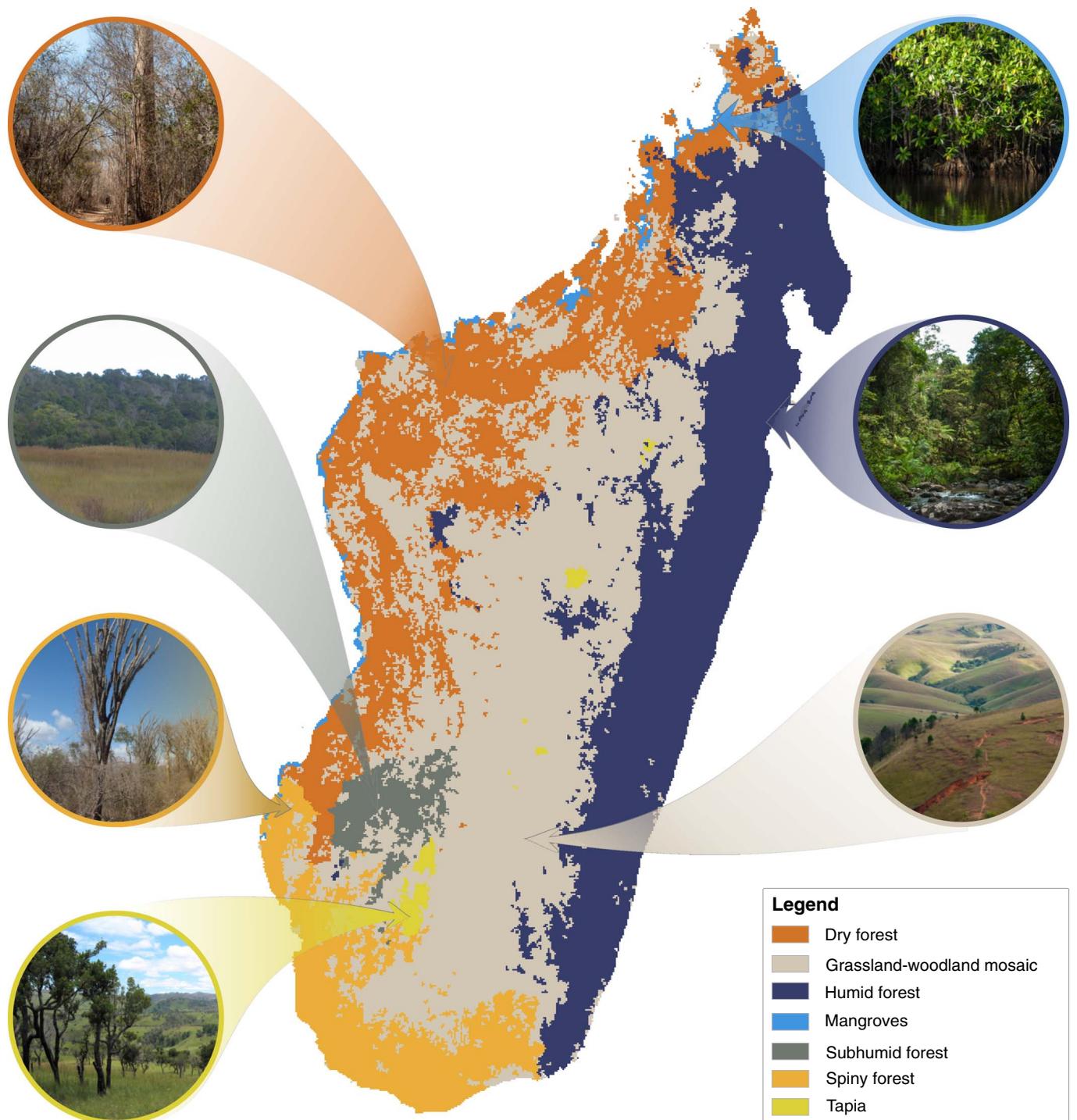


Fig. 2. Map of predominant vegetation types, expanded and simplified from Moat and Smith (21).

(Fig. 4) (46, 47). Despite the global significance of Malagasy biodiversity, many taxonomic groups remain poorly known, and Madagascar ranks among the top countries for the predicted percentage of terrestrial vertebrates lacking scientific description (48). Most species are represented by only a small number of records in global natural history collections

and some groups remain practically unknown, particularly fungi and most invertebrates. Estimates place the global number of fungi at >6.3 million species (49), and Madagascar is likely to hold a large proportion of this diversity. However, to date <2000 fungal species and species hypotheses—the latter defined by genetic reference sequences (50)—have been

reported in public databases (51, 52) and checklists (53, 54).

Concerted efforts, including taxonomic research, improved digital access to natural history collections, and application of molecular techniques for species identification and delimitation, have resulted in a substantial increase in the number of records and species

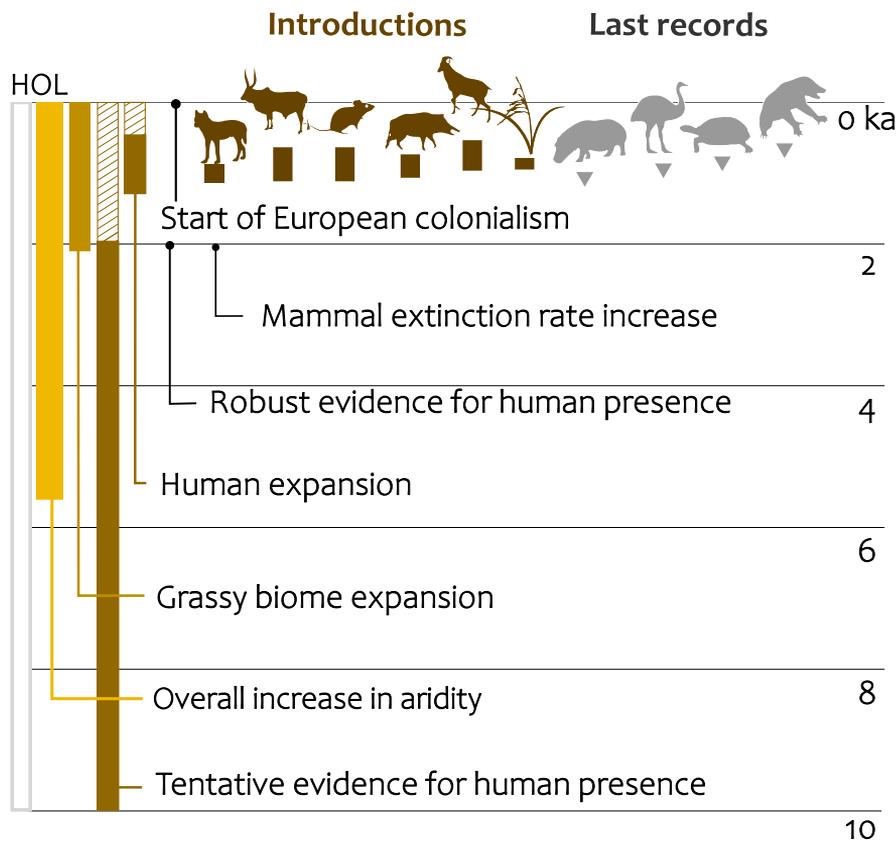


Fig. 3. Human arrival. Holocene events and environmental changes around the time of human arrival. Dates for human introductions of dogs, zebu cattle, rats, bushpigs, goats, and rice are provided as well as last dated records of megafauna (hippopotamus, elephant birds, giant tortoises, and giant lemurs) (22).

new to science in recent years, even in relatively conspicuous groups such as reptiles and amphibians (Fig. 5). However, many species remain undescribed across most taxonomic groups (55, 56). For example, as of June 2021, there were 369 described native Malagasy amphibians (57) but the true number has been estimated to be well over 500 (58). The figures for undescribed species of arthropods could be orders of magnitude higher. Of the estimated 1300 species of ants alone (59), only 781 have been formally described (60).

