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

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Title: Madagascar's extraordinary biodiversity: Threats and opportunities

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Abstract:

Madagascar's unique biota is heavily impacted by human activity and under intense threat. Here, we review the current state of knowledge on the conservation status of Madagascar's terrestrial and freshwater biodiversity by presenting data and analyses on documented and predicted species-level conservation status, the most prevalent and relevant threats, *ex situ* collections and programs, and the coverage and comprehensiveness of protected areas. The existing terrestrial protected area network in Madagascar covers 10.4% of its land area and includes at least part of the range of the majority of described native species of vertebrates with known distributions (97.1% of freshwater fishes, amphibians, reptiles, birds and mammals combined) and plants (67.7%). The overall figures are higher for threatened species (97.7% of threatened vertebrates and 79.6% of threatened plants occurring within at least one protected area). IUCN Red List assessments and Bayesian neural network analyses for plants identify overexploitation of biological resources and unsustainable agriculture as the most prominent threats to biodiversity. We highlight five opportunities for action at multiple levels to ensure that conservation and ecological restoration objectives, programs and activities take account of complex underlying and interacting factors and produce tangible benefits for the biodiversity and people of Madagascar.

One Sentence Summary: Current knowledge on Madagascar's biodiversity and its decline indicates an urgent need for inclusive actions.

Main text:

Madagascar's biota, the result of millions of years of evolution in relative isolation, is both unique and under threat. At the same time as the scientific description of new species is accelerating (*1*), so is the overall rate of extinction (*2*), and many species may be disappearing before they are even documented. In this review, we aim to consolidate information on the conservation status of some of the main elements of Madagascar's biodiversity, evaluate the many and varied threats faced by species assessed under the criteria for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, and provide some perspectives on future opportunities to ensure the future of this hyperdiverse and unique biota.

Threats to Madagascar's biodiversity

Madagascar's biodiversity is in decline, with some groups more threatened than others (Fig. 1). In our review of threatened species, we follow the IUCN Red List data (*3*) and threat categories (*4*), unless otherwise specified. Threatened species are those listed as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU). At one extreme, 22% (35 species) of assessed birds are threatened, while, at the other end of the scale, approximately 73% (66 species) of freshwater fishes and 75% (173 species) of magnoliid plants are threatened. Trees are particularly important in terms of their broad ecological functions and human uses, and 63% of the 3,118 assessed tree species in Madagascar are threatened (*5*). Humans have impacted the environment since arrival on Madagascar, not only in recent years. To avoid a shifting baseline effect, it is necessary to view changes in light of human settlement beginning hundreds or even thousands of years ago (*1*). For example, despite the relatively low proportion of bird species currently threatened with extinction, Madagascar has already lost at least 14 species (7% of all species) that were present when humans first settled the island (Fig. 1). The rate of anthropogenic extinction is even higher in mammals, with 23 species (10%) extirpated since first human settlement. Vertebrate extinctions include the loss of lineages representing millions of years of evolution – e.g., the sloth-, koala- and monkey-lemurs (families Palaeopropithecidae, Megaladapidae, and Archaeolemuridae) and two species of hippopotamus (family Hippopotamidae). The extinction of four species of elephant birds (order Aepyornithiformes) represents the global loss of a functionally unique clade (*6*, *7*). Extinctions, especially those of megafauna such as these, have broad scale implications for ecosystem functioning (*6-8*).

In total, 13 endemic animal species are listed as Extinct (EX), defined as extinctions after 1500 AD, and an additional 33 are listed as Extinct Prehistorically [EP], defined as anthropogenic extinctions prior to 1500 AD (see (*9*) for a full list of documented anthropogenic extinctions before 1500 AD). A further nine have been categorized as Critically Endangered (Possibly Extinct) – CR(PE). For plants, no species has been assessed as Extinct, and only one species (*Aloe silicicola*) is categorized as Extinct in the Wild (EW). A further 118 plant species are listed by IUCN as CR(PE) (111 spp.) or Critically Endangered (Possibly Extinct in the Wild) – CR(PEW) (7 spp.). Of those currently listed as CR(PE), five species are present in *ex situ* living collections, and their status should therefore be updated to CR(PEW) (*3*, *10*).

Malagasy species feature prominently among animal groups that have been considered by the EDGE of Existence program (*11-13*), which ranks species according to their evolutionary distinctiveness and the level of threat they face (EDGE = Evolutionary Distinct and Globally Endangered). Almost one in five species of amphibians (18 spp.), reptiles (17 spp.), and mammals

(17 spp.) in the top 100 EDGE species of each group are found in Madagascar (*13*). Yet only one in 20 (4 spp.) of the top 100 EDGE species of birds are found on the island.

Given the narrow geographic range of many Malagasy species (e.g., (*14*)), numerous undetected anthropogenic extinctions are likely to have taken place (*15*), such as CR *Aloe* species, which may have become extinct in the wild since they were last recorded. This may be especially pronounced in groups with high levels of micro-endemism, for example freshwater fishes and amphibians (*16*). Ascertaining extinction events is difficult due to sampling biases, insufficient taxonomic knowledge regarding the morphological features of extant species, and the challenges of comparisons with fossil and subfossil remnants in certain groups, such as frogs (e.g., (*17*)).

Reliability of species conservation assessments

Conservation assessments rely on taxonomic classification, and different opinions on species limits and numbers may influence the proportion of threatened species (e.g., (*18*)). This proportion may also be biased by an over-assessment of well-known and widespread taxa, or, alternatively, range-restricted species that are more likely to be threatened. To investigate indications of bias, we calculated the fraction of threatened species across different plant groups based on two sets of species: taxa with full threat-status assessments in the Red List compiled by the IUCN and their partners (*19*); and those estimated with a Bayesian neural network approach (Fig. 1; (*9*, *20*)), which inferred the threat status for all remaining species. Using this method, we predicted the threat status of 8,821 species with an estimated test accuracy of >65%. All taxa with a full threat-status assessment were included, although some assessments may be out of date and could underestimate threat levels.

The neural network approach combined with current IUCN assessments revealed a similar fraction of species inferred to be threatened across most taxonomic groups (Fig. 1). Large deviations from the proportion of threatened species in the current IUCN assessments occur in the ferns and lycophytes, and to a lesser extent the magnoliids. The neural network results combined with the known IUCN categories predicted a far higher proportion of threatened ferns and lycophytes (146 of 306 spp; 47.7% [95%CI: 38.5-56.7%]) than reflected in published IUCN assessments (1 of 33 spp; 3.0%), suggesting a bias towards assessing more common species. In the magnoliids, the combined results predict a lower proportion of threatened species (211 of 294 spp; 71.8% [95%CI: 68.0-75.9%]) compared to published IUCN assessments alone (173 of 225 spp; 76.9%), suggesting a bias towards assessing rare species in that group.

Genetic erosion

The reduction of genetic diversity within species resulting from the extirpation of subpopulations is a crucial, yet easily overlooked, facet of biodiversity loss that is often a precursor to extinction. Genetic erosion has negative effects on the individual fitness, the health of populations, and a species' ability to adapt to changing environments, reducing their resilience to further change, and potentially incurring extinction debt (*21*, *22*). In practice, genetic factors are not directly incorporated into IUCN assessments, which are based on measures of the probability of extinction due to population declines, restricted geographic ranges, and small population sizes (*23*).

