REVIEW

BIODIVERSITY

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

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Madagascar's biota is hyperdiverse and includes exceptional levels of endemicity. 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 transformation 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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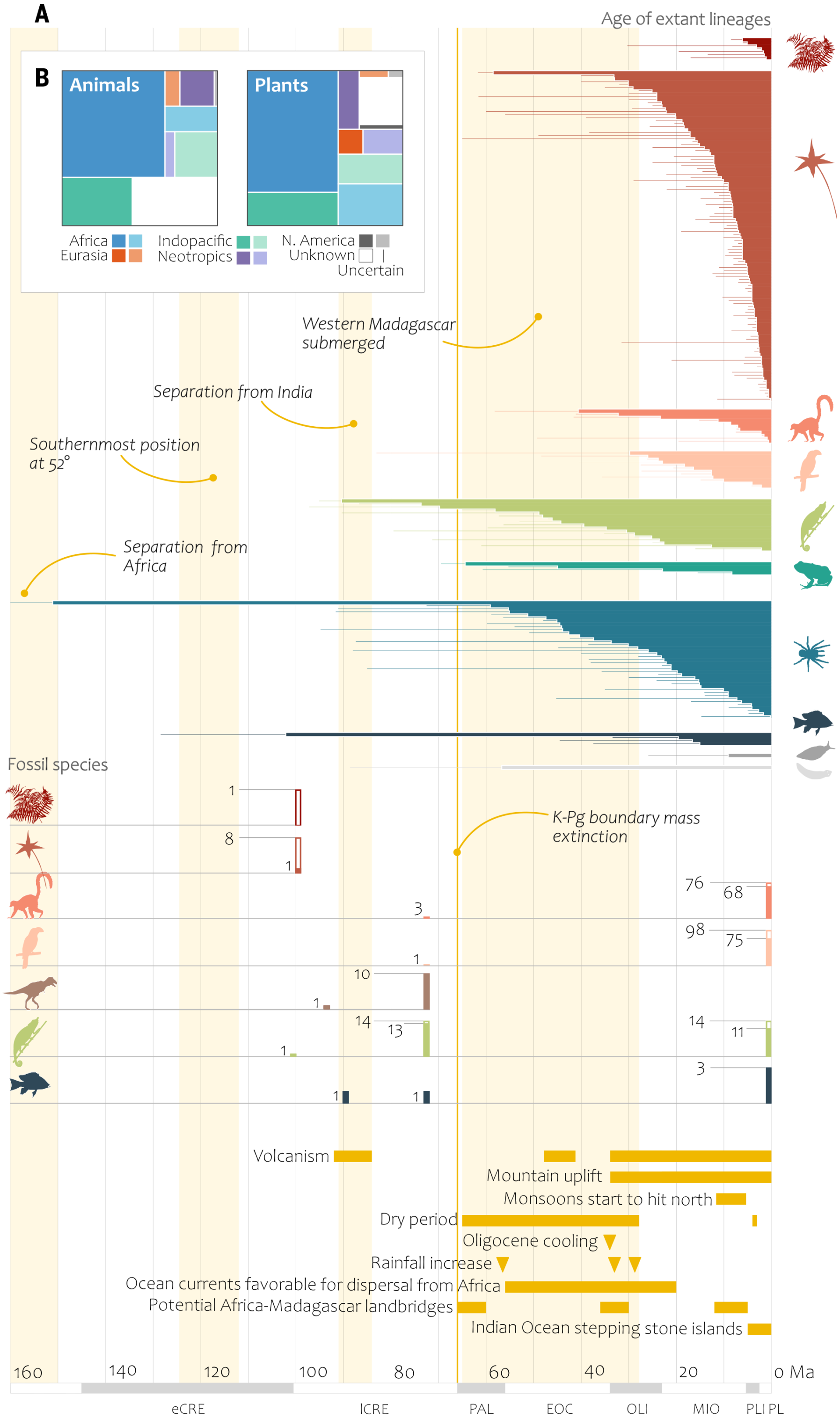

Fig. 1. Timing and origins of Madagascar's biodiversity. (**A**) Geological and environmental events in relation to the age of multiple organismal groups. The dark yellow horizontal bars at the bottom show the timing of landscape and climatic events. Vertical yellow shading along the panel corresponds 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; lCRE, 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.