For Malagasy grasses, concerted herbarium digitization efforts over just three years resulted in a 43% increase in georeferenced species records. This more than doubled the median number of records per species and improved the resolution of species richness patterns (28, 61). In better-studied groups such as lemurs, continued advancements in our understanding of their distribution, ecology, and genetic diversity allow us to better understand their evolutionary history and inform conservation strategies (62). Together, these efforts show the crucial role of field- and collections-based research in advancing biodiversity knowledge and understanding of spatial patterns of richness, endemism, and speciation, while providing

opportunities to further investigate the ecological roles of species across Madagascar's ecosystems.

Extensive endemism

Among the 1314 native species of terrestrial and freshwater vertebrates (4), levels of endemism are extremely high (90% overall); all native nonflying terrestrial mammals and native amphibians are found nowhere else on Earth, and 56% of birds, 81% of freshwater fishes, 95% of mammals, and 98% of reptile species are endemic (4, 63–68) (Fig. 4). Little is known about endemism in insects, but data from the few well-studied groups on the island suggest that it is similarly high (69, 70). Endemism among Madagascar's animals is not limited to lower taxonomic levels: Among birds, the island contains one endemic order (Mesitornithiformes) and three endemic families (Brachypteraciidae, Philepittidae, and Bernieridae) (71). Among mammals, higher-level endemism includes the superfamily Lemuroidea, the families Myzopodidae (sucker-footed bats), Eupleridae (native Carnivora), and Tenrecidae (tenrecs), and the subfamily Nesomyinae (nesomyine rodents) (66, 68, 72, 73). For amphibians, in the family Mantellidae (mantellid frogs) all but three species (endemic

to the Comoro islands) (74, 75) are endemic to Madagascar; there are also three endemic subfamilies: Cophylinae (narrow-mouthed frogs), Dyscophinae (tomato frogs), and Scaphiophryninae (rain frogs) (63).

Malagasy flora is also highly diverse and mostly endemic (76). It is estimated that over 14,000 vascular plant species occur on the island (76), including 11,516 described native species, of which 82% are endemic (22, 77). When the estimated 2550 species that remain to be scientifically described are factored in, the level of endemism could rise to 87% (76). Among the island's flowering plants (angiosperms), there are 310 endemic genera, ca. 19% of the generic diversity (11); and five endemic families (Asteropeiaceae, Barbeuiaceae, Physenaceae, Sarcolanaceae, and Sphaerosepalaceae). Five families dominate the flora in terms of species richness: Orchidaceae (orchid family, 922 spp., 84% endemic), Rubiaceae (coffee family, 806 spp., 93% endemic), Fabaceae (pea family, 603 spp., 76% endemic), Poaceae (grass family, 541 spp., 50% endemic, 40% after specialist taxonomic evaluation) (78), and Asteraceae (daisy family, 529 spp., 83% endemic) (5, 76, 77, 79). These are also the five largest families globally but all five are disproportionately species rich in Madagascar relative to the land area (~0.4% of Earth's total). The Malagasy bryophyte flora is less well studied but is also diverse: of the 1215 described bryophyte species (767 mosses, 443 liverworts, and 5 hornworts), 28% are endemic (80).

Endemism in Malagasy fungi is hard to assess given that so little is known about the total diversity of species. However, 14% of the species in the Global Biodiversity Information Facility (GBIF) and almost 75% of the fungal species hypotheses detected by environmental sequencing have not been reported as occurring outside of Madagascar (22). A recent molecular assessment of fruiting fungi and root samples from five forest sites in Madagascar based on Internal Transcribed Spacer data (12) found similar levels of endemism, with 65% of sequences not known from outside the country and 10% of species potentially new to science, with much of the new diversity extrapolated from ectomycorrhizal samples. This further highlights the possible magnitude of unknown diversity among Malagasy fungi.

Spatial patterns of Malagasy biodiversity

Biodiversity is not evenly distributed across Madagascar, with much of the island's biota occurring in humid forests in the east as well as on the eastern flanks of the Central Highlands and in some northern areas such as the Tsaratanana and Marojeje Massifs (79–82) (Fig. 4). Overall patterns of species richness correspond closely to collection effort, and the variation in sampling frequency across the country therefore makes it difficult to ascertain true patterns of diversity in many groups

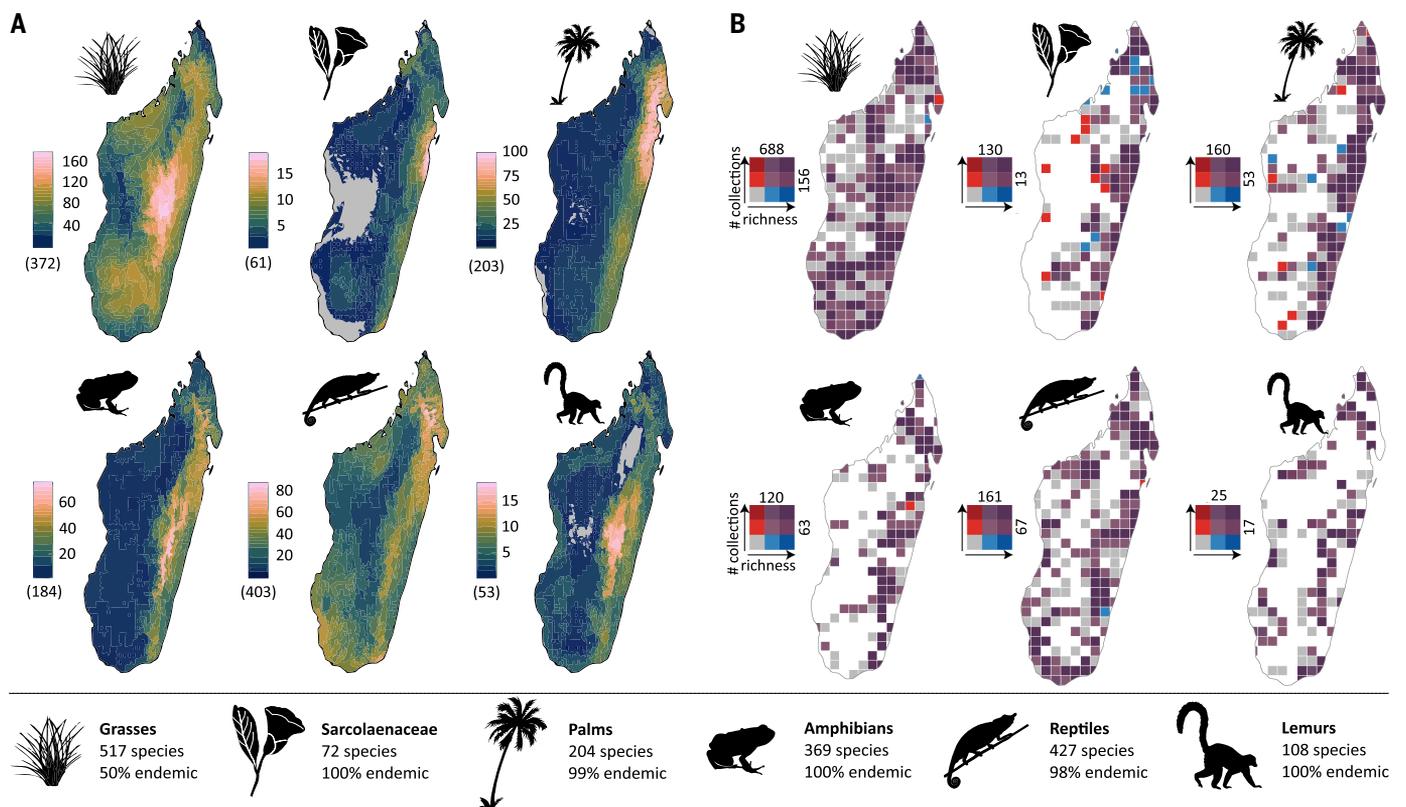


Fig. 4. Diversity patterns. (A) Species richness and endemism of six taxonomic groups in Madagascar. Native terrestrial and freshwater species counts and percentages of endemic species are based on estimates using author-curated data compiled from *The New Natural History of Madagascar* (126), and the *Catalogue of the Vascular Plants of Madagascar* (77). Species richness maps were generated from species distribution models based on specimen occurrence records and bioclimatic

data; non-native and marine taxa are not included (22). Numbers in parentheses below color ramps are the number of species used to generate the species richness maps. (B) Patterns of species richness and collection effort for the same six taxonomic groups. Map grid cells are 25 × 25 km; cell colors correspond to species richness and collection number per cell, based on specimen occurrence records. Gray denotes an absence of records for that cell.