The reduction in population sizes of wild plants and animals, together with their fragmentation and isolation, is generally expected to increase inbreeding and genetic load, reducing genetic diversity and fitness over time (*22, 24*). The few studies of intraspecific diversity in Malagasy species to date reveal that some species have maintained high genetic diversity in spite of habitat fragmentation (e.g., (*25, 26*)), whereas others have relatively low diversity, possibly as a result of anthropogenic effects (e.g., (*25, 27-29*)). Results differ even within species, such as in the palm *Beccariophoenix madagascariensis*, in which only some populations show strong signals of inbreeding, reflected by an excess of homozygotes (*30*). It is important to note that under some circumstances, population decline may outstrip the speed with which genetic diversity is eroded due to inbreeding. Estimates of heterozygosity may therefore not indicate the true genetic health and long-term prospects of populations when considered in isolation (*31*, *32*).

A more powerful, although less explored, approach is to use coalescence-based demographic modeling, which uses genome-wide data to estimate the longer-term trends in population size, providing more information than metrics of contemporary genetic diversity alone (*25*, *33*). In *Cheirogaleus* dwarf lemurs, genomic analysis suggests that four species have experienced population size declines in the last 50,000 years, with one decline (*C.* cf. *medius*) starting as long as 300,000 years ago – all clearly in pre-human times and resulting in lower genetic diversity (*29*). In contrast, another genomic study shows that five out of ten analyzed plant species with varying extinction risk have experienced substantial population declines since human colonization of Madagascar (*25*). In the golden-crowned sifaka (*Propithecus tattersalli*) (*26*), mouse lemurs (*Microcebus* spp.) (*28*), *Mantella* frogs (*34*), and the Milne-Edwards' sportive lemur (*Lepilemur edwardsi*) (*35*) demographic declines also appear to have taken place after the arrival of humans on the island (although the inherent uncertainties of mutation rates in the microsatellite data used makes the timing of these declines less certain).

The risks of inbreeding and increased genetic load may represent substantial and likely underestimated longer-term threats to the survival of Malagasy species. This is especially relevant considering the high level of fragmentation of native habitats in some vegetation types, such as the humid forests, and is worthy of further investigation.

Predicting future extinction: direct drivers of loss

Identifying direct threats is part of the IUCN Red List Assessment process, and even species that are not explicitly threatened (i.e., those that are Least Concern [LC], Near Threatened [NT], or Data Deficient [DD]) can still have threats listed. Here we discuss these threats and how they apply to all species. Our analysis of IUCN assessments indicates that overexploitation and agriculture are the most frequently listed threats to Malagasy fauna (excluding invertebrates) and flora (Fig. 2), mirroring global findings (*36*). Overexploitation is unsustainable biological resource use as defined by the IUCN (*37*), including hunting and collecting for subsistence use or national/international trade. Overexploitation is linked in some cases to illegal harvesting – for example, the illegal logging of rosewood for trade (*Dalbergia* spp.) – which is banned under the Convention on International Trade in Endangered Species of Wild Fauna and Flora since 2013 and under Malagasy law since 2010.

We estimated that 62.1% of vertebrates and 87.1% of plants are threatened by overexploitation and that 56.8% of vertebrates and 87.8% of plants are threatened by agriculture. These two major threats, almost equal in magnitude (Fig. 2), have different modes of impact – overexploitation is more targeted and tends to occur over relatively restricted areas compared to the broad effects of land clearance for agriculture.

Agriculture, and to a lesser extent overexploitation, are also the primary causes of deforestation in Madagascar. Approximately 44% of the land area covered by native forest in 1953 was deforested by 2014 (*38*). The rate of deforestation has steadily increased, reaching 99.0 kha/yr between 2010 and 2014 (*38*), and according to Global Forest Watch remains very high at 72.9 kha/yr (2014–2020) (*39*). Deforestation in Madagascar reflects global patterns (*40*) and is primarily driven by the small-scale but widespread practice of swidden agriculture (also known as shifting cultivation; in Madagascar referred to as *tavy* for rice cultivation in humid and subhumid areas, and *hatsake* for cassava and maize in dry and subarid areas). Additionally, cash crop production, particularly maize and peanut, has become a major driver of deforestation (*41*), alongside the production of products for international markets, such as forest-derived vanilla (*42*). The most frequent threats listed for plants and vertebrates suggest that this trend of increasing deforestation rates will continue, with forest loss and degradation a consequence of clearance of land for agriculture, potentially associated with small-scale fire activity (*43*) and overexploitation through selective logging and highly targeted activities such as the collection of palm hearts. Additionally, natural system modifications (threats from actions that convert or degrade habitat, e.g., anthropogenic fire in forests or changes in water management; Fig. 2), adds to deforestation and threatens 23.2% of vertebrates and is estimated to threaten 68.9% of plants. Some predictions indicate that in the absence of an effective strategy against deforestation, 38–93% of forest present in 2000 will be no longer present in 2050 (*41*).

For vertebrates, the greatest threat after overexploitation and agriculture is ‘invasive and problematic species and emerging infectious diseases’ (referred to as invasives/diseases in Fig. 2), which impacts 27% of all species (360 spp.; Fig. 2). This category includes non-native invasive species, as well as problematic native species and diseases of any origin. Changes in habitat due to the spread of non-native plant species can have a large effect, and one study reports that of a total of 546 naturalized non-native plants in Madagascar, 101 have been found to display invasive characteristics (*44*). Many non-native plants, such as the Mexican yellow pine (*Pinus patula*) in terrestrial systems (*45*), and common water hyacinth (*Pontederia crassipes*) in freshwater systems (*46*), are aggressively invasive and transformative in semi-natural habitats, and are clearly impacting native fauna and flora. Even within reserves and protected areas, the issue can be pronounced. For example, three species of invasive/problematic plants – strawberry guava (*Psidium cattleyanum*), Molucca raspberry (*Rubus moluccanus*), and wild cardamom (*Aframomum angustifolium*) – together occupy 17.6% of the Betampona Nature Reserve (*47*) and are also widespread in Ranomafana National Park and other protected areas.

Not all impacts are negative, however, and there is some evidence to suggest that, due to their potential for faster growth, some non-native plants are better able to combat the rapid fragmentation of native vegetation, and may be beneficial for endemic vertebrates, providing refuge, food, and vegetation corridors, while also improving human livelihoods (*48*). The potential for such species to become invasive or readily burn must however be fully considered before embarking on any planting initiatives (*49*). In addition, effects must be considered at different scales. For examples, the presence of strawberry guava has been reported to locally increase species richness in frugivores, but as they are primary dispersers of the seed this further contributes to the spread and to associated changes in floral and faunal community structure and reduction in taxonomic richness (*50*).

