REVIEW SUMMARY

BIODIVERSITY

Madagascar's extraordinary biodiversity: Threats and opportunities

Hélène Ralimanana* ***et al.***

BACKGROUND: Madagascar is one of the world's foremost biodiversity hotspots. Its unique assemblage of plants, animals, and fungi—the majority of which evolved on the island and occur nowhere else—is both diverse and threatened. After human arrival, the island's entire megafauna became extinct, and large portions of the current flora and fauna may be on track for a similar fate. Conditions for the long-term survival of many Malagasy species are not currently met because of multiple anthropogenic threats.

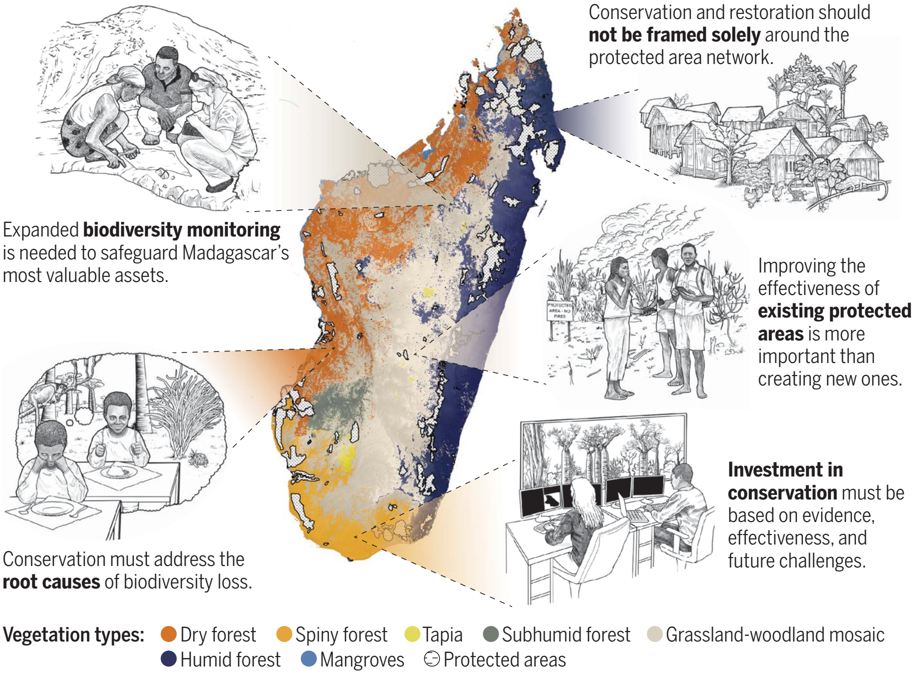
ADVANCES: We review the extinction risk and threats to biodiversity in Madagascar, using available international assessment data as well as a machine learning analysis to predict the extinction risks and threats to plant species lacking assessments. Our compilation of global International Union for Conservation of Nature (IUCN) Red List assessments shows that overexploitation alongside unsustainable agricultural practices affect 62.1 and 56.8% of vertebrate species, respectively, and each affects nearly 90% of all plant species. Other threats have a relatively minor effect today but are expected to increase in coming decades. Because only one-third (4652) of all Malagasy plant species have been formally assessed, we carried out a neural network analysis to predict the putative status and threats for 5887 unassessed species and to evaluate biases in current assessments. The percentage of plant species currently assessed as under threat is probably representative of actual numbers, except in the case of the ferns and lycophytes, where significantly more species are estimated to be threatened. We find that Madagascar is home to a disproportionately high number of Evolutionarily Distinct and Globally Endangered (EDGE) species. This further highlights the urgency for evidence-based and effective in situ and ex situ conservation.

Despite these alarming statistics and trends, we find that 10.4% of Madagascar's land area is protected and that the network of protected areas (PAs) covers at least part of the range of 97.1% of terrestrial and freshwater vertebrates with known distributions (amphibians, freshwater fishes, reptiles, birds, and mammal species combined) and 67.7% of plant species (for threatened species, the percentages are 97.7% for vertebrates and 79.6% for plants). Complementary to this, ex situ collections hold 18% of vertebrate species and 23% of plant species. Nonetheless, there are still many threatened species that do not occur within PAs and are absent from ex situ collections, including one amphibian, three mammals, and seven reptiles, as well as 559 plants and more yet to be assessed. Based on our updated vegetation map, we find that the current PA network provides good coverage of the major habitats, particularly mangroves, spiny forest, humid forest, and tapia, but subhumid forest and grassland-woodland mosaic have very low areas under protection (5.7 and 1.8% respectively).

OUTLOOK: Madagascar is among the world's poorest countries, and its biodiversity is a key resource for the sustainable future and well-being of its citizens. Current threats to Madagascar's biodiversity are deeply rooted in historical and present social contexts, including widespread inequalities. We therefore propose five opportunities for action to further conservation in a just and equitable way.

First, investment in conservation and restoration must be based on evidence and effectiveness and be tailored to meet future challenges through inclusive solutions. Second, expanded biodiversity monitoring, including increased dataset production and availability, is key. Third, improving the effectiveness of existing PAs—for example through community engagement, training, and income opportunities—is more important than creating new ones. Fourth, conservation and restoration should not focus solely on the PA network but should also include the surrounding landscapes and communities. And finally, conservation actions must address the root causes of biodiversity loss, including poverty and food insecurity.

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. Protecting Madagascar's biodiversity while promoting social development for its people is a matter of the utmost urgency ■



Conservation and restoration should **not be framed solely** around the protected area network.

Expanded **biodiversity monitoring** is needed to safeguard Madagascar's most valuable assets.

Improving the effectiveness of **existing protected areas** is more important than creating new ones.

Investment in conservation must be based on evidence, effectiveness, and future challenges.

Conservation must address the **root causes** of biodiversity loss.

Vegetation types: ● Dry forest ● Spiny forest ● Tapia ● Subhumid forest ● Grassland-woodland mosaic ● Humid forest ● Mangroves ○ Protected areas

Visual representation of five key opportunities for conserving and restoring Madagascar's rapidly declining biodiversity identified in this Review. The dashed lines point to representative vegetation types where these recommendations could have tangible effects, but the opportunities are applicable across Madagascar.

ILLUSTRATION: INESSA VOET

The complete list of authors and their affiliations is available in the full article online.