(Fig. 4). Species diversity patterns in amphibians, reptiles, and primates are closely mirrored by corresponding phylogenetic diversity patterns (fig. S3). An exception occurs in water beetles, where phylogenetic diversity is negatively correlated to species richness and endemism, purportedly because narrow endemism in this group is the result of recent radiations (83). The few studies investigating the distribution of phylogenetic diversity in plants present varied patterns, some resembling those of vertebrate groups, whereas others differ markedly (84, 85).

The high species richness and endemism of many lineages in the humid forests of eastern and northern Madagascar reflect the role of these ecosystems both as forest refugia during glacial maxima (82, 86, 87), and centers of recent and rapid evolutionary radiations (88–90). This scenario is supported by the presence in these areas of high but clustered phylogenetic diversity in reptiles, mammals, and, to a certain extent, amphibians (fig. S3). The grassland-woodland mosaic vegetation of the Central Highlands is marked by its own distinctive endemism despite relatively low species richness

(78, 91). Certain groups, including reptiles and some plant families, such as Fabaceae, Euphorbiaceae, and Malvaceae, show additional centers of diversity in spiny forests that dominate the island's southwest region (77, 79, 81) (Fig. 4).

Species endemism across taxa and regions has arisen through multiple mechanisms, including allopatric speciation across mountain ranges (92), between isolated inselbergs (93), and in fragments of forests and wetlands created during the wet-dry cycles of the Quaternary (94, 95). Narrow endemism is also linked to adaptive radiation across the island's steep environmental gradients (81, 94, 96).

Human use of biodiversity

Madagascar's rich biodiversity, particularly its diverse flora, has provided many opportunities for human utilization. Although biodiversity is “useful” in many ways (e.g., ecosystem services or nature's contributions to people, either material or non-material), here we report “utilized species” as those having a documented direct use by humans. Of the 40,283 plant species documented as used by humans worldwide (97), 1916 (5%) are found in Madagascar—of

these, 1596 are thought to be native and 597 endemic to the island (98). Hundreds of utilized species have also been introduced, such as the Mesoamerican vanilla orchid (*Vanilla planifolia*), brought to Madagascar from the island of Réunion by the French in the mid-1800s, following the discovery of a method to speed up hand pollination by Edmond Albius in 1841 (99). Vanilla is the second most expensive spice in the world, and Madagascar has become the largest producer globally (100). Vanilla agroforestry is currently expanding, especially in northeastern (Sava region) and eastern (Analanjiroro and Atsinanana regions) Madagascar, which can pose additional threats to biodiversity in some cases. However, it can also generate opportunities for conservation and restoration when undertaken in sustainable and safe settings and accounting for local land use history (100–102). Beyond the widespread cultivation of a few introduced species, the goods and services provided by Madagascar's flora are especially important for subsistence in many rural communities (103).

Documented utilized endemic plants include 310 species used for materials (e.g., woods,

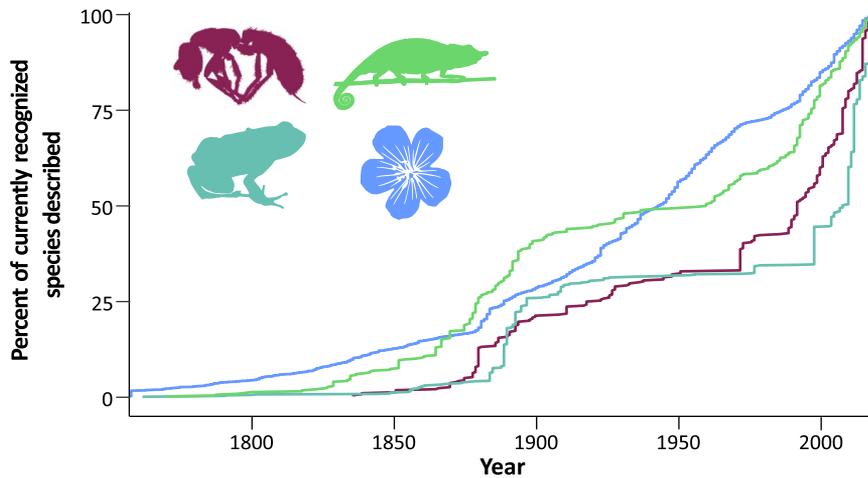


Fig. 5. Rates of scientific documentation. Percentage of described Malagasy ants, amphibians, reptiles, and vascular plants through time, based on year of basionym publication (22).

fibers, resins) (104), 91 edible species, and an additional 120 crop wild relatives that represent genetic reservoirs for the improvement of food crops. Among the most important edible groups, 38 species of yams (*Dioscorea* spp.) are native to Madagascar, 31 of which are endemic (105). Most have edible tubers and are widely consumed throughout the island, especially when primary crops fail (105, 106). Crop wild relatives with potential for commercial benefits include Madagascar's 65 species of coffee, *Coffea* spp. (107–109), which could be used as gene and trait sources for the improvement of the two non-native but commercially grown coffee species, robusta (*C. canephora*) and Arabica (*C. arabica*), for example to confer greater climate resilience (110).

Many of Madagascar's 204 native palm species (99% of which are endemic) are used by people and often for multiple purposes, e.g., construction materials, fibers, medicine, and food (111). Structural constraints of palms mean that palm exploitation is often fatal to the trees. Consequently, palm populations are often denuded in otherwise intact habitats as a result of selective extraction, which contributes to palms being among the most threatened of the assessed plant groups in Madagascar, with more than 83% of species evaluated as threatened (112).

At least 221 endemic plant species have been documented as having medicinal value (97, 113–115). These include several species of *Zanthoxylum*, which have antiplasmodial properties and are used locally to treat malaria (116), and the widely cultivated Madagascar periwinkle (*Catharanthus roseus*), which contains diverse and abundant alkaloids used in the treatment of some cancers and other diseases such as diabetes, high blood pressure, and asthma (117). Many plant species are used solely in traditional medicine practices in Madagascar.

Although scientific knowledge remains incomplete on the topic, medicinal plant species have been documented as being used for a wide range of health conditions across many regions and ecosystems (103, 118–120), highlighting the effective and potential value of Malagasy plant diversity for humanity.

The human uses of animals are not as extensive as those of plants, but hunting for meat, especially forest-dwelling species, provides an important source of nutrition and protein for some communities (121, 122) and exerts considerable pressure on wild populations (123–125). Consumption of insects—particularly orthopterans, lepidopterans, and coleopterans—is also widespread. Beyond what we report, there are certainly additional potential uses of plants that have yet to be published or discovered, and additional uses of currently utilized species that have not been documented by scientists. The data reported here are certainly underestimates.

Madagascar's rich biodiversity has diverse values. Among them, the multitude of known and potential uses reported here reinforce the imperative to conserve the unique Malagasy biota in the face of major threats such as habitat loss and overexploitation (2).

Concluding remarks

Our synthesis shows that the depth and breadth of Madagascar's remarkable biodiversity—the product of millions of years of evolution in relative isolation (Figs. 1 and 2)—is still being uncovered. Although the scientific community has accumulated a great amount of information on some taxonomic groups, others remain relatively unknown, particularly fungi and most invertebrates. Fundamental information on biodiversity and its uses is essential for guiding conservation action (2). The gathering and analysis of these data must therefore con-

tinue and accelerate, through equitable practices, if we are to safeguard the multifaceted aspects of Madagascar's unique biota.