Non-native vertebrates have also had marked and diverse impacts, which we also here illustrate with some examples. Introduced rats (*Rattus rattus*; present since at least the 14th century) are now ubiquitous, even in remote areas, and there is evidence that their presence is associated with declines in native small mammals (*51*). In freshwater habitats, competition and predation by exotic fish species is considered a major factor in the decline of native freshwater fish (*52*), which have been completely replaced by non-native species across much of the Central Highlands and western areas (*53*). While not yet listed in current assessments, the recent invasion of the toxic Asian common toad (*Duttaphrynus melanostictus*), along with the predicted vulnerability of most native vertebrates to its toxins (*54*), is expected to represent a new threat to many nocturnal carnivores. The effects of other introduced and naturalized animals on native biodiversity are not well studied; this includes widely occurring species such as dogs (*Canis familiaris*), cats (*Felis catus*), the common myna (*Acridotheres tristis*), and the marbled crayfish (*Procambarus virginalis*). The threat of emerging infectious diseases is primarily driven by the occurrence of the chytrid fungus *Batrachochytrium dendrobatidis*, widely documented across Madagascar over the last decade and a potential threat to all amphibians, although no mass mortalities associated with chytridiomycosis have been reported in the country (*55*). Species often face multiple threats at the same time, although the impact of each threat can vary between species (Fig. 2).

Among vertebrates, amphibians have the highest number of IUCN-identified threats per species (Fig. 2A), with a mean of 4.8 threats per species, followed by mammals (mean 2.5 threats/species), and reptiles (mean 2.2 threats/species). For plants (Fig. 2B), magnoliids have the most threats per species (mean 2.9 threats/species), followed by rosids (mean 2.8 threats/species), and other eudicots (mean 2.8 threats/species). Although there might be some variation in the perception and documentation of threats between the specialists carrying out assessments, all follow the same protocols (*4*).

The number and relative impact of these threats may change in coming decades. The impact of climate change on Malagasy biodiversity remains understudied and it is not currently indicated in

IUCN assessments as a major threat. However, this impact is expected to increase in the future (*56*-*59*), and could potentially result in synergistic negative effects with unsustainable agriculture associated with land clearance, invasive alien species, and inappropriate management of fire regimes that can increase future fire risk (*43, 56*, *57*, *60*). Extinctions in one group could also have effects on others that depend on them, such as in cases of strong plant–animal mutualisms (*61*, *62*). Although coextinction is hard to quantify, with substantial knowledge and data gaps (*63*), models suggest that the effects of extinction can be amplified as a result of the interactions between species within and between trophic levels, with the potential to lead to secondary and even cascading extinctions (*64*, *65*).

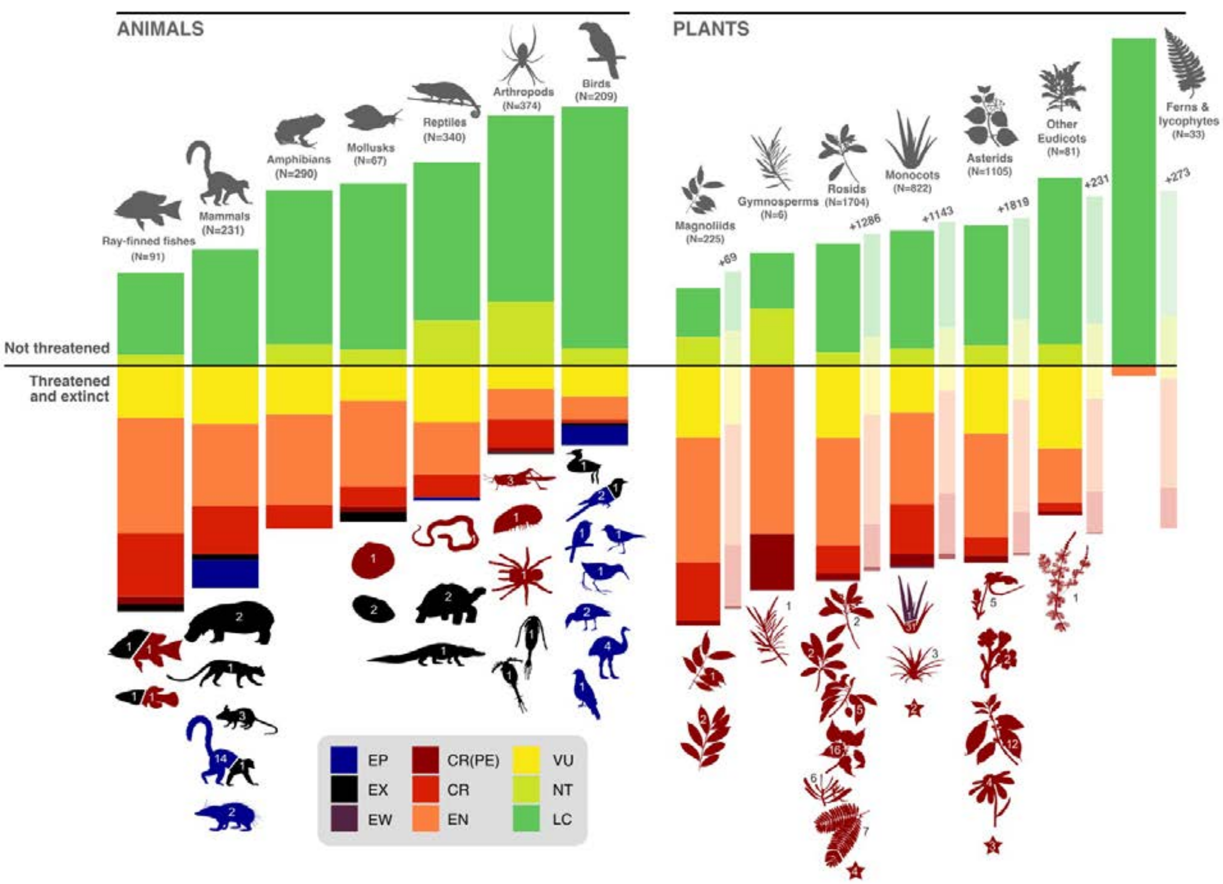

Fig. 1. Madagascar's threatened and lost biodiversity. IUCN Red List assessment categories of major groups of plants and animals from Madagascar. Assessment categories and coloration follow the standards used by the IUCN Red List. Category distributions for animal groups include ray-finned fishes, (Actinopterygii, freshwater species only, N=91), mammals (Mammalia, N=231 species), amphibians (Amphibia, N=296), mollusks (Mollusca, N=67), reptiles (Reptilia, N=340), arthropods (Arthropoda, N=374), and birds (Aves, N=209). Category distributions for plants, indicated with saturated, wider bars, include magnoliids (N=225), gymnosperms (N=6), rosids (N=1,704), monocots (N=822), asterids (N=1,105 species), other eudicots (N=81), and ferns & lycophytes (N=33). Thinner, unsaturated bars indicate the relative proportion of plant taxa in each threat category for IUCN Red List assessments combined with the taxa where the threat category was predicted in a Bayesian neural network analysis: asterids (N=2,924 species), rosids (N=2,990), other eudicots (N=312), magnoliids (N=294), monocots (N=1,965), and ferns & lycophytes (N=306). The number indicated above each bar with "+" is the number of taxa for which the threat category was predicted using the neural network analysis. IUCN Red List Assessment categories include Least Concern (LC) and Near Threatened (NT), together making up the "not threatened" category; while Vulnerable (VU); Endangered (EN); Critically Endangered (CR); Critically Endangered, Possibly Extinct (CR(PE)); Extinct in the Wild (EW); Extinct (EX; i.e., extinct after 1500 CE), and Extinct Prehistorically (EP; sensu (*66*), i.e., extinct before 1500 CE but with dated records within the last 130,000 years) make up the group "threatened and extinct." Silhouettes below the bars depict taxonomic orders with EP, EX, EW, and CR(PE) species, with the number of species in each category per order. For some plant groups, additional orders with single CR(PE) species are indicated with a star. Depicted orders are, from left to right and top to bottom: Perciformes, Cyprinodontiformes, Cetartiodactyla, Carnivora, Rodentia, Primates, Afrosoricida, Venerida, Unionoida, Perciformes,

Cyprinodontiformes, Squamata, Testudines, Crocodilia, Orthoptera, Spirobolida, Araneae, Calanoida, Cyclopoida, Podicipediformes, Cuculiformes, Coraciiformes, Charadriiformes, Gruiformes, Anseriformes, Aepyornithiformes, Accipitriformes, Laurales, Magnoliales, Pinales, Oxalidales, Sapindales, Myrtales, Malvales, Malpighiales, Fabales, Asparagales, Poales, Ericales, Boraginales, Gentianales, Asterales, Saxifragales.