*Corresponding authors: Hélène Ralimanana (h.ralimanana@kew.org); Alexandre Antonelli (a.antonelli@kew.org)

Cite this article as H. Ralimanana *et al.*, *Science* **378**, eadf1466 (2022). DOI: 10.1126/science.adf1466

READ THE FULL ARTICLE AT
https://doi.org/10.1126/science.adf1466

REVIEW

BIODIVERSITY

Madagascar's extraordinary biodiversity: Threats and opportunities

Hélène Ralimanana[1]*†, Allison L. Perrigo[2,3]†, Rhian J. Smith[3,4]†, James S. Borrell[4], Søren Faurby[2,3], Mamy Tiana Rajaonah[1], Tianjanahary Randriamboavonjy[1], Maria S. Vorontsova[4], Robert S. C. Cooke[2,3,5], Leanne N. Phelps[6,7], Ferran Sayol[3,8], Niels Andela[9], Tobias Andermann[2,3,10,11], Andotiana M. Andriamanohera[1], Sylvie Andriambololonera[12], Steven P. Bachman[4], Christine D. Bacon[2,3], William J. Baker[4], Francesco Belluardo[13,14,15], Chris Birkinshaw[12,16], Stuart Cable[4], Nataly A. Canales[17], Juan D. Carrillo[3,11,18,19], Rosie Clegg[4,20], Colin Clubbe[4], Angelica Crottini[13,14,15], Gabriel Damasco[2,21], Sonia Dhanda[4], Daniel Edler[2,3,22], Harith Farooq[2,3,23], Paola de Lima Ferreira[2,3,24], Brian L. Fisher[25], Félix Forest[4], Lauren M. Gardiner[26], Steven M. Goodman[27,28], Olwen M. Grace[4], Thaís B. Guedes[29], Jan Hackel[4], Marie C. Henniges[4,30], Rowena Hill[4,30], Caroline E. R. Lehmann[6,7], Porter P. Lowry II[16,31], Lovanomenjanahary Marline[1,3,27], Pável Matos-Maraví[3,24], Justin Moat[4], Beatriz Neves[3,32], Matheus G. C. Nogueira[3,32], Renske E. Onstein[33,34], Alexander S. T. Papadopulos[35], Oscar A. Perez-Escobar[4], Peter B. Phillipson[16,31], Samuel Pironon[4,36], Natalia A. S. Przelomska[4,37], Marina Rabarimanarivo[12], David Rabehevitra[1], Jeannie Raharimampionona[12], Fano Rajaonary[12], Landy R. Rajaovelona[1], Mijoro Rakotoarinivo[38], Amédée A. Rakotoarisoa[1], Solofo E. Rakotoarisoa[1], Herizo N. Rakotomalala[1], Franck Rakotonasolo[1], Berthe A. Ralaiveloarisoa[1], Myriam Ramirez-Herranz[3,39,40], Jean Emmanuel N. Randriamamonjy[1], Vonona Randrianasolo[1], Andriambolantsoa Rasolohery[41], Anitry N. Ratsifandrihamanana[42], Noro Ravololomanana[12], Velosoa Razafiniary[1], Henintsoa Razanajatovo[1], Estelle Razanatsoa[43], Malin Rivers[44], Daniele Silvestro[2,3,11,19], Weston Testo[2,3,28], Maria F. Torres Jiménez[2,3,45], Kim Walker[4,46], Barnaby E. Walker[4], Paul Wilkin[4], Jenny Williams[4], Thomas Ziegler[47,48], Alexander Zizka[49], Alexandre Antonelli[2,3,4,50]*†

Madagascar's unique biota is heavily affected by human activity and is 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 statuses, 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). International Union for Conservation of Nature (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.

Madagascar's biota, the result of millions of years of evolution in relative isolation, is both unique and under threat. At the same time that 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, whereas at the other end of the scale, 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 3118 assessed tree species in Madagascar are threatened (*5*). Humans have affected the environment since their earliest 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 the 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 before 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 EX, 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 species) or as Critically Endangered (Possibly Extinct in the Wild) [CR(PEW)] (seven species). Of those currently listed as CR(PE), five species are present in ex situ living collections, and their statuses 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 = Evolutionarily Distinct and Globally Endangered). Almost one in five species of amphibians (18 species), reptiles (17 species), and mammals (17 species) in the top 100 EDGE species of each group are found in Madagascar (*13*). Yet, only 1 in 20 (four species) of the top 100 EDGE species of birds are found on the island.

Given the narrow geographic range of many Malagasy species [such as (*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 because of 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 (*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 [such as (*18*)]. This proportion may also be biased by an overassessment 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 on the basis of 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 8821 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, in 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 species; 47.7% [95% confidence interval (CI): 38.5 to 56.7%]} than reflected in published IUCN assessments (1 of 33 species; 3.0%), which suggests a bias toward assessing more common species. In the magnoliids, the combined results predict a lower proportion of threatened species [211 of 294 species; 71.8% (95% CI: 68.0 to 75.9%)] compared with published IUCN assessments alone (173 of 225 species; 76.9%), which suggests a bias toward 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 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 resulting from 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 despite habitat fragmentation (*25*, *26*), whereas others have relatively low diversity, possibly as a result of anthropogenic effects (*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 as a result of 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 past 50,000 years, with one decline (*Cheirogaleus* cf. *medius*) starting as long as 300,000 years ago—all clearly in prehuman times and resulting in lower genetic diversity (*29*). By contrast, another genomic study shows that 5 out of 10 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