REFERENCES AND NOTES

1. A. D. Barnosky et al., Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787 (2017). doi: [10.1126/science.aah4787](https://doi.org/10.1126/science.aah4787); pmid: [28183912](https://pubmed.ncbi.nlm.nih.gov/28183912/)
2. H. Ralimanana et al., *Science* **378**, adf1466 (2022). doi: [10.1126/science.adf1466](https://doi.org/10.1126/science.adf1466)
3. N. A. Wells, in *The Natural History of Madagascar*. S. M. Goodman, J. P. Benstead, Eds. (Univ. of Chicago Press, 2003), pp. 16–34.
4. H. Ralimanana et al., Madagascar's extraordinary biodiversity: a data repository, Version 6, Zenodo (2022); <https://doi.org/10.5281/zenodo.5017212>.
5. L. Gautier, P. P. Lowry II, S. M. Goodman, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 452–464.
6. A. Crottini et al., Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K-T boundary in Madagascar. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 5358–5363 (2012). doi: [10.1073/pnas.1112487109](https://doi.org/10.1073/pnas.1112487109); pmid: [22431616](https://pubmed.ncbi.nlm.nih.gov/22431616/)
7. K. E. Samonds et al., Imperfect isolation: Factors and filters shaping Madagascar's extant vertebrate fauna. *PLoS ONE* **8**, e62086 (2013). doi: [10.1371/journal.pone.0062086](https://doi.org/10.1371/journal.pone.0062086); pmid: [23626770](https://pubmed.ncbi.nlm.nih.gov/23626770/)
8. K. E. Samonds, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 69–73.
9. E. F. A. Toussaint, M. Fikáček, A. E. Z. Short, India–Madagascar vicariance explains cascade beetle biogeography. *Biol. J. Linn. Soc. Lond.* **118**, 982–991 (2016). doi: [10.1111/bj12791](https://doi.org/10.1111/bj12791)
10. A. D. Yoder, M. D. Nowak, Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annu. Rev. Ecol. Syst.* **37**, 405–431 (2006). doi: [10.1146/annurev.ecolsys.37.091305.110239](https://doi.org/10.1146/annurev.ecolsys.37.091305.110239)
11. S. Buerki, D. S. Devey, M. W. Callmander, P. B. Phillipson, F. Forest, Spatio-temporal history of the endemic genera of Madagascar. *Bot. J. Linn. Soc.* **171**, 304–329 (2013). doi: [10.1111/boj.12008](https://doi.org/10.1111/boj.12008)
12. M. Rivas-Ferreiro, L. M. Suz, S. M. Skarha, F. Rakotonasolo, B. T. M. Dentinger, ITS-based assessment of Madagascar's fungal diversity and arrival of EcM fungi to the island. *bioRxiv* 2022.2003.2009.483579 [Preprint] (2022); doi: [10.1101/2022.03.09.483579](https://doi.org/10.1101/2022.03.09.483579)
13. J. R. Ali, M. Huber, Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653–656 (2010). doi: [10.1038/nature08706](https://doi.org/10.1038/nature08706); pmid: [20090678](https://pubmed.ncbi.nlm.nih.gov/20090678/)
14. J. C. Masters et al., Biogeographic mechanisms involved in the colonization of Madagascar by African vertebrates: Rifting, rafting and runways. *J. Biogeogr.* **48**, 492–510 (2021). doi: [10.1111/jbi.14032](https://doi.org/10.1111/jbi.14032)
15. J. R. Ali, S. B. Hedges, A review of geological evidence bearing on proposed Cenozoic land connections between Madagascar and Africa and its relevance to biogeography. *Earth Sci. Rev.* **232**, 104103 (2022). doi: [10.1016/j.earscirev.2022.104103](https://doi.org/10.1016/j.earscirev.2022.104103)
16. B. H. Warren, D. Strasberg, J. H. Bruggemann, R. P. Prys-Jones, C. Thébaud, Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics* **26**, 526–538 (2010). doi: [10.1111/j.1096-0031.2009.00300.x](https://doi.org/10.1111/j.1096-0031.2009.00300.x); pmid: [34875766](https://pubmed.ncbi.nlm.nih.gov/34875766/)
17. S. N. Stephenson et al., Cenozoic Dynamic Topography of Madagascar. *Geochem. Geophys.* **22**, e2020GC009624 (2021). doi: [10.1111/j.1096-0031.2009.00300.x](https://doi.org/10.1111/j.1096-0031.2009.00300.x); pmid: [34875766](https://pubmed.ncbi.nlm.nih.gov/34875766/)
18. G. G. Roberts, J. D. Paul, N. White, J. Winterbourne, Temporal and spatial evolution of dynamic support from river profiles: A framework for Madagascar. *Geochem. Geophys.* **13**, e2020GC009624 (2012). doi: [10.1111/j.1096-0031.2009.00300.x](https://doi.org/10.1111/j.1096-0031.2009.00300.x); pmid: [34875766](https://pubmed.ncbi.nlm.nih.gov/34875766/)
19. H. Humbert, in *Notice de la carte de Madagascar*, H. Humbert, G. Cours-Darne, Eds. (Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry, 1965), vol. hors série, pp. 46–78.
20. P. P. Lowry II, G. E. Schatz, P. B. Phillipson, in *Natural change and human impact in Madagascar*, S. M. Goodman, B. Patterson, Eds. (Smithsonian Institution Press, 1997), pp. 93–123.