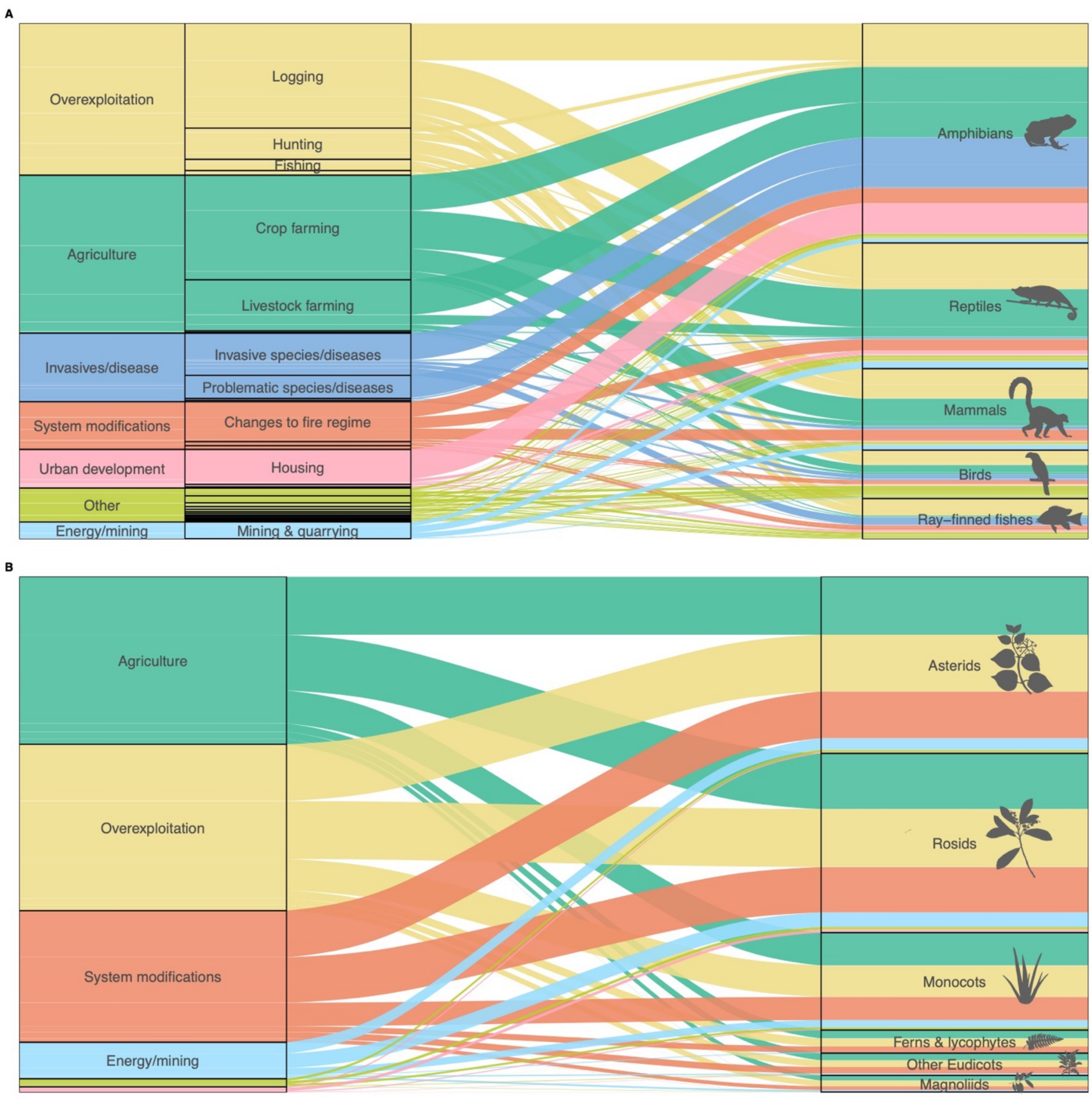

Fig. 2. Threats to Malagasy biodiversity. Alluvial plots showing threats, as defined by the IUCN, and their associations with major groups of terrestrial and freshwater (A) vertebrates (1,332 species with IUCN assessments, of which 993 species have at least one listed threat) and (B) plants (9,268 species with IUCN assessments or predictions, all of which have at least one listed threat; includes gymnosperms [6 species], which could not be visualized). Widths of the boxes/lines reflect the number of species impacted by each threat. Threats for vertebrates are further divided into sub-threats, whereas only the highest threat classification was available for assessed plants. The estimates for plants include predictions for unassessed species based on a Bayesian neural network analysis (*9*). The color scheme is consistent across panels. The "Other" threat class includes Pollution, Climate change, Transportation, and Human disturbance, plus Invasives/diseases for plants. Some threat classes have been renamed for brevity/clarity, including the IUCN category "biological resource use", which is labeled "overexploitation" here and in the text, for brevity and in line with IPBES terminology (*36*).

Conservation efforts and effectiveness

Protected Areas

Protected areas (PAs) are the central political and scientific accomplishment of Madagascar's conservation strategy. The network has been continuously developed since the first PA was established in 1927 (*67-71*). Our data compilation shows that the network now encompasses 10.4% of the land area of Madagascar, having grown by more than a third over the last two decades (Fig. 3). This recent and extensive designation of new PAs was carried out via a multi-stakeholder consultative process, in combination with data and literature analyses, through the Durban Vision initiative conceived in 2003. In addition to preserving diverse ecosystems and landscapes, the focus has been on species groups for which sufficient diversity and distribution data were available, primarily vertebrates (including birds, mammals, amphibians, and reptiles), and some plant groups. Despite the production of considerable new data since the Durban Vision began (e.g., many newly described species; (*1*), the network designed during that process remains highly taxonomically comprehensive. From a global perspective, the PA network also excels at capturing the vast majority of Madagascar's many EDGE species: 14 out of 18 amphibians, 15 out of 17 reptiles, 16 out of 17 mammals, and all four birds (*13*).

As of November 2020, there were 110 terrestrial PAs with permanent protected status in Madagascar, covering 61,300 km^2 across the country (Fig. 3) (*70, 72, 73*). Eleven of these are "orphan PAs" – sites abandoned by their former managers with responsibility reverting to the Ministry of Environment and Sustainable Development (*70*). An additional 89 sites (15,200 km^2), predominantly comprising Key Biodiversity Areas (KBAs), are not under formal protection (*70, 72, 74*, *75*).