---

[1]Royal Botanic Gardens, Kew, Kew Madagascar Conservation Centre, Antananarivo, Madagascar. [2]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden. [3]Gothenburg Global Biodiversity Centre, University of Gothenburg, Gothenburg, Sweden. [4]Royal Botanic Gardens, Kew, Richmond, Surrey, UK. [5]UK Centre for Ecology and Hydrology, Wallingford, UK. [6]School of GeoSciences, University of Edinburgh, Edinburgh, UK. [7]Royal Botanic Garden Edinburgh, Edinburgh, UK. [8]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK. [9]School of Earth and Environmental Sciences, Cardiff University, Cardiff, Wales, UK. [10]Department of Organismal Biology, SciLifeLab, Uppsala University, Uppsala, Sweden. [11]Department of Biology, University of Fribourg, Fribourg, Switzerland. [12]Missouri Botanical Garden, Madagascar Program, Antananarivo, Madagascar. [13]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, Vairão, Portugal. [14]Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal. [15]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal. [16]Missouri Botanical Garden, St. Louis, MO, USA. [17]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark. [18]CR2P, Muséum National d'Histoire Naturelle, Paris, France. [19]Swiss Institute of Bioinformatics, Fribourg, Switzerland. [20]Department of Geography, University of Exeter, Exeter, Devon, UK. [21]Departamento de Botânica e Zoologia, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil. [22]Integrated Science Lab, Department of Physics, Umeå University, Umeå, Sweden. [23]Faculty of Natural Sciences, Lúrio University, Pemba, Cabo Delgado Province, Mozambique. [24]Biology Centre CAS, Institute of Entomology, České Budějovice, Czech Republic. [25]California Academy of Sciences, San Francisco, CA, USA. [26]Cambridge University Herbarium, Department of Plant Sciences, University of Cambridge, Cambridge, UK. [27]Association Vahatra, Antananarivo, Madagascar. [28]Field Museum of Natural History, Chicago, IL, USA. [29]Instituto de Biologia, Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil. [30]School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK. [31]Institut de Systématique, Évolution, et Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, Paris, France. [32]Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. [33]Naturalis Biodiversity Center, Leiden, Netherlands. [34]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [35]School of Natural Sciences, Bangor University, Bangor, Gwynedd, Wales, UK. [36]UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC), Cambridge, UK. [37]Department of Anthropology, Smithsonian National Museum of Natural History, Washington, DC, USA. [38]Department of Plant Biology and Ecology, University of Antananarivo, Antananarivo, Madagascar. [39]Instituto de Ecología y Biodiversidad, University of La Serena, La Serena, Chile. [40]Programa de Doctorado en Biología y Ecología Aplicada, Universidad Católica del Norte, Universidad de La Serena, La Serena, Chile. [41]Ileiry Geospatial Services, Antananarivo, Madagascar. [42]WWF, Antananarivo, Madagascar. [43]Plant Conservation Unit, Department of Biological Sciences, University of Cape Town, South Africa. [44]Botanic Gardens Conservation International, Kew, Richmond, Surrey, UK. [45]Institute of Biosciences, Life Sciences Centre, Vilnius University, Vilnius, Lithuania. [46]Royal Holloway, University of London, Egham, Surrey, UK. [47]Cologne Zoo, Cologne, Germany. [48]Institute of Zoology, University of Cologne, Cologne, Germany. [49]Department of Biology, Philipps-University Marburg, Marburg, Germany. [50]Department of Biology, University of Oxford, Oxford, UK.

***Corresponding author. Email: h.ralimanana@kew.org (H.R.); a.antonelli@kew.org (A.A.)**

†These authors contributed equally to this work.