21. J. Moat, P. Smith, *Atlas de La Vegetation de Madagascar*. (Royal Botanic Gardens, Kew, 2007).
22. Materials, methods, and supplementary data are available as supplementary materials.
23. L. Gautier, A. J. Tahinarivony, P. Ranirison, S. Wohlhauser, in *The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota*, S. M. Goodman, M. J. Raheerilalao, S. Wohlhauser, Eds. (Association Vahatra, 2018).
24. D. A. Keith *et al.*, The IUCN Global Ecosystem Typology v1.01: Descriptive profiles for Biomes and Ecosystem Functional Groups. (IUCN, CEM, 2020).
25. D. Edler, T. Guedes, A. Zizka, M. Rosvall, A. Antonelli, Infomapp Bioregions: Interactive Mapping of Biogeographical Regions from Species Distributions. *Syst. Biol.* **66**, 197–204 (2017). doi: [10.1093/sysbio/syw087](https://doi.org/10.1093/sysbio/syw087); pmid: [27694311](https://pubmed.ncbi.nlm.nih.gov/27694311/)
26. R. E. Dewar, A. F. Richard, Evolution in the hypervariable environment of Madagascar. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 13723–13727 (2007). doi: [10.1073/pnas.0704346104](https://doi.org/10.1073/pnas.0704346104); pmid: [17698810](https://pubmed.ncbi.nlm.nih.gov/17698810/)
27. K. B. Karsten, L. N. Andriamandimbarisoa, S. F. Fox, C. J. Raxworthy, A unique life history among tetrapods: An annual chameleon living mostly as an egg. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 8980–8984 (2008). doi: [10.1073/pnas.0802468105](https://doi.org/10.1073/pnas.0802468105); pmid: [18591659](https://pubmed.ncbi.nlm.nih.gov/18591659/)
28. C. E. R. Lehmann, C. L. Solofondranohatra, J. A. Morton, L. N. Phelps, H. Ralimanana, J. Razanatsoa, V. Rakotoarimanana, S. S. Vorontsova, in *The New Natural History of Madagascar* S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 152–168.
29. B. E. Crowley, L. R. Godfrey, J. P. Hansford, K. E. Samonds, Seeing the forest for the trees—and the grasses: Revisiting the evidence for grazer-maintained grasslands in Madagascar's Central Highlands. *Proc. Biol. Sci.* **288**, 20201785 (2021). pmid: [33978523](https://pubmed.ncbi.nlm.nih.gov/33978523/)
30. M. Ohba, K. E. Samonds, M. LaFleur, J. R. Ali, L. R. Godfrey, Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **441**, 688–695 (2016). doi: [10.1016/j.palaeo.2015.10.028](https://doi.org/10.1016/j.palaeo.2015.10.028)
31. K. Douglass *et al.*, A critical review of radiocarbon dates clarifies the human settlement of Madagascar. *Quat. Sci. Rev.* **221**, 105878 (2019). doi: [10.1016/j.quascirev.2019.105878](https://doi.org/10.1016/j.quascirev.2019.105878)
32. J. Hansford *et al.*, Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. *Sci. Adv.* **4**, eaat6925 (2018). doi: [10.1126/sciadv.aat6925](https://doi.org/10.1126/sciadv.aat6925); pmid: [30214938](https://pubmed.ncbi.nlm.nih.gov/30214938/)
33. R. E. Dewar, A. F. Richard, Madagascar: A history of arrivals, what happened, and will happen next. *Annu. Rev. Anthropol.* **41**, 495–517 (2012). doi: [10.1146/annurev-anthro-092611-145758](https://doi.org/10.1146/annurev-anthro-092611-145758)
34. D. Pierron *et al.*, Genomic landscape of human diversity across Madagascar. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E6498–E6506 (2017). pmid: [28716916](https://pubmed.ncbi.nlm.nih.gov/28716916/)
35. D. A. Burney, G. S. Robinson, L. P. Burney, *Sporormiella* and the late Holocene extinctions in Madagascar. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 10800–10805 (2003). doi: [10.1073/pnas.1534700100](https://doi.org/10.1073/pnas.1534700100); pmid: [12960385](https://pubmed.ncbi.nlm.nih.gov/12960385/)
36. B. E. Crowley, K. E. Samonds, Stable carbon isotope values confirm a recent increase in grasslands in northwestern Madagascar. *Holocene* **23**, 1066–1073 (2013). doi: [10.1177/0959683613484675](https://doi.org/10.1177/0959683613484675)
37. B. E. Crowley, A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quat. Sci. Rev.* **29**, 2591–2603 (2010). doi: [10.1016/j.quascirev.2010.06.030](https://doi.org/10.1016/j.quascirev.2010.06.030)
38. J. P. Hansford, A. M. Lister, E. M. Weston, S. T. Turvey, Simultaneous extinction of Madagascar's megaherbivores correlates with late Holocene human-caused landscape transformation. *Quat. Sci. Rev.* **263**, 106996 (2021). doi: [10.1016/j.quascirev.2021.106996](https://doi.org/10.1016/j.quascirev.2021.106996)
39. B. E. Crowley *et al.*, Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. *Ecography* **40**, 901–912 (2017). doi: [10.1111/ecog.02376](https://doi.org/10.1111/ecog.02376)
40. S. W. Hixon *et al.*, Late Holocene spread of pastoralism coincides with endemic megafaunal extinction on Madagascar. *Proc. Biol. Sci.* **288**, 20211204 (2021). pmid: [34284627](https://pubmed.ncbi.nlm.nih.gov/34284627/)
41. L. R. Godfrey *et al.*, A new interpretation of Madagascar's megafaunal decline: The "Subsistence Shift Hypothesis". *J. Hum. Evol.* **130**, 126–140 (2019). doi: [10.1016/j.jhevol.2019.03.002](https://doi.org/10.1016/j.jhevol.2019.03.002); pmid: [31010539](https://pubmed.ncbi.nlm.nih.gov/31010539/)
42. M. Virah-Sawmy, K. J. Willis, L. Gillson, Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. *J. Biogeogr.* **37**, 506–519 (2010). doi: [10.1111/j.1365-2699.2009.02203.x](https://doi.org/10.1111/j.1365-2699.2009.02203.x)
43. A. Crowther *et al.*, Ancient crops provide first archaeological signature of the westward Austronesian expansion. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6635–6640 (2016). doi: [10.1073/pnas.1522714113](https://doi.org/10.1073/pnas.1522714113); pmid: [27247383](https://pubmed.ncbi.nlm.nih.gov/27247383/)
44. C. Radimilahy, *L' Ancienne Métallurgie du Fer a Madagascar*. British Archaeological Reports International Series 422 (BAR Publishing, 1988), pp. 246.
45. L. Rakotzafy, S. M. Goodman, Contribution à l'étude zoarchéologique de la région du Sud-ouest et extrême Sud de Madagascar sur la base des collections de l'ICMAA de l'Université d'Antananarivo, (2005).
46. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000). doi: [10.1038/35002501](https://doi.org/10.1038/35002501); pmid: [10706275](https://pubmed.ncbi.nlm.nih.gov/10706275/)
47. S. M. Goodman, J. R. Rakotoson, P. M. Razafimahatratra, M. J. Raheerilalao, in *The terrestrial protected areas of Madagascar: Their history, description, and biota*, S. M. Goodman, M. J. Raheerilalao, S. Wohlhauser, Eds. (Association Vahatra, 2018), pp. 33–78.
48. M. R. Moura, W. Jetz, Shortfalls and opportunities in terrestrial vertebrate species discovery. *Nat. Ecol. Evol.* **5**, 631–639 (2021). doi: [10.1038/s41559-021-01411-5](https://doi.org/10.1038/s41559-021-01411-5); pmid: [33753900](https://pubmed.ncbi.nlm.nih.gov/33753900/)
49. P. Baldrian, T. Větrovský, C. Lepinay, P. Kohout, High-throughput sequencing view on the magnitude of global fungal diversity. *Fungal Divers.* **114**, 539–547 (2021). doi: [10.1007/s13225-021-00472-Y](https://doi.org/10.1007/s13225-021-00472-Y)
50. U. Kjörlig *et al.*, Towards a unified paradigm for sequence-based identification of fungi. *Mol. Ecol.* **22**, 5271–5277 (2013). doi: [10.1111/mec.12481](https://doi.org/10.1111/mec.12481); pmid: [24112409](https://pubmed.ncbi.nlm.nih.gov/24112409/)
51. Index Fungorum. (Index Fungorum Partnership, 2021); <http://www.indexfungorum.org/>.
52. Plutof. (Plutof, 2020); <https://plutof.ut.ee/>.