The long-term security and effective management of Madagascar's PAs is therefore crucial to addressing the country's biodiversity challenges. Providing evidence of their effectiveness and co-benefits, such as ecosystem service provision, will be critical to securing ongoing support and management from local communities, as well as from local and national governments. However, measuring PA effectiveness is challenging (e.g., at avoiding deforestation, or providing alternative livelihoods) while accounting for numerous covariates (*76*), particularly in Madagascar with comparatively little long-term biodiversity monitoring data (*77*). Recent counterfactual analyses (*78*) have sought to address this question by identifying protected and non-protected sites that are similar across multiple social and environmental variables, and then comparing indicators of conservation effectiveness, such as deforestation rate. These analyses indicate that PAs have a small, but significant, effect at reducing deforestation (*9*).

We show that since 1990, human impacts have measurably increased across all terrestrial PAs (Table S8 (*9*)), a trend documented worldwide (*76*). Human activity by local communities inside PAs is not necessarily detrimental to biodiversity, and land use and conservation are therefore not mutually exclusive. Nevertheless, land conversion and unsustainable exploitation remain major drivers of biodiversity loss. This suggests that protecting and realizing the potential of Madagascar's comprehensive PA network will require the application of rigorous monitoring and evaluation strategies, matched with extensive community collaboration, to understand co-benefits and minimize detrimental human impacts.

Scores for deforestation and management effectiveness – for example, from the self-reported Management Effectiveness Tracking Tool (*79*) – have been the main metrics used to monitor effectiveness to date. However, these are not always reliable indicators of management effectiveness (*77*). New and expanded capacity of variables such as remote-sensed fire and stable night lights, with increased temporal resolution, offer promising new monitoring opportunities. How fire is associated with land transformation in Madagascar has been discussed in the literature but only recently quantitatively assessed (*43*), demonstrating that tree loss anomalies are highest in environments where landscapes-scale fire (>21 ha) does not occur, and where the role of small-scale fires (<21 ha) requires close and urgent investigation. We show that trends in anthropogenic fire are variable, increasing in some areas of forest vegetation in the north, east, and west but decreasing in grassland-woodland mosaic vegetation across central Madagascar (Fig. 4A, B). Forest loss also reflects this pattern, primarily occurring in the humid forest biome in the east, but also in dry forest and spiny forest in the west (Fig. 4C, D). Deforestation and land use conversion remain key challenges to conservation in Madagascar, and improved remote-sensing will accelerate monitoring and developing understanding on the effectiveness of PAs and other conservation measures.

Ex situ *conservation and restoration*

Living plant collections in botanic gardens and seed banks represent invaluable sources of taxonomic and genetic diversity for immediate conservation and research, and should continue to support restoration efforts. Globally, 29.6% of all known native Malagasy plant species (23.1% of endemic species and 23.1% of native threatened species) are held in botanic gardens, with 15.5% held in Madagascar (*10*), where their cultivation is sometimes linked to educational programs and community engagement, essential to raising awareness of biodiversity and conservation issues. The Millennium Seed Bank Partnership in Madagascar, initiated in 1996, hosts collections of an estimated 3,500 native Malagasy species, including members of four of the five endemic plant families and all seven of the iconic baobab species (*Adansonia* spp.). The single Malagasy plant species listed as Extinct in the Wild, *Aloe silicicola*, now only survives in one living collection outside Madagascar.

For native terrestrial and freshwater vertebrates, 9% of amphibians, 17% of mammals, 20% of reptiles, 21% of freshwater fishes, and 33% of birds are currently held in zoological collections (18% overall) (*9*, *80*). Many are part of active breeding programs: a subset of these (3% of amphibians, 7% of reptiles, 11% of freshwater fishes, 13% of mammals, and 23% of birds) were successfully bred during 2020 (*9*). Unsurprisingly, the species held in captive breeding facilities are biased towards the more charismatic, well-known taxa (*81*). For example, among amphibians, 13 of the 34 species in zoos belong to the genus *Mantella*, a group of strikingly colored diurnal frogs, even though *Mantella* contains only 4% of Madagascar’s amphibian fauna. Freshwater fishes, amphibians, and reptiles are highly suitable for targeted *ex situ* breeding and reintroduction programs (*82-85*). For species in these groups and others with high levels of micro-endemism, such conservation programs continue to represent a major safeguard against extinction (*86*). This complies with the One Plan Approach to species conservation proposed by the IUCN SSC Conservation Planning Specialist Group, which supports the development of conservation and management plans for all populations of a species, even outside of their natural range (*87*). It should be noted that the success of reintroduction relies also on the maintenance of natural habitat and functional diversity at potential reintroduction sites, along with minimizing risks associated with invasive species and infectious diseases. In addition, particularly for mammals, vulnerability of captive-bred populations to predation can also jeopardize the success of reintroductions (*88*).

Progress towards international conservation commitments

Madagascar continues to make progress towards Convention on Biological Diversity targets, but like most countries falls short of meeting them in full (*89*). Of particular relevance here is that Madagascar did not formally meet Aichi Target 11 to protect at least 17% of its total land area (Fig. 3) – as was the case for 48% of the parties reporting their progress (*89*). If areas designated as important for biodiversity but not currently under formal protection were also given protection, the total percentage of PA coverage would rise from the current 10.4% to 13% (Fig. 3B). However, given that even the existing network is widely considered to be chronically under-resourced, this action is not a priority for the near future (*90, 91*).

Target 4 of the Global Strategy for Plant Conservation seeks to protect 15% of each vegetation type. This has been achieved for mangrove (currently at 29.4%), spiny forest (21.5%), humid forest (18.5%), and tapia (17.9%), but not for dry forest (13.3%), subhumid forest (5.7%), and grassland-woodland mosaic (1.8%) (Table S6 (*9*)). However, expansion of the areas of those vegetation types under protection may not be feasible due to limited financial resources, the large degree of fragmentation and geographical spread of habitats, and the long administrative process involved in extending PAs or designating additional areas, as well as a lack of political will. It also may not be desirable until it can be demonstrated that the existing PAs are well-resourced, achieving conservation objectives and providing benefits to communities. Restoration within currently protected areas may provide a longer-term pathway to meeting this goal, particularly where there are rapidly realizable socio-economic benefits such as sustainable silk production from wild native silkworms (*Borocera cajani*) associated with tapia (*Uapaca bojeri*) in the Itremo Massif PA and Ambatofinandrahana KBA. Other targets are more difficult to assess due to lack of data. For example, there is very little evidence to assess success in the control of invasive alien species, with some exceptions such as the ongoing but promising house crow (*Corvus splendens*) eradication (*92*).

Although most of the Aichi and GSPC targets were either not achieved or cannot be assessed, a marked success is that Madagascar has comfortably achieved GSPC Target 7 (at least 75% of known threatened plant species conserved *in situ*), with our analyses indicating this percentage is currently at 80%.