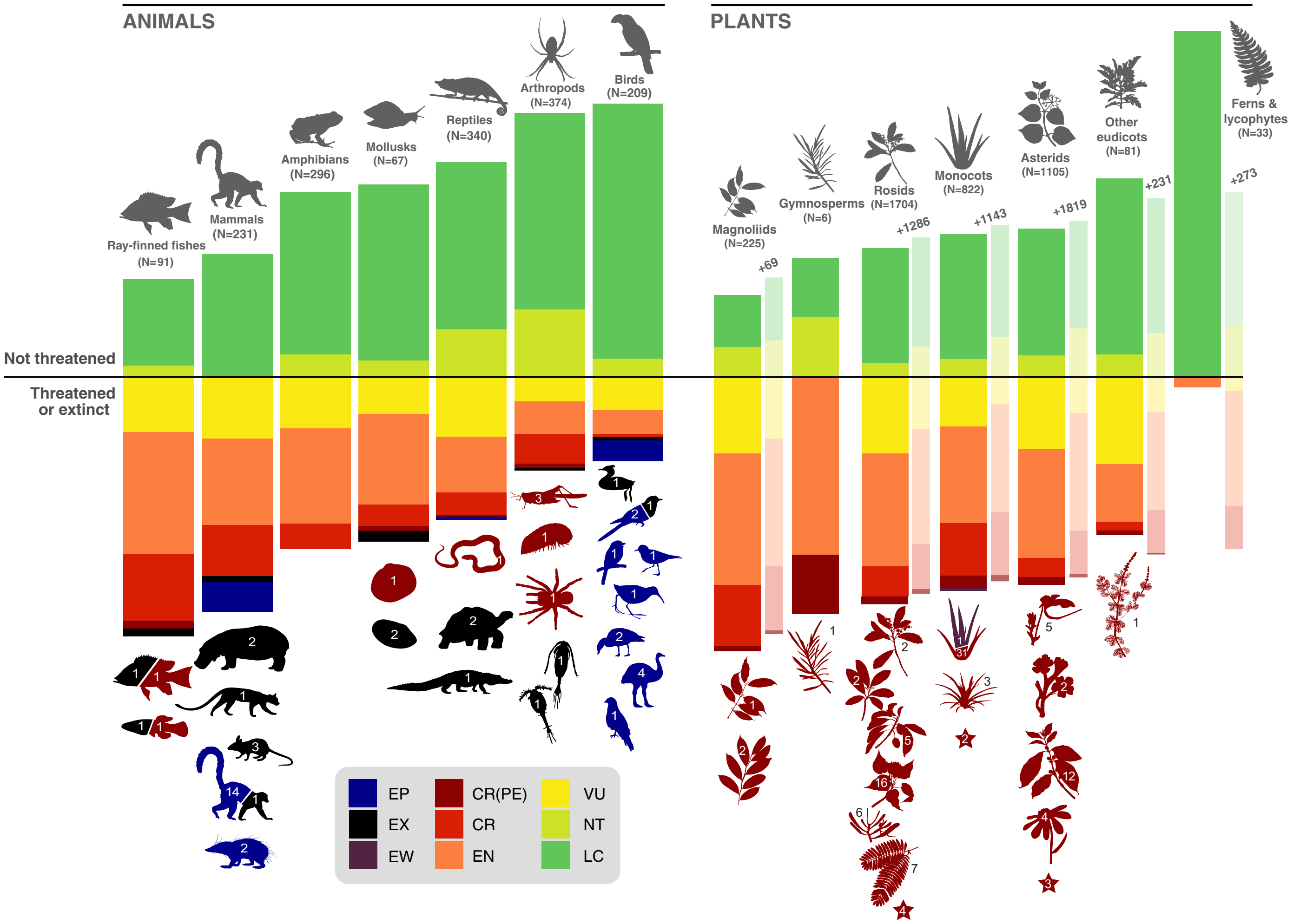


Fig. 1. Madagascar's threatened and lost biodiversity. IUCN Red List assessment categories of major groups of plants and animals from Madagascar. Assessment categories and coloration follow the standards used by the IUCN Red List. Category distributions for animal groups include ray-finned fishes (Actinopterygii, freshwater species only, *N* = 91 species), mammals (Mammalia, *N* = 231), 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* = 1704), monocots (*N* = 822), asterids (*N* = 1105), other eudicots (*N* = 81), and ferns and 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* = 2924), rosids (*N* = 2990), other eudicots (*N* = 312), magnoliids (*N* = 294), monocots (*N* = 1965), and ferns and lycophytes (*N* = 306). The number indicated above each bar with a plus symbol is the number of taxa for which the threat category was predicted using the neural network analysis. IUCN Red List assessment categories include LC and NT, together making up the not threatened category, whereas VU, EN, CR, CR(PE), EW, EX (i.e., extinct after 1500 CE), and EP (*126*) (i.e., extinct before 1500 CE but with dated records within the past 130,000 years) make up the threatened and extinct category. 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, 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, and Saxifragales.

that are not explicitly threatened [i.e., those that are assessed as 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 and international trade. Overexploitation is linked in some cases to illegal harvesting—for example, the illegal logging of rosewood for trade (*Dalbergia* spp.)—which has been 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 with the broad effects of land clearance for agriculture.

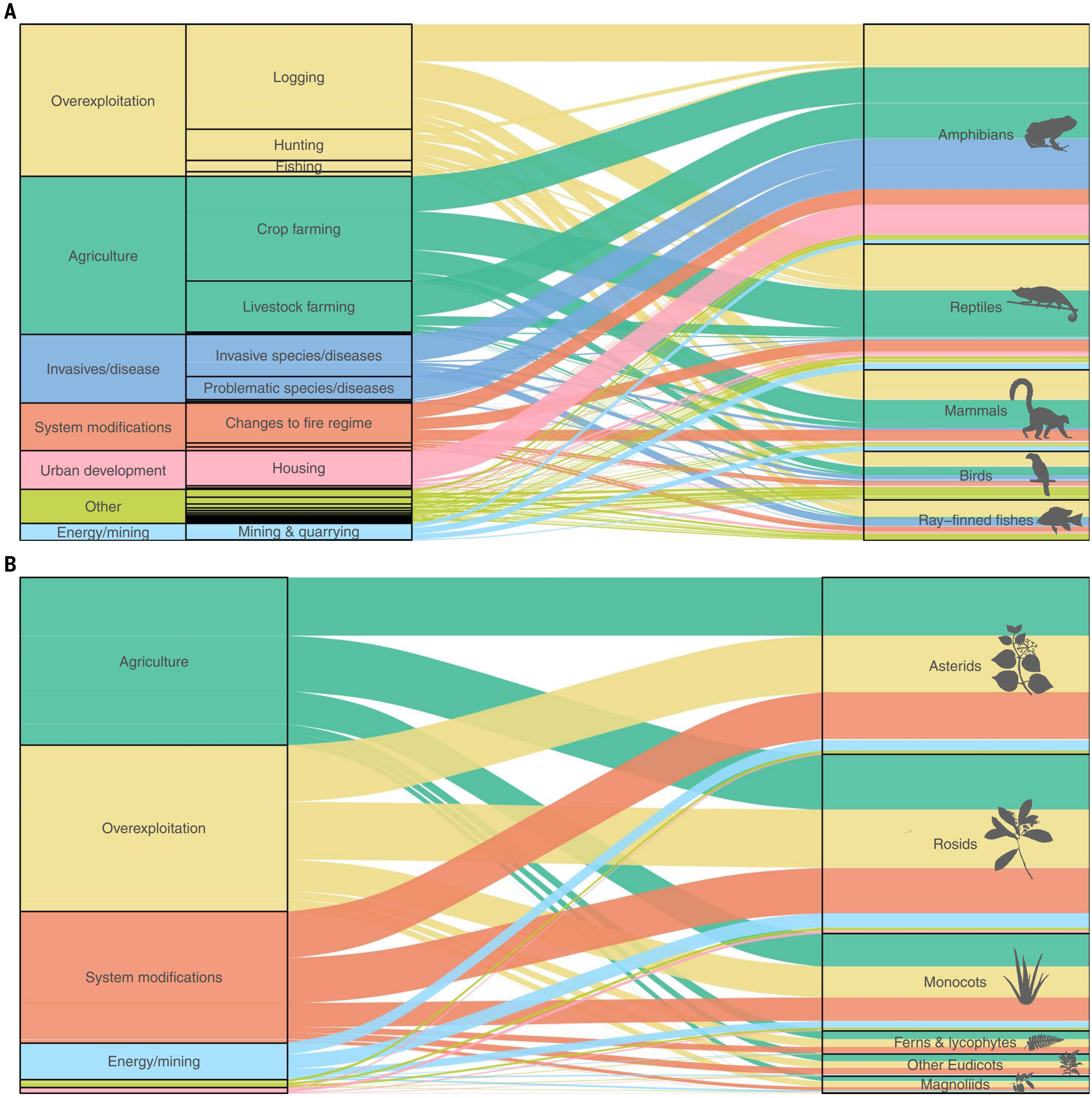


Fig. 2. Threats to Malagasy biodiversity. (**A** and **B**) Alluvial plots showing threats, as defined by the IUCN, and their associations with major groups of terrestrial and freshwater vertebrates (A) (1332 species with IUCN assessments, of which 993 species have at least one listed threat) and plants (B) [9268 species with IUCN assessments or predictions, all of which have at least one listed threat; includes gymnosperms (six species), which could not be visualized]. Widths of the boxes and lines reflect the number of species affected by each threat. Threats for vertebrates are further divided into subthreats, 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 and diseases for plants. Some threat classes have been renamed for brevity and clarity, including the IUCN category "biological resource use," which is referred to as overexploitation here and in the text for brevity and in line with Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) terminology (*36*).

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/year between 2010 and 2014 (*38*) and, according to Global Forest Watch, remains very high at 72.9 kha/year (2014 to 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 the 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) add to deforestation, threaten 23.2% of vertebrates, and are estimated to threaten 68.9% of plants. Some predictions indicate that in the absence of an effective strategy against deforestation, 38 to 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 affect 27% of all species (360 species; Fig. 2). This category includes non-native invasive species as well as problematic native species and diseases of any origin. Changes in habitat because of 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 the common water hyacinth (*Pontederia crassipes*) in freshwater systems (*46*), are aggressively invasive and transformative in seminatural habitats and are clearly affecting native fauna and flora. Even within reserves and protected areas (PAs), the issue can be pronounced. For example, three species of invasive or 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 PAs.