53. A. Aptroot, Preliminary checklist of the lichens of Madagascar, with two new thelotrema Graphidaceae and 131 new records. *Willdenowia* **46**, 349–365 (2016). doi: [10.3372/wi.46.46304](https://doi.org/10.3372/wi.46.46304)
54. A. Aptroot, F. Schumm, Lichenized ascomycetes: Lichens, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 499–510.
55. Z. T. Nagy, G. Sonet, F. Glaw, M. Vences, First Large-Scale DNA Barcoding Assessment of Reptiles in the Biodiversity Hotspot of Madagascar, Based on Newly Designed COI Primers. *PLOS ONE* **7**, e34506 (2012).
56. D. R. Vieites *et al.*, Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 8267–8272 (2009). doi: [10.1073/pnas.0810821106](https://doi.org/10.1073/pnas.0810821106); pmid: [19416818](https://pubmed.ncbi.nlm.nih.gov/19416818/)
57. Univ. of California, Amphibiaweb. (2021); <https://amphibiaweb.org/>.
58. R. G. B. Perl *et al.*, DNA barcoding Madagascar's amphibian fauna. *Amphib.-Reptil.* **35**, 197–206 (2014). doi: [10.1163/15685381-00002942](https://doi.org/10.1163/15685381-00002942)
59. B. L. Fisher, C. Peeters, *Ants of Madagascar: A Guide to the 62 Genera*. (Association Vahatra, 2019), pp. 260.
60. B. Bolton, An online catalog of the ants of the world. (2022); <https://antcat.org>.
61. M. S. Vorontsova *et al.*, Inequality in plant diversity knowledge and unrecorded plant extinctions: An example from the grasses of Madagascar. *Plants People Planet* **3**, 45–60 (2021). doi: [10.1002/ppp3.10123](https://doi.org/10.1002/ppp3.10123)
62. J. P. Herrera, Prioritizing protected areas in Madagascar for lemur diversity using a multidimensional perspective. *Biol. Conserv.* **207**, 1–8 (2017). doi: [10.1016/j.biocon.2016.12.028](https://doi.org/10.1016/j.biocon.2016.12.028)
63. F. Glaw, A. Crottini, A. Rakotoarison, M. D. Scherz, M. Vences, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1305–1322.
64. J. S. Sparks, M. L. J. Stiasny, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1245–1260.
65. M. Vences, A. Raselimanana, in *The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota*, S. M. Goodman, M. J. Raheerilalao, S. Wohlhauser, Eds. (Association Vahatra, 2018), pp. 289–327.
66. I. Tattersal, F. Cuozzo, in *The terrestrial protected areas of Madagascar: Their History, Description, and Biota*, S. M. Goodman, M. J. Raheerilalao, S. Wohlhauser, Eds. (Association Vahatra, 2018), pp. 403–421.
67. M. V. F. Glaw, C. J. Raxworthy, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1423–1442.
68. S. M. Goodman, V. Soarimalala, in *New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1737–1769.
69. B. L. Fisher, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 847–853.
70. R. Paulian, P. Viette, in *The Natural History of Madagascar*, S. M. Goodman, J. P. Benstead, Eds. (Chicago Univ. Press, 2003), pp. 503–511.
71. R. J. Safford, S. M. Goodman, M. J. Raheerilalao, A. F. A. Hawkins, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1553–1602.
72. D. E. Wilson, D. M. Reeder, Eds., *Mammal Species of the World: A Taxonomic and Geographic Reference (3rd ed)*, (Johns Hopkins Univ. Press, 2005).
73. C. J. Burgin, J. P. Colella, P. L. Kahn, N. S. Upham, How many species of mammals are there? *J. Mammal.* **99**, 1–14 (2018). doi: [10.1093/jmammal/gyx147](https://doi.org/10.1093/jmammal/gyx147)
74. F. Glaw, O. Hawlitschek, K. Glaw, M. Vences, Integrative evidence confirms new endemic island frogs and transmarine dispersal of amphibians between Madagascar and Mayotte (Comoros archipelago). *Naturwissenschaften* **106**, 19 (2019). doi: [10.1007/s00114-019-1618-9](https://doi.org/10.1007/s00114-019-1618-9); pmid: [31041592](https://pubmed.ncbi.nlm.nih.gov/31041592/)
75. D. R. Vieites, S. Nieto-Román, M. P. Fernández, J. H. Santos-Santos, Hidden in plain sight: A new frog species of the genus *Blommersia* from the oceanic island of Mayotte, Comoros archipelago. *ZooKeys* **994**, 149–166 (2020). doi: [10.3897/zookeys.994.57012](https://doi.org/10.3897/zookeys.994.57012); pmid: [33273885](https://pubmed.ncbi.nlm.nih.gov/33273885/)
76. P. P. Lowry II, P. B. Phillipson, L. Andrimaheravaro, G. E. Schatz, F. Rajoanary, S. Andriambolohera, in *The terrestrial protected areas of Madagascar: Their History, Description, and Biota*, S. M. Goodman, M. J. Raheerilalao, S. Wohlhauser, Eds. (Association Vahatra, 2018), pp. 243–255.
77. Madagascar Catalogue, Catalogue of the Vascular Plants of Madagascar (Missouri Botanical Garden, 2021); <http://legacy.tropicos.org/Project/Madagascar>. [accessed 12 May 2022].
78. M. S. Vorontsova *et al.*, Madagascar's grasses and grasslands: Anthropogenic or natural? *Proc. Biol. Sci.* **283**, 20152262 (2016). pmid: [26791612](https://pubmed.ncbi.nlm.nih.gov/26791612/)
79. M. W. Callmander *et al.*, The endemic and non-endemic vascular flora of Madagascar updated. *Plant Ecol. Evol.* **144**, 121–125 (2011). doi: [10.5091/plecevo.2011.513](https://doi.org/10.5091/plecevo.2011.513)
80. L. Marline, C. Ah-Peng, T. A. J. Hedderson, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 510–520.
81. J. L. Brown, A. Cameron, A. D. Yoder, M. Vences, A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nat. Commun.* **5**, 5046 (2014). doi: [10.1038/ncomms6046](https://doi.org/10.1038/ncomms6046); pmid: [25297804](https://pubmed.ncbi.nlm.nih.gov/25297804/)
82. M. Rakotoarivony *et al.*, Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar: A tropical biodiversity hotspot. *Proc. Biol. Sci.* **280**, 20123048 (2013). pmid: [23427173](https://pubmed.ncbi.nlm.nih.gov/23427173/)
83. B. Isambert *et al.*, Endemism and evolutionary history in conflict over Madagascar's freshwater conservation priorities. *Biol. Conserv.* **144**, 1902–1909 (2011). doi: [10.1016/j.biocon.2011.04.016](https://doi.org/10.1016/j.biocon.2011.04.016)
84. S. Buerki *et al.*, Incorporating evolutionary history into conservation planning in biodiversity hotspots. *Philos. Trans. R. Soc. B* **370**, 20140014 (2015). doi: [10.1098/rstb.2014.0014](https://doi.org/10.1098/rstb.2014.0014); pmid: [25561675](https://pubmed.ncbi.nlm.nih.gov/25561675/)
85. A. Soulebeau, R. Pellens, P. P. Lowry, X. Aubriot, M. E. K. Evans, T. Haevermans, in *Biodiversity Conservation and Phylogenetic Systematics: Preserving our evolutionary heritage in an extinction crisis*, R. Pellens, P. Grandcolas, Eds. (Springer, 2016), pp. 355–374.
86. C. J. Raxworthy, R. A. Nussbaum, Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. *J. Zool.* **235**, 525–558 (1995). doi: [10.1111/j.1469-7998.1995.tb01767.x](https://doi.org/10.1111/j.1469-7998.1995.tb01767.x)
87. N. Ray, J. M. Adams, A GIS-based Vegetation Map of the World at the Last Glacial Maximum (25,000–15,000 BP). *Internet Archaeol.* **11**, ia.11.2 (2001). doi: [10.1111/ia.11.2](https://doi.org/10.1111/ia.11.2)
88. H. N. Andriananjamanantsoa, S. Engberg, E. E. Louis Jr., L. Brouillet, Diversification of *Angraecum* (Orchidaceae, Vandaeae) in Madagascar: Revised phylogeny reveals species accumulation through time rather than rapid radiation. *PLOS ONE* **11**, e0163194 (2016). doi: [10.1371/journal.pone.0163194](https://doi.org/10.1371/journal.pone.0163194); pmid: [27669569](https://pubmed.ncbi.nlm.nih.gov/27669569/)
89. F. T. Burbrink *et al.*, The origins and diversification of the exceptionally rich gerrhonotines (Colubroidea: Lamprophiidae: Pseudohyphinae) in Madagascar. *Syst. Biol.* **68**, 918–936 (2019). doi: [10.1093/sysbio/syz026](https://doi.org/10.1093/sysbio/syz026); pmid: [31188455](https://pubmed.ncbi.nlm.nih.gov/31188455/)