Realizing benefits of biodiversity for people

The majority of Madagascar's over 28 million inhabitants live outside of, but often very close to, PAs (*93*) (Figs. 3A; S1). These communities face challenges connected to widespread poverty, which itself is related to degradation of natural capital in the landscape, limited access to formal education and health care, crime, corruption, weak governance, and regulatory issues including land tenure (*15*, *94*, *95*). For example, southern Madagascar is severely affected by food and water insecurity, which catalyzes political and social instability, exacerbates economic insecurity, and has led to large-scale migration within the country (*96*). This instability likewise hampers the operations of local, national, and international conservation organizations, which could be compounded further by adverse effects from climate change (*59*). As the human population in the country is expected to reach 42–105 million by the end of this century, of which half will be under 15 years of age, and with the majority under the poverty threshold (*97*), the conservation success of PAs will be inextricably linked to the effective provision of livelihoods, food security, and natural capital – a situation echoed across all Malagasy ecosystems and the world over (*98*).

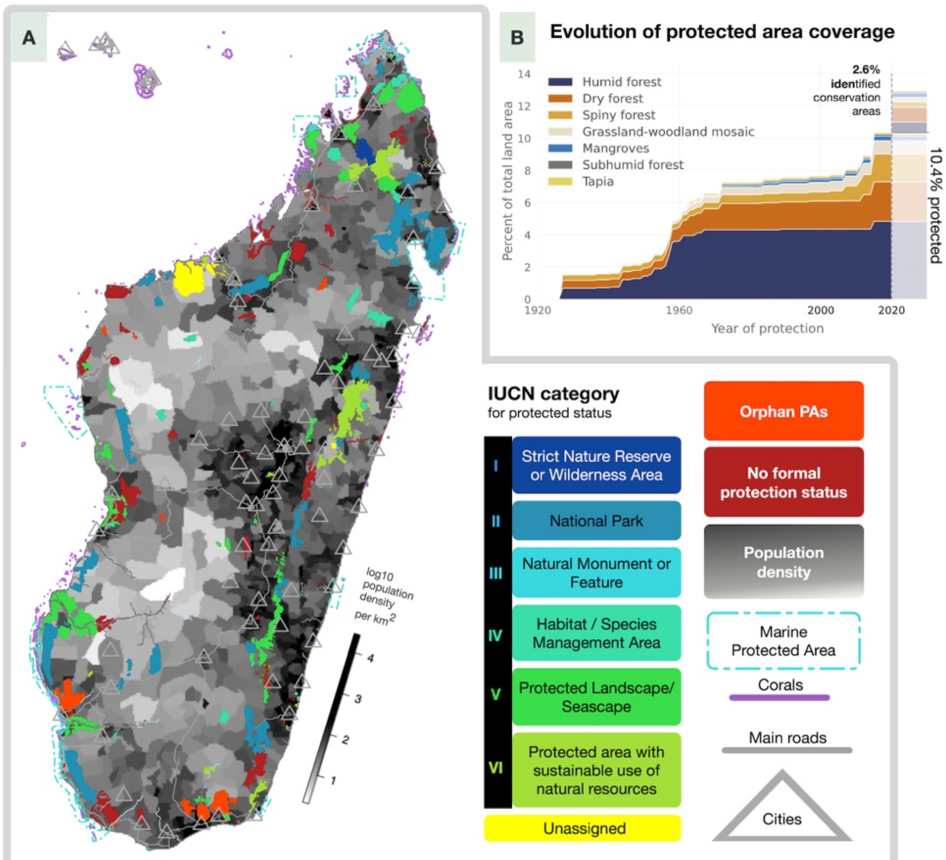

Fig. 3. Madagascar's terrestrial protected areas (PAs) in the context of human population density and changes in coverage of vegetation type over time. (A) PAs with IUCN protected status (*99*), "orphan" status, or no formal protection status (e.g., unprotected Key Biodiversity Areas [KBAs]), shown in the context of nearby marine PAs, surrounding bathymetry (*100*), coral reefs (*101*), cities, roads, and population density (*102*). (B) The evolution of PA coverage over time, showing the potential increase in area protected that could be gained if the designated areas (those identified as important for biodiversity but not currently under formal protection, mostly KBAs) were protected in the future (*74*, *75*).

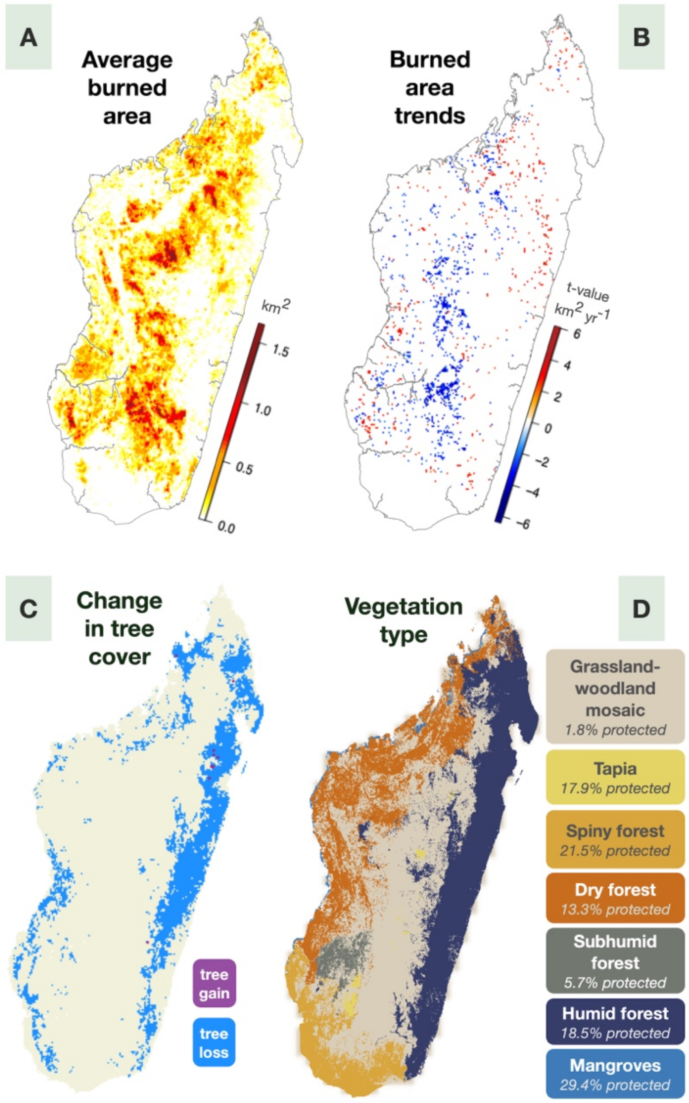

Fig 4. Recent changes and patterns in burned area and tree cover in Madagascar. (A) Average burned area in the period 2003–2019. (B) Statistically significant trends in burned area (MODIS) (*103*) from 2006–2016, not explained by precipitation change (TRMM) (*104*), dates chosen for comparison with Goodman et al. (*72*). Red indicates an increasing trend; blue indicates a decreasing trend. (C) Change in tree cover from 2000–2012 (*105*). (D) Vegetation map, inferred

and simplified from Moat & Smith (*106*). The legend indicates the percentage of each vegetation category currently covered by the protected area network.