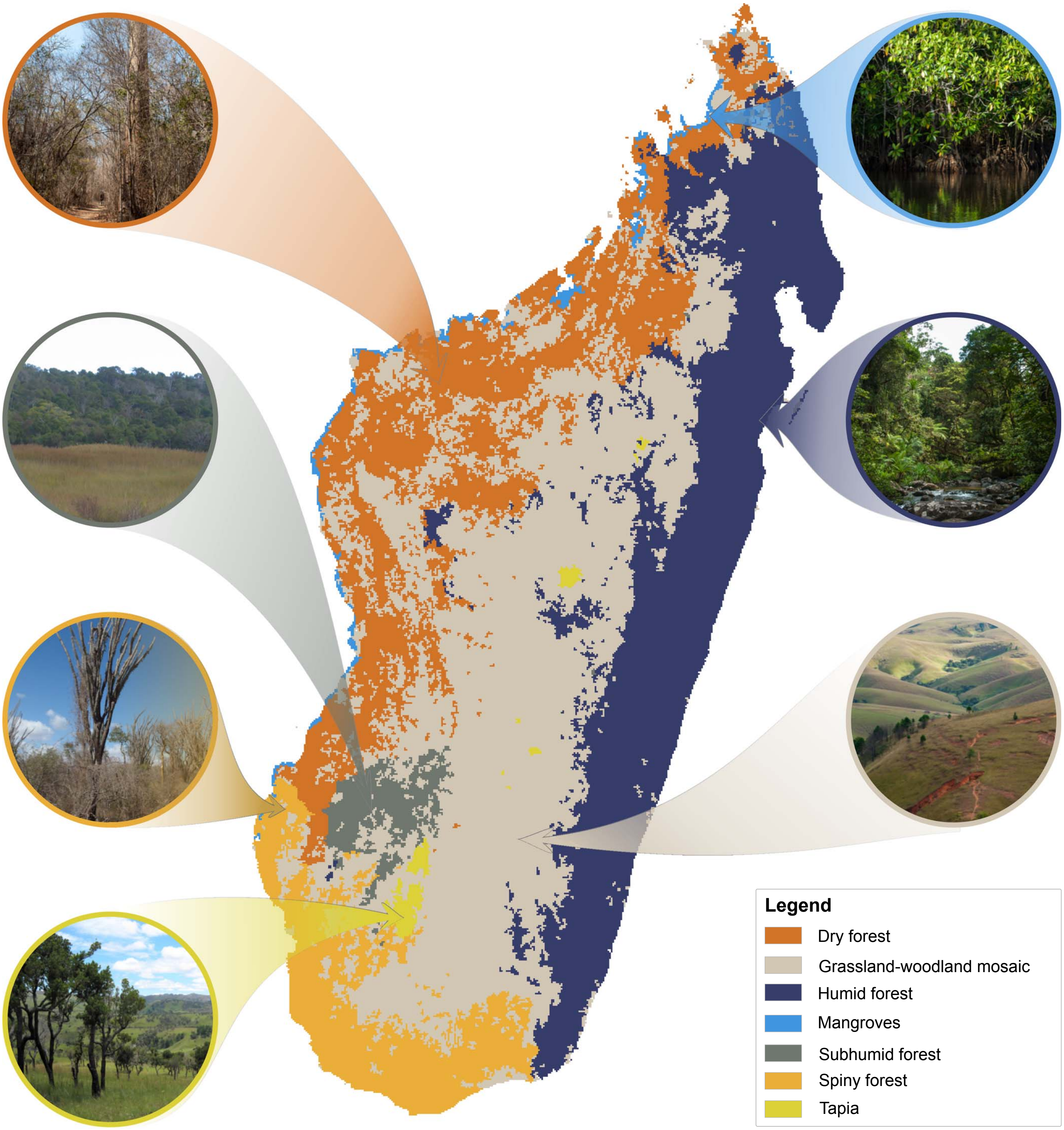

Fig. 2. Map of predominant vegetation types, expanded and simplified from Moat and Smith (21).