Not all impacts are negative, however, and there is some evidence to suggest that, because of 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 example, the presence of strawberry guava has been reported to locally increase species richness in frugivores, but because they are primary dispersers of the seed, this further contributes to the spread of and associated changes in floral and faunal community structure and reduction in taxonomic richness (*50*).

Non-native vertebrates have also had marked and diverse effects, which we illustrate here 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*). Although 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 past 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 effect 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 of 2.5 threats per species) and reptiles (mean of 2.2 threats per species). For plants (Fig. 2B), magnoliids have the most threats per species (mean of 2.9 threats per species) followed by rosids (mean of 2.8 threats per species) and other eudicots (mean of 2.8 threats per 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 effect 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*).

Conservation efforts and effectiveness

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 (*66*–*70*). 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 past two decades (Fig. 3). This recent and extensive designation of new PAs was carried out through a multistakeholder 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 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 of 18 amphibians, 15 of 17 reptiles, 16 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) (*69*, *71*, *72*). Eleven of these are orphan PAs—sites abandoned by their former managers, with responsibility reverting to the Ministry of Environment and Sustainable Development (*69*). An additional 89 sites (15,200 km^2), predominantly made up of Key Biodiversity Areas (KBAs), are not under formal protection (*69*, *71*, *73*, *74*).

The long-term security and effective management of Madagascar's PAs is therefore crucial to addressing the country's biodiversity

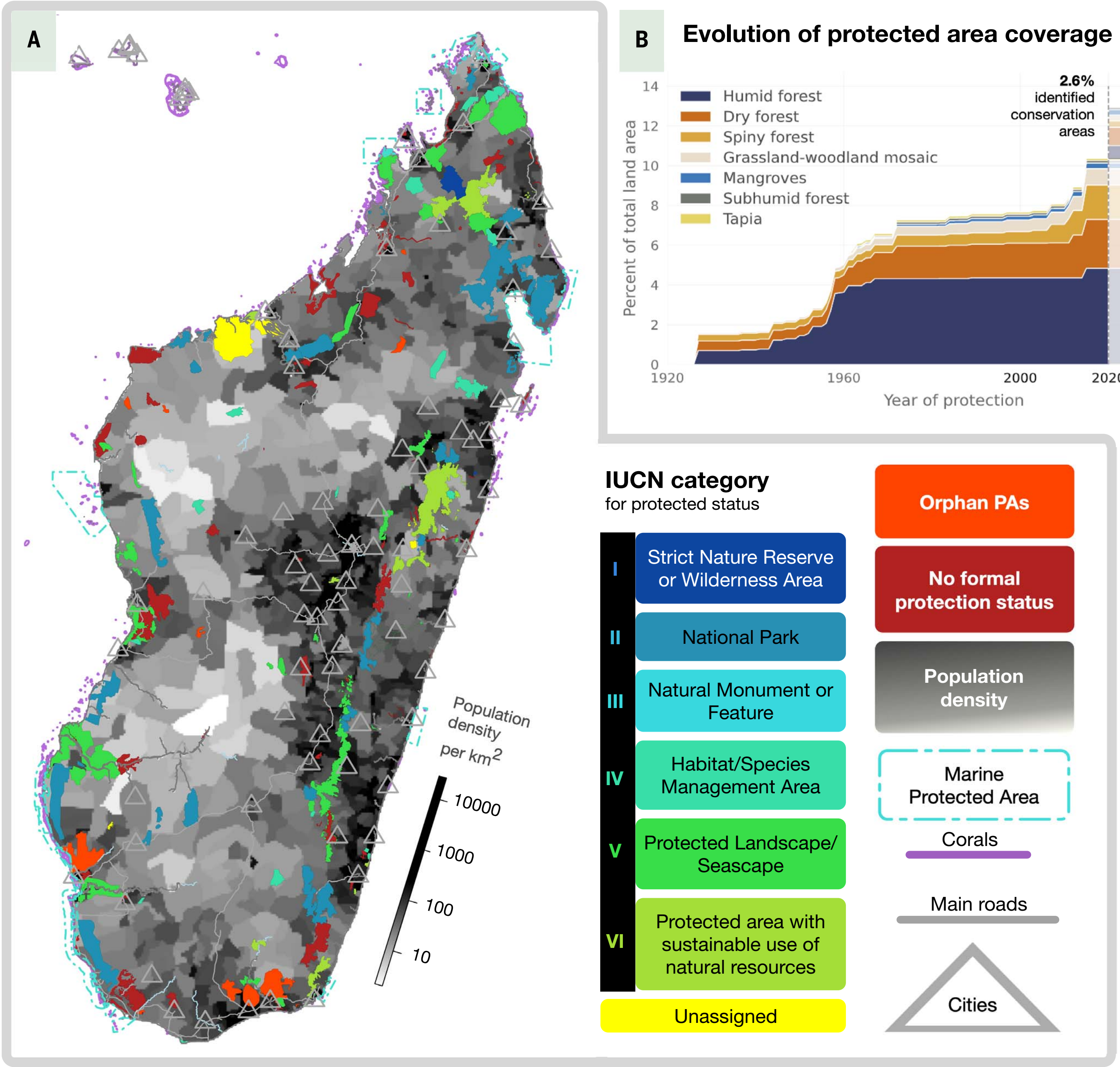


Fig. 3. Madagascar's terrestrial PAs in the context of human population density and changes in coverage of vegetation type over time. (**A**) PAs with IUCN protected status (*127*), orphan status, or no formal protection status (e.g., unprotected KBAs) shown in the context of nearby marine PAs, surrounding bathymetry (*128*), coral reefs (*129*), cities, roads, and population density (*130*). (**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 (*73*, *74*).

challenges. Providing evidence of their effectiveness and cobenefits, 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., its effectiveness at avoiding deforestation or providing alternative livelihoods) while accounting for numerous covariates (*75*), particularly in Madagascar with comparatively little long-term biodiversity monitoring data (*76*). Recent counterfactual analyses (*77*) have sought to address this question by identifying protected and nonprotected 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 important role in reducing deforestation (*9*).

We show that since 1990, human impacts have measurably increased across all terrestrial PAs (table S8) (*9*), a trend documented worldwide (*75*). 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 cobenefits and minimize detrimental human effects.