Looking back, moving forward

Despite decades of research and applied conservation programs supported through substantial financial investments (*95*, *107*), Madagascar’s remarkable biodiversity continues to face severe challenges (Figs. 1, 2). It is reasonable to ask whether more of the same – even if better resourced and underpinned with greater scientific understanding and technology – is likely to deliver a tangible reversal in Madagascar’s trajectory of biodiversity loss, or whether new approaches are required to bring transformative change (*108*), including greater emphasis on monitoring interventions and addressing underlying drivers through key leverage points. The responsibility for averting humanitarian and biodiversity crises is a shared global challenge (*36*, *109*), with solutions needed at all societal levels – including via local communities, engagement of the private sector, sound leadership and policy from regional and national government, steady international support for conservation, and increased recognition of how historic and ongoing global and national inequalities have contributed to the current situation. Scientific data and evidence will continue to make a vital contribution, but it is crucial that this is done in an interdisciplinary context, with open communication channels to relevant government departments and third sector organizations.

Decades of progress in biodiversity science and conservation

We now have a clearer and more detailed understanding than ever before of the past and present diversity and distribution of Madagascar's biodiversity, and the threats it faces (*1*) (Fig. 1). The underlying data are the product of decades of research – with an increasing number of Malagasy biologists involved. This body of research and the evidence we have collated and presented here makes a clear case for Madagascar as one of the world's foremost conservation priorities.

Despite multiple competing demands on land, the Malagasy government, in collaboration with a broad group of conservation organizations and donors, has succeeded in designating 10.4% of the country as terrestrial PAs in a network that is largely representative of Madagascar's diverse biomes (Fig. 3, 4). Most terrestrial and freshwater vertebrate species with known distributions have ranges that overlap with least one PA (94.7% of reptiles, 97.2% of amphibians, 98.1% of mammals, 98.9% of freshwater fishes, 100% of birds, and 97.1% for all groups combined), as do the majority of plants, but to a lesser extent (67.7%) (*9*). For threatened species with known distributions, the percentages are similar for vertebrates (94.3% of reptiles, 99.3% of amphibians, 97.7% of mammals, 100% of freshwater fishes, 100% of birds, and 97.7% for all groups combined) and markedly higher for plants (79.6%). Nonetheless, there are still many threatened species with ranges that do not overlap with existing PA network, including one amphibian, three mammals, seven reptiles, and 559 plants (*9*), and many more that have not yet been assessed but may be threatened. The ranges of all birds overlapped with at least one PA; this was also true when we filtered the analysis to only include resident and breeding areas (*9*).

Since the loss of Madagascar's terrestrial megafauna (here defined as vertebrates above 10 kg), there have been few documented modern extinctions, but many species have perilously reduced population sizes. The continued increase in new species descriptions suggests there may be undocumented extinctions, especially in poorly studied taxa (*1*). Despite this, with limited resources and/or capacity, Madagascar has made important progress towards achieving international climate, biodiversity, and sustainable development goals, providing a foundation on which to build in the coming decades.

Success stories for individual species highlight how positive collaborative efforts can avert extinction. Examples include work on the Madagascar pochard (*Aythya innotata*) (*110*), which shows a 30% probability that extinction was prevented due to conservation action, the success story of the community-based protection of the tahina palm or dimaka (*Tahina spectabilis*) where local communities were involved in propagation and population reinforcement (*111*), and the work to prevent the extinction of the ploughshare tortoise (*Astrochelys yniphora*) through a captive breeding program (*112*).

Other notable successes have come from Madagascar's "biodiversity conservation boom", which started in the 1980s, including a growth in the number of students pursuing university-level education in environmental sciences, biodiversity conservation and management, and related fields, at both public and private universities. The result is an increasingly robust national capacity for the conservation and management of biodiversity that extends to international conservation organizations, which have been able to actively recruit Malagasy professionals to the highest administrative and executive positions. Going beyond this, the gap in scientific leadership that underpins conservation evidence is being incrementally filled by Malagasy biodiversity scientists. Researchers from outside Madagascar are increasingly collaborating with Malagasy researchers for mutual benefit. The requirement for international collaborators to provide financial and technical support for Malagasy researchers and their research infrastructure via collaboration protocols, set out in the national strategy for scientific research in Madagascar (*113*), reinforces the importance of this.

As in many low-income countries, insufficient public funding means that the number of Malagasy professionals is still insufficient to serve the country's needs, there are relatively few PhD positions available to students, and those that are trained at higher levels often move away from academia and into the private sector. Access to up-to-date biodiversity data has also been a limiting factor (*15*). A further challenge is how to successfully engage multiple parts of society in conservation. Efforts that are genuinely socially integrated have been shown to produce more effective and resilient practices, policies, and decision-making, especially in the face of unstable environmental, political, and health situations (*114*). The Madagascar Fauna and Flora Group, the Lemur Conservation Foundation, Durrell Wildlife Conservation Trust, The Peregrine Fund Madagascar, Madagascar Biodiversity Center, and Madagasikara Voakajy, as well as the work of the Royal Botanic Gardens, Kew, and Missouri Botanical Garden, are all examples of successful collaborations involving researchers, conservation partners and local communities to protect biodiversity and empower local people.

The future of biodiversity in Madagascar

Meeting the Convention on Biological Diversity's Post-2020 Global Biodiversity Framework 2030 targets and milestones and achieving the 2050 goals (*115*) will be challenging – in Madagascar and globally. Evaluating successes and failures over previous decades and learning from these to prioritize effective conservation investment will be particularly important. To embrace diverse views and promote inclusivity in the identification of future directions, we discussed our results and current literature among our co-authors and consulted with Malagasy and external researchers, conservation leaders, and politicians, to arrive at five main opportunities for the future, which we now present.

1) Investment in conservation and restoration must be based on evidence, effectiveness, and future challenges. Since the 1980s, billions of US dollars from international donors and conservation organizations, in cooperation with the Malagasy government, have been dedicated to protecting the country’s biodiversity and creating today’s network of PAs (*107, 116*). However, the effectiveness of many interventions is poorly understood because impact evaluations are absent or lacking rigor. Evaluating the effectiveness of conservation activities is challenging, but the subject of increasingly sophisticated research efforts (*76, 78, 117*). Nevertheless, it is imperative investments reinforce evidence-based and regularly evaluated interventions, requiring greater collaboration and co-design between local communities, regional and national authorities, researchers, the private sector, and other stakeholders. A particular opportunity is to frame these evaluations around community-based conservation interventions that address challenges faced by people and nature in unison. For example, nature-based solutions (*118*) for diversified, locally adapted and sustainable agriculture can help address livelihood needs, while more efficient stoves can substantially decrease the demand on charcoal from native forests for cooking and heating, and further may reduce the health hazards of smoke inhalation. Such initiatives increase food and energy security (*119*) while providing resilience to climate stochasticity (*120*). Similarly, coordinated, community-based fire management and awareness raising can be used to help mitigate risk to fire-sensitive forests. On-site management is especially important for fire mitigation, as a study during the COVID 19 pandemic has shown (*121*). Fire management also presents the opportunity to mitigate the impact of exotic species by targeting the removal of flammable invasives (e.g., *Pinus*), and guide appropriate tree-planting initiatives to avoid fire-prone plantations near areas of particular biological importance. Such measures can improve the quality of grazing land for livestock, while reducing carbon emissions from fire and helping to protect biodiverse habitats.