90. C. R. Hutter, S. M. Lambert, Z. F. Andriampemanana, F. Glaw, M. Vences, Molecular phylogeny and diversification of Malagasy bright-eyed tree frogs (Mantelliidae: *Boophis*). *Mol. Phylogenet. Evol.* **127**, 568–578 (2018). doi: [10.1016/j.jmpev.2018.05.027](https://doi.org/10.1016/j.jmpev.2018.05.027); pmid: 29894731
91. M. S. Vorontsova et al., in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 585–598.
92. K. C. Wollenberg et al., Patterns of endemism and species richness in Malagasy cophylinae frogs support a key role of mountainous areas for speciation. *Evolution* **62**, 1890–1907 (2008). doi: [10.1111/j.1558-5646.2008.00420.x](https://doi.org/10.1111/j.1558-5646.2008.00420.x); pmid: 18485110
93. M. N. Rabarimanarivo et al., The extraordinary botanical diversity of inselbergs in Madagascar. *Candollea* **74**, 65–84 (2019).
94. M. Vences, K. C. Wollenberg, D. R. Vieites, D. C. Lees, Madagascar as a model region of species diversification. *Trends Ecol. Evol.* **24**, 456–465 (2009). doi: [10.1016/j.tree.2009.03.011](https://doi.org/10.1016/j.tree.2009.03.011); pmid: 19500874
95. L. Wilmé, S. M. Goodman, J. U. Ganzhorn, Biogeographic evolution of Madagascar's microendemic biota. *Science* **312**, 1063–1065 (2006). doi: [10.1126/science.1122806](https://doi.org/10.1126/science.1122806); pmid: 16709785
96. R. G. Pearson, C. J. Raxworthy, The evolution of local endemism in Madagascar: Watershed versus climatic gradient hypotheses evaluated by null biogeographic models. *Evolution* **63**, 959–967 (2009). doi: [10.1111/j.1558-5646.2008.00596.x](https://doi.org/10.1111/j.1558-5646.2008.00596.x); pmid: 19210532
97. M. Diazgranados et al., World Checklist of Useful Plant Species, Version 2.1.1, Knowledge Network for Biocomplexity (2020); doi: [10.5063/F1CV4G34](https://doi.org/10.5063/F1CV4G34).
98. WCPV, World Checklist of Vascular Plants, version 2.0. (2020); <https://wcvp.science.keew.org/>.
99. S. Ramachandra Rao, G. A. Ravishanker, Vanilla flavour: Production by conventional and biotechnological routes. *J. Sci. Food Agric.* **80**, 289–304 (2000). doi: [10.1002/1097-0010\(200002\)80:3<289:ADJ-SA543>3.0.CO;2](https://doi.org/10.1002/1097-0010(200002)80:3<289:ADJ-SA543>3.0.CO;2)
100. D. S. Correll, Vanilla-its botany, history, cultivation and economic import. *Econ. Bot.* **7**, 291–358 (1953). doi: [10.1007/BF02930810](https://doi.org/10.1007/BF02930810)
101. D. Hending, A. Andrianiaina, Z. Rakotomalala, S. Cotton, The use of vanilla plantations by lemurs: Encouraging findings for both lemur conservation and sustainable agroforestry in the Sava Region, Northeast Madagascar. *Int. J. Primatol.* **39**, 141–153 (2018). doi: [10.1007/s10764-018-0022-1](https://doi.org/10.1007/s10764-018-0022-1)
102. D. A. Martin et al., Bird diversity and endemism along a land-use gradient in Madagascar: The conservation value of vanilla agroforests. *Biotropica* **53**, 179–190 (2021). doi: [10.1111/btp.12859](https://doi.org/10.1111/btp.12859)
103. T. N. Randrianarivony et al., The most used medicinal plants by communities in Mahaboboka, Amoronabo, Mikoboka, Southwestern Madagascar. *J. Ethnobiol. Ethnomed.* **13**, 19 (2017). doi: [10.1186/s13002-017-0147-x](https://doi.org/10.1186/s13002-017-0147-x); pmid: 28279184
104. N. Rakotoarivelo et al., Ethnobotanical and economic value of *Ravenala madagascariensis* Sonn. in Eastern Madagascar. *J. Ethnobiol. Ethnomed.* **10**, 57 (2014). doi: [10.1186/1746-4269-10-57](https://doi.org/10.1186/1746-4269-10-57); pmid: 25027625
105. P. Wilkin et al., in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 545–551.
106. V. H. Jeannoda et al., Les ignames (*Dioscorea* spp.) de Madagascar: Espèces endémiques et formes introduites; diversité, perception, valeur nutritionnelle et systèmes de gestion durable. *Rev. Écol.* **62**, 191–207 (2007).
107. A. P. Davis, R. Govaerts, D. M. Bridson, P. Stoffelen, An annotated taxonomic conspectus of the genus *Coffea* (Rubiaceae). *Bot. J. Linn. Soc.* **152**, 465–512 (2006). doi: [10.1111/j.1095-8339.2006.00584.x](https://doi.org/10.1111/j.1095-8339.2006.00584.x)
108. A. P. Davis, F. Rakotonasolo, Six new species of coffee (*Coffea*) from northern Madagascar. *Kew Bull.* **76**, 497–511 (2021). doi: [10.1007/s12225-021-09952-5](https://doi.org/10.1007/s12225-021-09952-5)
109. A. P. Davis, F. Rakotonasolo, P. De Block, *Coffea toshii* sp. nov. (Rubiaceae) from Madagascar. *Nord. J. Bot.* **28**, 134–136 (2010). doi: [10.1111/j.1756-1051.2010.00710.x](https://doi.org/10.1111/j.1756-1051.2010.00710.x)
110. A. P. Davis et al., High extinction risk for wild coffee species and implications for coffee sector sustainability. *Sci. Adv.* **5**, eaav3473 (2019). doi: [10.1126/sciadv.aav3473](https://doi.org/10.1126/sciadv.aav3473); pmid: 30746478
111. J. Dransfield, H. Beentje, *The Palms of Madagascar*. (Royal Botanic Gardens and The International Palm Society, 1995).
112. M. Rakotoarivony, J. Dransfield, S. P. Bachman, J. Moat, W. J. Baker, Comprehensive Red List assessment reveals exceptionally high extinction risk to Madagascar palms. *PLOS ONE* **9**, e103684 (2014). doi: [10.1371/journal.pone.0103684](https://doi.org/10.1371/journal.pone.0103684); pmid: 25075612
113. O. M. Grace et al., Plant Power: Opportunities and challenges for meeting sustainable energy needs from the plant and fungal kingdoms. *Plants People Planet* **2**, 446–462 (2020). doi: [10.1002/ppp3.10147](https://doi.org/10.1002/ppp3.10147)
114. E. Nic Lughadha et al., Extinction risk and threats to plants and fungi. *Plants People Planet* **2**, 389–408 (2020). doi: [10.1002/ppp3.10146](https://doi.org/10.1002/ppp3.10146)
115. T. Ulian et al., Unlocking plant resources to support food security and promote sustainable agriculture. *Plants People Planet* **2**, 421–445 (2020). doi: [10.1002/ppp3.10145](https://doi.org/10.1002/ppp3.10145)
116. M. Randrianarivelojosa et al., Plants traditionally prescribed to treat tazo (malaria) in the eastern region of Madagascar. *Malar. J.* **2**, 25–25 (2003). doi: [10.1186/1475-2875-2-25](https://doi.org/10.1186/1475-2875-2-25); pmid: 12921540
117. S. Das, A. B. Sharangi, Madagascar periwinkle (*Catharanthus roseus* L.): Diverse medicinal and therapeutic benefits to humankind. *J. Pharmacogn. Phytochem.* **6**, 1695–1701 (2017).
118. N. H. Rakotoarivelo et al., Medicinal plants used to treat the most frequent diseases encountered in Ambalabe rural community, Eastern Madagascar. *J. Ethnobiol. Ethnomed.* **11**, 68 (2015). doi: [10.1186/s13002-015-0050-2](https://doi.org/10.1186/s13002-015-0050-2); pmid: 26369781
119. A. Miora Henintsoa et al., Medicinal plants from the Ankaratra Mountain in Madagascar: Diversity and uses. *Research Square*, (2022).
120. M. Razafindraibe et al., Medicinal plants used by women from Agnalazaha littoral forest (Southeastern Madagascar). *J. Ethnobiol. Ethnomed.* **9**, 73 (2013). doi: [10.1186/1746-4269-9-73](https://doi.org/10.1186/1746-4269-9-73); pmid: 24188563
121. C. Borgerson et al., The use of natural resources to improve household income, health, and nutrition within the forests of Kianjavato, Madagascar. *Madag. Conserv. Dev.* **13**, 45 (2018). doi: [10.4314/mcd.v13i1.6](https://doi.org/10.4314/mcd.v13i1.6)
122. C. D. Golden, L. C. H. Fernald, J. S. Brashares, B. J. R. Rasolofoniaina, C. Kremen, Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 19653–19656 (2011). doi: [10.1073/pnas.1112586108](https://doi.org/10.1073/pnas.1112586108); pmid: 22106297
123. C. D. Golden, C. DeSisto, C. Borgerson, H. J. Randriamady, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 204–217.
124. Z. J. Farris et al., Hunting, exotic carnivores, and habitat loss: Anthropogenic effects on a native carnivore community, Madagascar. *PLOS ONE* **10**, e0136456 (2015). doi: [10.1371/journal.pone.0136456](https://doi.org/10.1371/journal.pone.0136456); pmid: 26375991
125. R. K. B. Jenkins et al., Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLOS ONE* **6**, e27570 (2011). doi: [10.1371/journal.pone.0027570](https://doi.org/10.1371/journal.pone.0027570); pmid: 22194787
126. S. M. Goodman, in *The New Natural History of Madagascar* (Princeton University Press, 2022), pp. 2246.