Scores for deforestation and management effectiveness—for example, from the self-reported Management Effectiveness Tracking Tool (78)—have been the main metrics used to monitor effectiveness to date. However, these are not always reliable indicators of management effectiveness (76). 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 has only recently been 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. 4, A and 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. 4, C and D). Deforestation and land use conversion remain key challenges to conservation in Madagascar, and improved remote sensing will accelerate monitoring and developing an understanding of 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 3500 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 EW, *Aloe silicicola*, now only survives in one living collection outside Madagascar.

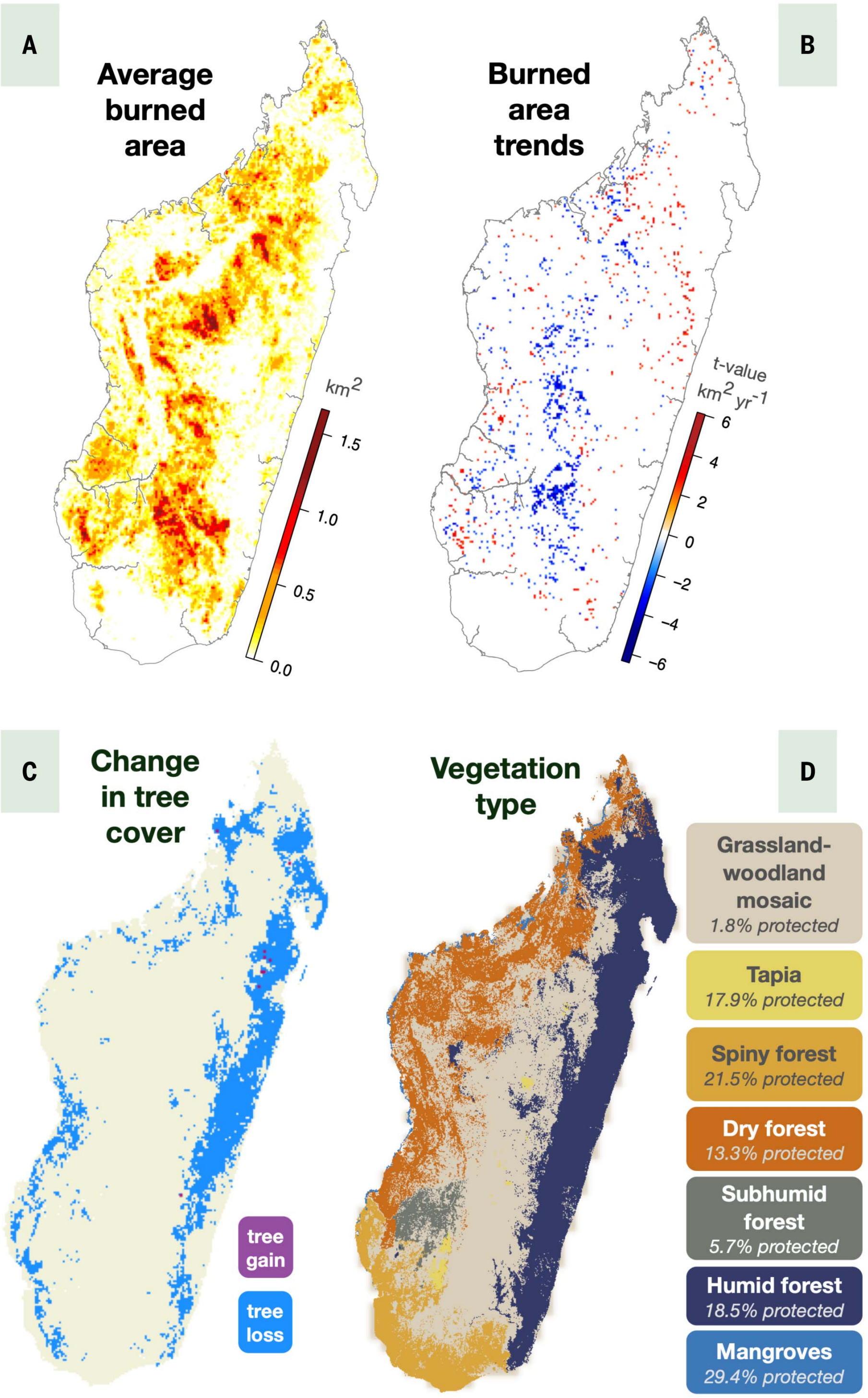


Fig. 4. Recent changes and patterns in burned area and tree cover in Madagascar. (**A**) Average burned area in the period 2003 to 2019. (**B**) Statistically significant trends in burned area (MODIS) (131) from 2006 to 2016, not explained by precipitation change (TRMM) (132), dates chosen for comparison with Goodman *et al*. (71). Red indicates an increasing trend, and blue indicates a decreasing trend. (**C**) Change in tree cover from 2000 to 2012 (133). (**D**) Vegetation map, inferred and simplified from Moat and Smith (134). The legend indicates the percentage of each vegetation category currently covered by the PA network.

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, 79). Many are part of active breeding programs, but only 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 toward the more charismatic, well-known taxa (80). 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 (*81*–*84*). For species in these groups and others with high levels of micro-endemism, such conservation programs continue to represent a major safeguard against extinction (*85*). 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 (*86*). 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 the minimization of 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 (*87*).

Progress toward international conservation commitments

Madagascar continues to make progress toward Convention on Biological Diversity targets but, like most countries, falls short of meeting them in full (*88*). Of particular relevance 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 (*88*). 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 (*89*, *90*).

Target 4 of the Global Strategy for Plant Conservation (GSPC) 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 because of 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 current PAs may provide a longer-term pathway to meeting this goal, particularly where there are rapidly realizable socioeconomic 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 because of a 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 (*91*). 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 that this percentage is currently at 80%.

Realizing the benefits of biodiversity for people

The majority of Madagascar's more than 28 million inhabitants live outside of, but often very close to, PAs (*92*) (Fig. 3A and fig. S1). These communities face challenges connected to widespread poverty, which itself is related to the 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*, *93*, *94*). 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 (*95*). 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*). Because the human population in the country is expected to reach 42 to 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 (*96*), 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 (*97*).