2) Expanded biodiversity monitoring is key to safeguarding Madagascar’s most valuable natural assets. Existing biodiversity data are sufficient to characterize major conservation challenges and robustly support the orientation of conservation efforts in Madagascar. Calling for the collection of additional data risks delivering diminished returns on investment for conservation planning (*122*). Nevertheless, from collating the information for this review, we acknowledge a clear need to address gaps in understudied ecosystems, taxa, and genetically distinct populations, noting that many newly described species are already threatened (*123*) and in need of immediate protection. Monitoring is also crucial for the detection of new non-native and potentially invasive species, as well as providing important data for the management of those that have already taken hold. Increasing connections with international trading partners without concurrent improvements in capacity for biosecurity increases Madagascar’s vulnerability to such species (*124*), and strategies to monitor and mitigate these risks while delivering near-term benefits are needed.

Although there are initiatives that provide broad overviews of conservation effectiveness (e.g. (*117*)), many conservation interventions lack impact evaluations, in part due to a lack of robust, long-term monitoring data for biodiversity and social outcomes. The major gap is a lack of capacity for robust biodiversity monitoring. An example of the increasing value of data and coherency in conservation efforts is the development of the Madagascar Protected Areas website (*125*), which consolidates much of the information about Madagascar’s extensive network of PAs. But as with many initiatives, the key is in long-term financing and maintenance of these portals and ensuring that data flows freely and openly to similar, global initiatives like Protected Planet (*73*).

Biological monitoring needs to be based on consistent, repeatable methodologies, with shared data. This information provides the science-based evidence needed to leverage international funding and government policy support. Monitoring is one area where new technologies will play a key role, such as through the increasing availability of near real-time satellite images and small and cost-effective unmanned aerial vehicles, which can increase visual access to remote areas (*126*). Similarly, DNA-based biodiversity surveys, including environmental sampling, can greatly improve the speed of site-inventories and identification of unknown and understudied taxa. Advances in monitoring must be delivered with improved and centralized management. This should include open-source and transdisciplinary data on biodiversity, social and conservation governance and performance. These data should be in formats that are accessible and useful to practitioners, to identify relevant baselines, and support evidence-based decisions for conservation and restoration.

3) Improving the effectiveness of existing PAs is more important than creating new ones. Madagascar has an extensive, evidence-based, and highly representative network of terrestrial PAs (Fig. 3, 4). Madagascar's existing PAs already include at least partial ranges of a substantial proportion of Malagasy taxa, including most Malagasy EDGE species. Focusing on improving their quality and effectiveness will likely lead to positive biodiversity outcomes (*127*), further increasing the already measurable impact that PAs have had on biodiversity. By strengthening PAs, biodiversity can be conserved across ecosystem, species, and genetic levels, all of which are integral in long-term conservation, as discussed above. Investment in restoration of degraded areas within and beyond the existing network (see Opportunity 4 below) will provide multiple benefits for biodiversity and people. This could help increase the resilience of habitats to future drivers of biodiversity loss including climate change, while increasing potential ranges of many species in parallel. Demonstrating the benefits of strengthened PAs to people is a likely prerequisite for societal support to maintain and improve upon the existing network, while mitigating risk of future

downgrading, downsizing, or degazettement (legal removal of conservation status) (*128*). Financial benefits that come with strengthened PAs must be distributed appropriately and equitably within the country's political and social contexts, with the full inclusion of local communities at all stages (*127*, *129*).

4) Conservation and restoration should not focus solely on the PA network. Madagascar's PAs are islands of natural capital in a landscape of degraded natural resources (*130*) and therefore provide vital resources for communities living adjacent to them. Traditional "fortress conservation" – seeking to protect areas by limiting access – is therefore both undesirable and unlikely to be effective. To further reduce the detrimental human impacts that exist in all PAs (*107*) (Table S8 (*9*)), we argue for strategies to enhance the natural capital of the surrounding landscapes, to reduce pressure on PAs as providers of basic resources, and to increase buffer zones for the species that live in and around them. This could include increasing ecosystem provision, such as productive soils, food, fibers, and other materials and services such as water flow regulation and carbon capture. Such measures would serve to address some of the largest threats to species, including the expansion of agriculture and overexploitation (Fig. 2).

In particular, ecological restoration could benefit people and biodiversity, particularly when targeted to the 89.6% of the country that is not protected. It offers potential to provide new livelihood opportunities that are far from, and independent of, the resources within PAs, further reducing pressure on the system (*131*). Importantly, restoration should not only target those ecosystems that traditionally receive the most conservation attention because they hold the greatest biodiversity, for example forests. Other vegetation types such as grasslands, where most agriculture takes place, are equally vital. Restoration should be carried out following best practice and in places where people will benefit most, not necessarily only adjacent to PAs. Further, restoration should include maximizing biodiversity recovery to meet multiple goals, using resilient species, and working together with local communities (*49, 132*).

For the species and their inherent genetic diversity not covered by the PA network, particularly those that are challenging to conserve, such as freshwater fishes and palms, *ex situ* conservation in zoological and botanical gardens is a vital tool to support conservation and restoration. For plants, efforts should especially focus on the 32.3% of plant species that fall outside of the PA network, and the species that have cultural or economic value for people (e.g., crop wild relatives). Promoting biobanking for animals and intensifying it for seeds, spores, and fungi will not only support conservation but also contribute material and knowledge to restoration and research (*88*).

5) Conservation actions must address the root causes of biodiversity loss. Our analysis showed that the most frequently listed threats to Madagascar's biodiversity come from overexploitation and agriculture, predominantly a result of forest loss and potentially tied to increases in small-scale anthropogenic fire in forests (Fig. 4A, B; see also (*43*)), significantly affecting humid forest areas in the east and dry forest and spiny forest in the west (Fig. 4C, D). This trend is likely to continue unless the root causes of this forest loss are addressed. Conservationists and their funders must recognize that food, social security, health, and well-being are the utmost priorities for rural communities, and that PAs will always be vulnerable when surrounded by impoverished people living in landscapes with eroded natural capital (*133*). Politicians and economists must recognize that sustainable and equitable development in Madagascar is inextricably linked to, and dependent on, the maintenance of ecosystem function and the goods and services they provide. Initiatives that address these issues by working with local communities to identify tailored solutions in health,

education, and green entrepreneurship are increasingly successful and should be expanded, but generally lack data and evidence from monitoring (see Opportunity 2). Promising approaches include voluntary savings and loans; inclusive, sustainable agricultural development schemes that promote stable land ownership and build – rather than destroy – natural capital and the ecosystem services it provides; implementation of conservation interventions, including research and monitoring; and PA management that maximizes local employment (*107*, *132*). Such efforts will facilitate improved livelihoods for many, while reducing pressure on the PAs themselves, bringing tangible benefits to communities, and contributing to sustainable management (*107*, *134*).

Conclusions

The alarming status of Madagascar's biodiversity is the result of multifaceted, unsustainable practices including historic and contemporary exploitation. In the eyes of much of the world, Madagascar's biodiversity is a unique global asset that needs "saving"; in the daily lives of many of the Malagasy people, it is a rapidly diminishing source of the most basic needs for subsistence. Achieving a sustainable future that benefits people and biodiversity is possible by building on, and expanding, integrated, inclusive conservation efforts. Biodiversity is the greatest opportunity and most valuable asset for Madagascar's future development.

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Supplementary Materials

Materials and Methods

Figure S1

Tables S1–S8

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