ACKNOWLEDGMENTS

A. Davis (RBG Kew) provided information on Rubiaceae, P. Kirk (RBG Kew) provided data from Index Fungorum, L. M. Suz (RBG Kew) provided information on mycorrhizal fungi, and S. N. Stephenson (University of Oxford) provided feedback on Malagasy geology. We thank J. Aronson (Missouri Botanical Garden), D. Ashley (UK Ambassador to Madagascar and Comoros), J. P. G. Jones (Bangor University), A. Lehavana (Missouri Botanical Garden), J. Ratsimbazafy (Houston Zoo and the Groupe d'Etude et de Recherche sur les Primates de Madagascar), S. Ratsirahonana (Fondation pour les Aires Protégées et la Biodiversité de Madagascar), and G. E. Schatz (Missouri Botanical Garden) for their insightful feedback on the first draft of the manuscript, and three anonymous reviewers for valuable feedback. We stress that all views expressed in this article are only those of the authors. **Funding:** A.A. acknowledges financial support from the Swedish Research Council (2019-05191), the Swedish Foundation for Strategic Research (FFL15-0196) and a grant from the Kew Foundation. T.A. was supported by the SciLifeLab and Wallenberg Data Driven Life Science Program, grant KAW 2020.0239. C.D.B. and M.F.T.J. were supported by a grant from the Swedish Research Council to C.D.B., grant 2017-04980. F.B. was supported by Fundação para a Ciência e a Tecnologia, grant PD/BD/128493/2017. J.B., J.H., S.P., and B.E.W. were supported by a Future Leader Fellowship from RBG Kew. N.A.C. was financed by H2020 MSCA-ITN-ETN PlantID, a European Union's Horizon 2020 research and innovation programme under grant agreement 765000. J.D.C. was supported by the Swiss National Science Foundation, grant P400PB_186733 and P4P4PB_191987. A.C. was supported by Portuguese National Funds through the Foundation for Science and Technology, FCT, grant 2020.00823.CEECIND and project PTDC/BIA-EVL/31254/2017. G.D. was supported by Vinnova, grant 2019-02717. D.E. was supported by the Swedish Research Council, grant 2016-00796, and the Swedish Foundation for Strategic

Research, grant FFL15-0196. S.F. was supported by the Swedish Research Council, grant 2017-03862. B.L.F. was supported by National Science Foundation, grant DEB-1655076. P.L.F. was supported by the MEMOVA project, EU Operational Programme Research, Development and Education, grant CZ.02.2.69/0.0/0.0/0.0/18_053/0016982. T.B.G. is supported by a young researcher grant from São Paulo Research Foundation (FAPESP, #2021/07161-6, #2022/09428-2), Brazil. M.C.H. and R.H. are Natural Environment Research Council funded Ph.D. students with the London NERC DTP (NERC Ref: NE/L002485/1). P.M.M. was funded by the Czech Science Foundation, grant GJ20-18566Y. B.N. was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brasil (CAPES) – (PDSE 88881.132750/2016-01). R.E.O. acknowledges the support of iDiv funded by the German Research Foundation (DFG–FZT 118, 202548816). A.S.T.P. was supported by the Natural Environment Research Council (NERC), grant NE/R001081/1. L.N.P. was supported by a Swiss National Science Foundation Early Postdoc Mobility Grant, grant P2LAP2_187745. M.R.H. was supported by a beca de doctorado del Instituto de Ecología y Biodiversidad, Chile; Programa de Doctorado en Biología y Ecología Aplicada, Universidad Católica del Norte, Universidad de La Serena, La Serena, Chile Ph.D. and a ANID National Scholarship (grant 21181931); Institute of Ecology and Biodiversity (Project ANID FB210006). E.R. was supported by the NRF / SASSCAL (Southern African Science Service Centre), grant 118589, and the NRF / African Origins Platform, grant 117666. F.S. was supported by European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement, grant 838998. D.S. received funding from the Swiss National Science Foundation (PCEFP3_187012) and from the Swedish Research Council (VR: 2019-04739). M.S.V. was supported by a GBIF: Biodiversity Information for Development grant. K.W. was supported by a Techné Arts and Humanities Research Council Doctoral Training Partnership. P.W. was supported by the Darwin Initiative, grants 22-005 and EIDP0049. **Author contributions:** The paper was project-led, with overall writing responsibility, by A.A., A.L.P., H.Ral., and R.J.S. The content was divided into two sections, with corresponding working groups, each making full use of the expertise and direct in-country experience of the 25 Malagasy co-authors. The sections were organized, written, and led by A.C., A.L.P., H.Ral., J.H., R.J.S., and W.T. Formal analyses were carried out by D.E., H.F., J.M., M.S.V., O.A.P., R.H., S.P., T.A., and W.T. Visualizations and figures were done by D.E., H.F., M.F.J.T., O.A.P., and W.T. This paper and its sister manuscript on threats and opportunities (2) were based on the outputs of a consortium focusing on Madagascar's biodiversity. The data curation, investigation and resources therefore formed the foundation for the project as a whole and we therefore list all co-authors involved in these activities across both papers. Data curation was carried out by A.C., A.M.A., A.Rak., A.Ras., A.Z., B.A.R., B.L.F., B.N., C.D.B., D.E., G.D., D.R., E.R., F.Raj., F.Rak., F.S., H.N.R., H.Ral., H.Raz., J.D.C., J.E.N.R., J.H., J.M., K.W., L.M., L.N.P., L.R.R., M.F.T.J., M.G.C.N., M.Rab., M.R.H., M.Ri., M.S.V., M.T.R., N.A., N.A.C., N.A.S.P., N.R., O.A.P., P.L.F., P.M.M., P.B.P., P.W., R.C., R.E.O., R.H., S.A., S.C., S.D., S.E.R., S.M.G., S.P., T.B.G., T.R., T.Z., V.Ran., V.Raz., and W.T. Investigation was carried out by A.C., A.M.A., A.Rak., A.Ras., A.S.T.P., B.A.R., B.N., F.B., F.Rak., H.N.R., H.Raz., M.G.C.N., O.A.P., O.M.G., P.L.F., P.M.M., P.W., R.A., R.H., R.S.C., S.E.R., and T.B.G. Methodology was developed by A.C., A.Z., B.E.W., C.E.R.L., D.S., J.H., J.M., J.S.B., L.N.P., M.S.V., S.P.B., and T.A. Resources were provided by A.C., D.R., E.R., J.R., L.M., M.Rak., M.S.V., M.T.R., N.A.S.P., and T.R. Software was designed by A.Z., B.E.W., D.E., D.S., and H.F. Validations were carried out by A.C., D.E., J.M., and W.J.B. All co-authors were involved in the writing, revision and editing of the text. **Competing interests:** Authors declare no competing interests. **Data and materials availability:** All data is available in the main text or the Supplementary Materials. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.sciencemag.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abf0869

Materials and Methods

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MDAR Reproducibility Checklist

Submitted 8 September 2021; accepted 7 November 2022

10.1126/science.abf0869

Madagascar's extraordinary biodiversity: Evolution, distribution, and use

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Science, 378 (6623), eabf0869.

Protecting Madagascar

Madagascar has been isolated from mainland Africa and Asia for more than 80 million years and has developed a distinctive flora and fauna, with more than 90% of its species endemic to the island nation. It is also home to the Malagasy people, with a population of about 30 million, and was first colonized by humans around the first century BCE. The island's biodiverse wildlife is highly threatened, and much of its human population lives below the poverty line. In Reviews, Antonelli *et al.* and Ralimanana *et al.* characterize the biological history and diversity of the island and examine conservation status and actions required to protect biodiversity and improve living standards and well-being for the Malagasy people. —SNV

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