Looking back, moving forward

Despite decades of research and applied conservation programs supported through substantial financial investments (*94*, *98*), Madagascar's remarkable biodiversity continues to face severe challenges (Figs. 1 and 2). It is reasonable to ask whether more of the same tactics—even if better resourced and underpinned with greater scientific understanding and technology—are likely to deliver a tangible reversal in Madagascar's trajectory of biodiversity loss, or whether new approaches are required to bring transformative change (*99*), 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*, *100*), with solutions needed at all societal levels—including through local communities, engagement of the private sector, sound leadership and policy from regional and national governments, 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 (Figs. 3 and 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, although 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 the existing PA network, including one amphibian, three mammals, seven reptiles, and 559 plants (*9*) as well as 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 larger than 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 that there may be undocumented extinctions, especially in poorly studied taxa (*1*). Despite this, with limited resources and/or capacity, Madagascar has made important progress toward 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*) (*101*), which shows a 30% probability that extinction was prevented because of 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 (*102*); and the work to prevent the extinction of the ploughshare tortoise (*Astrochelys yniphora*) through a captive breeding program (*103*).

Other notable successes have come from Madagascar's biodiversity conservation boom, which started in the 1980s and included 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 through collaboration protocols—set out in the national strategy for scientific research in Madagascar (*104*)—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 (*105*). The Madagascar Fauna and Flora Group, the Lemur Conservation Foundation, the Durrell Wildlife Conservation Trust, The Peregrine Fund Madagascar, the Madagascar Biodiversity Center, and Madagasikara Voakajy, as well as the work of the Royal Botanic Gardens, Kew, and the 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 (*106*) 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 coauthors and consulted with Malagasy and external researchers, conservation leaders, and politicians to arrive at five main opportunities for the future, which we present here.

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 (*98*, *107*). 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 it is the subject of increasingly sophisticated research efforts (*75*, *77*, *108*). Nevertheless, it is imperative that 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 (*109*) for diversified, locally adapted, and sustainable agriculture can help address livelihood needs, whereas 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 (*110*) while providing resilience to climate stochasticity (*111*). 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 shown by a study conducted during the COVID-19 pandemic (*112*). Fire management also presents the opportunity to mitigate the effect 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 (*113*). 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 (*114*) and in need of immediate protection. Monitoring is also crucial for the detection of new non-native and potentially invasive species as well as for 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 (*115*), 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 (*108*), many conservation interventions lack impact evaluations, in part because of 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 (*116*), 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 in ensuring that data flow freely and openly to similar, global initiatives like Protected Planet (*72*).

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 (*117*). Similarly, DNA-based biodiversity surveys, including environmental sampling, can greatly improve the speed of site inventories and the 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, 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 (Figs. 3 and 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 (*118*), further increasing the already measurable effect 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 the risk of future downgrading, downsizing, or degazettement (legal removal of conservation status) (*119*). 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 (*118*, *120*).

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 (*121*) 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 (*98*) (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 (*122*). Notably, 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*, *123*).

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 (*87*).

5) Conservation actions must address the root causes of biodiversity loss. Our analysis shows 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. 4, A and B) [see also (*43*)], which significantly affects humid forest areas in the east and dry forest and spiny forest in the west (Fig. 4, C and 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 (*124*). 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 they 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 (*98*, *123*). 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 (*98*, *125*).

Conclusions

The alarming status of Madagascar's biodiversity is the result of multifaceted, unsustainable practices that include 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 the most valuable asset for Madagascar's future development.

REFERENCES AND NOTES

1. A. Antonelli *et al.*, Madagascar's extraordinary biodiversity: Evolution, distribution, and use. *Science* **378**, eabf0869 (2022). doi: 10.1126/science.abf0869
2. T. Andermann, S. Faurby, S. T. Turvey, A. Antonelli, D. Silvestro, The past and future human impact on mammalian diversity. *Sci. Adv.* **6**, eabb2313 (2020). doi: 10.1126/sciadv.abb2313; pmid: 32917612
3. IUCN, The IUCN Red List of Threatened Species, version 2021-1 (2021); https://www.iucnredlist.org.
4. IUCN, *IUCN Red List Categories and Criteria: Version 3.1, Second Edition* (Gland, 2012).
5. E. Beech *et al.*, *The Red List of Trees of Madagascar* (Botanic Gardens Conservation International, 2021).
6. S. M. Goodman, W. L. Jungers, *Les Animaux et Ecosystèmes de l'Holocene Disparus de Madagascar* (Association Vahatra, 2013).
7. F. Sayol, M. J. Steinbauer, T. M. Blackburn, A. Antonelli, S. Faurby, Anthropogenic extinctions conceal widespread

evolution of flightlessness in birds. *Sci. Adv.* **6**, eabb6095 (2020). doi: 10.1126/sciadv.abb6095; pmid: 33268368