(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

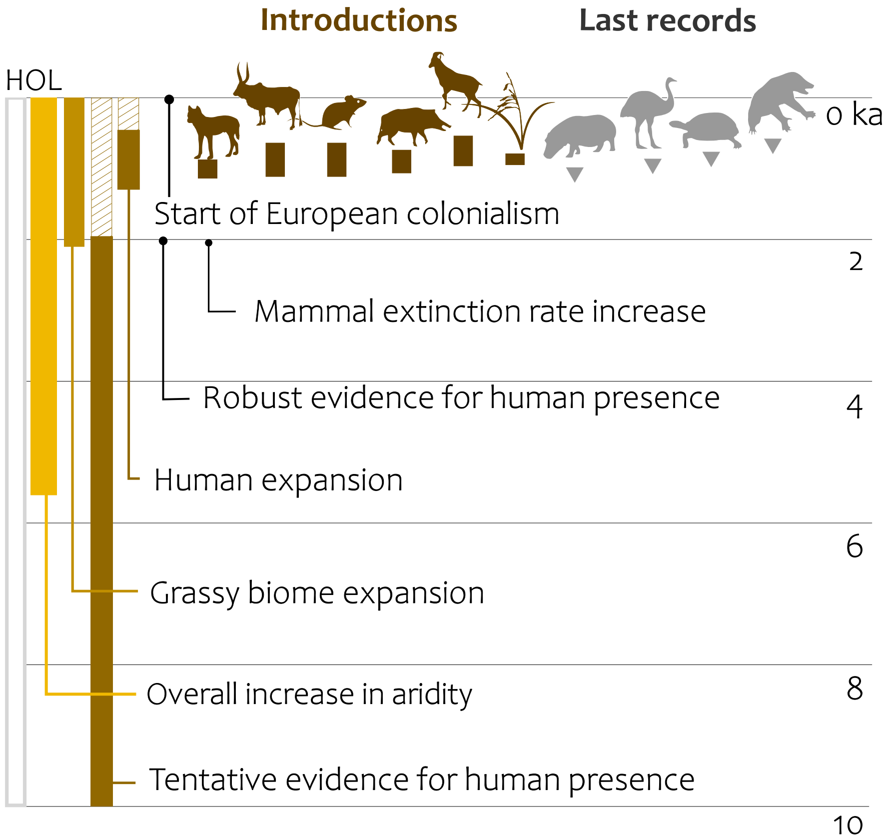

Fig. 3. Human arrival. Holocene events and environmental changes around the time of human arrival. Dates for human introductions of dogs, zebu cattle, rats, bushpigs, goats, and rice are provided as well as last dated records of megafauna (hippopotamus, elephant birds, giant tortoises, and giant lemurs)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

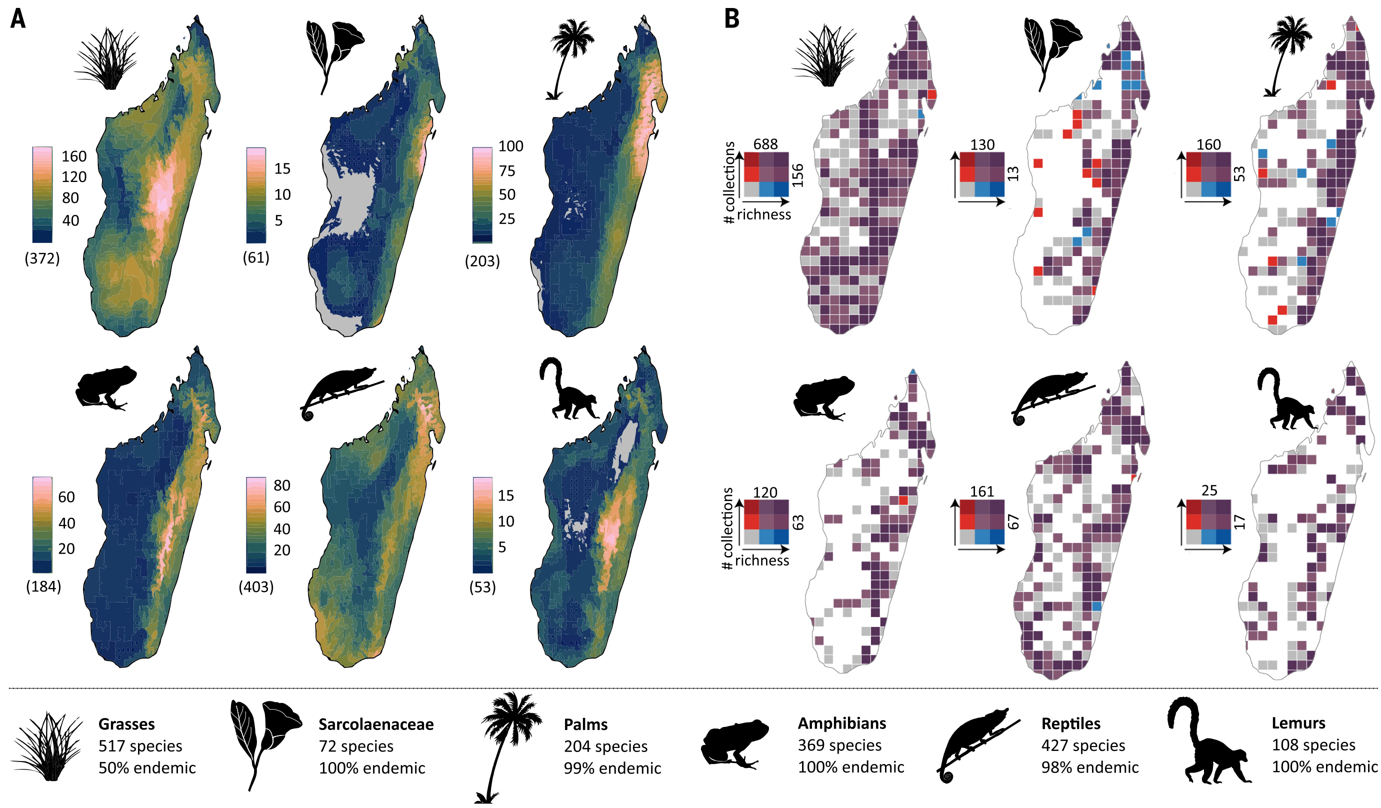

Fig. 4. Diversity patterns. (**A**) Species richness and endemism of six taxonomic groups in Madagascar. Native terrestrial and freshwater species counts and percentages of endemic species are based on estimates using author-curated data compiled from *The New Natural History of Madagascar* (*126*), 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 nonmaterial), 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 (Analanjirofo 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,

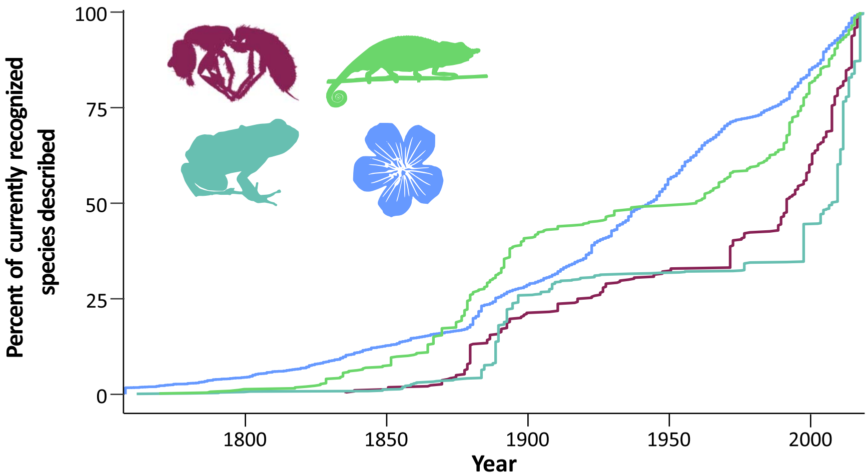

Fig. 5. Rates of scientific documentation. Percentage of described Malagasy ants, amphibians, reptiles, and vascular plants through time, based on year of basionym publication (*22*).

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

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SUPPLEMENTARY MATERIALS

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MDAR Reproducibility Checklist

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Science

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

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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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