8. Y. Malhi *et al*., Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 838–846 (2016). doi: 10.1073/pnas.1502540113; pmid: 26811442
9. Materials and methods and supplementary text are available as supplementary materials.
10. Botanic Gardens Conservation International, PlantSearch online database (2021); https://tools.bgci.org/plant_search.php.
11. Zoological Society of London, EDGE of Existence; https://www.edgeofexistence.org/.
12. N. J. B. Isaac, S. T. Turvey, B. Collen, C. Waterman, J. E. M. Baillie, Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLOS ONE* **2**, e296 (2007). doi: 10.1371/journal.pone.0000296; pmid: 17375184
13. Zoological Society of London, EDGE of Existence: Explore EDGE species by country (2021); https://www.edgeofexistence.org/explore-edge-species-country/.
14. A. Rakotoarison *et al*., Describing the smaller majority: Integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. *Vertebr. Zool.* **67**, 271–398 (2017).
15. 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
16. J. P. Benstead *et al*., Conserving Madagascar's Freshwater Biodiversity. *Bioscience* **53**, 1101–1111 (2003). doi: 10.1641/0006-3568(2003)053[1101:CMFB]2.0.CO;2
17. R. D. E. MacPhee, D. A. Burney, N. A. Wells, Early Holocene Chronology and environment of Ampasambazimb, a Malagasy subfossil lemur site. *Int. J. Primatol.* **6**, 463–489 (1985). doi: 10.1007/BF02735571
18. S. Faurby, W. L. Eiserhardt, J.-C. Svenning, Strong effects of variation in taxonomic opinion on diversification analyses. *Methods Ecol. Evol.* **7**, 4–13 (2016). doi: 10.1111/2041-210X.12449
19. IUCN, The IUCN Red List of Threatened Species, version 2020-3 (2020); https://www.iucnredlist.org.
20. A. Zizka, T. Andermann, D. Silvestro, *IUCNN* – Deep learning approaches to approximate species' extinction risk. *Divers. Distrib.* **28**, 227–241 (2021). doi: 10.1111/ddi.13450
21. P. de Villemereuil *et al*., Little adaptive potential in a threatened passerine bird. *Curr. Biol.* **29**, 889–894.e3 (2019). doi: 10.1016/j.cub.2019.01.072; pmid: 30799244
22. R. Lande, Genetics and demography in biological conservation. *Science* **241**, 1455–1460 (1988). doi: 10.1126/science.3420403; pmid: 3420403
23. M. C. Rivers, N. A. Brummitt, E. Nic Lughadha, T. R. Meagher, Do species conservation assessments capture genetic diversity? *Glob. Ecol. Conserv.* **2**, 81–87 (2014). doi: 10.1016/j.gecco.2014.08.005
24. B. Charlesworth, D. Charlesworth, The genetic basis of inbreeding depression. *Genet. Res.* **74**, 329–340 (1999). doi: 10.1017/S0016672399004152; pmid: 10689809
25. A. J. Helmstetter *et al*., The demographic history of Madagascan micro-endemics: Have rare species always been rare? *Proc. R. Soc. B* **288**, 20210957 (2021). doi: 10.1098/rspb.2021.0957; pmid: 34547905
26. E. Quéméré, X. Amelot, J. Pierson, B. Crouau-Roy, L. Chikhi, Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 13028–13033 (2012). doi: 10.1073/pnas.1200153109; pmid: 22826244
27. L. M. Gardiner, M. Rakotoarinivo, L. R. Rajaovelona, C. Clubbe, Population genetics data help to guide the conservation of palm species with small population sizes and fragmented habitats in Madagascar. *PeerJ* **5**, e3248 (2017). doi: 10.7717/peerj.3248; pmid: 28480141
28. G. L. Olivieri, V. Sousa, L. Chikhi, U. Radespiel, From genetic diversity and structure to conservation: Genetic signature of recent population declines in three mouse lemur species (*Microcebus* spp.). *Biol. Conserv.* **141**, 1257–1271 (2008). doi: 10.1016/j.biocon.2008.02.025
29. R. C. Williams *et al*., Conservation genomic analysis reveals ancient introgression and declining levels of genetic diversity in Madagascar's hibernating dwarf lemurs. *Heredity* **124**, 236–251 (2020). doi: 10.1038/s41437-019-0260-9; pmid: 31435007
30. A. Shapcott *et al*., Can we bring Madagascar's critically endangered palms back from the brink? Genetics, ecology and conservation of the critically endangered palm *Beccariophoenix madagascariensis*. *Bot. J. Linn. Soc.* **154**, 589–608 (2007). doi: 10.1111/j.1095-8339.2007.00676.x
31. P. A. Hagl *et al*., Geographical structure of genetic diversity in *Loudetia simplex* (Poaceae) in Madagascar and South Africa. *Bot. J. Linn. Soc.* **196**, 81–99 (2020). doi: 10.1093/botlinnean/boaa098
32. T. van der Valk, D. Díez-Del-Molino, T. Marques-Bonet, K. Guschanski, L. Dalén, Historical genomes reveal the genomic consequences of recent population decline in eastern gorillas. *Curr. Biol.* **29**, 165–170.e6 (2019). doi: 10.1016/j.cub.2018.11.055; pmid: 30595519
33. C. R. Peart *et al*., Determinants of genetic variation across eco-evolutionary scales in pinnipeds. *Nat. Ecol. Evol.* **4**, 1095–1104 (2020). doi: 10.1038/s41559-020-1215-5; pmid: 32514167
34. A. Crottini, P. Orozco-terWengel, F. C. E. Rabemananjara, J. S. Hauswaldt, M. Vences, Mitochondrial introgression, color pattern variation, and severe demographic bottlenecks in three species of malagasy poison frogs, genus *Mantella*. *Genes* **10**, 317 (2019). doi: 10.3390/genes10040317; pmid: 31018611
35. M. Craul *et al*., Influence of forest fragmentation on an endangered large-bodied lemur in northwestern Madagascar. *Biol. Conserv.* **142**, 2862–2871 (2009). doi: 10.1016/j.biocon.2009.05.026
36. S. Díaz *et al*., "Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services" (IPBES, 2019).
37. IUCN, Threats Classification Scheme, version 3.2 (2022); https://www.iucnredlist.org/resources/threat-classification-scheme.
38. G. Vieilledent *et al*., Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* **222**, 189–197 (2018). doi: 10.1016/j.biocon.2018.04.008
39. GFW, Global Forest Watch - Madagascar (2021); https://gfw.global/3uplmN5.
40. S. L. Maxwell, R. A. Fuller, T. M. Brooks, J. E. M. Watson, Biodiversity: The ravages of guns, nets and bulldozers. *Nature* **536**, 143–145 (2016). doi: 10.1038/536143a; pmid: 27510207
41. G. Vieilledent *et al*., It's not just poverty: Unregulated global market and bad governance explain unceasing deforestation in Western Madagascar. bioRxiv 2020.07.30.229104 [Preprint] (2020). https://doi.org/10.1101/2020.07.30.229104.
42. D. A. Martin *et al*., Land-use trajectories for sustainable land system transformations: Identifying leverage points in a global biodiversity hotspot. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2107747119 (2022). doi: 10.1073/pnas.2107747119; pmid: 35165148
43. L. N. Phelps *et al*., Madagascar's fire regimes challenge global assumptions about landscape degradation. *Glob. Change Biol.* **28**, 6944–6960 (2022). doi: 10.1111/gcb.16206; pmid: 35582991
44. C. A. Kull *et al*., The introduced flora of Madagascar. *Biol. Invasions* **14**, 875–888 (2012). doi: 10.1007/s10530-011-0124-6
45. R. Baohanta *et al*., Restoring native forest ecosystems after exotic tree plantation in Madagascar: Combination of the local ectotrophic species *Leptolena bojeriana* and *Uapaca bojeri* mitigates the negative influence of the exotic species *Eucalyptus camaldulensis* and *Pinus patula*. *Biol. Invasions* **14**, 2407–2421 (2012). doi: 10.1007/s10530-012-0238-5
46. A. Lehavana, "Distribution, ecological and economic impacts and competition of the invasive alien aquatic weeds (*Pontederia crassipes* Mart., *Pistia stratiotes* L., *Salvinia molesta* D.S. Mitch. and *Azolla filiculoides* Lam.) in Madagascar," thesis, Rhodes University, South Africa (2020).
47. A. Ghulam, I. Porton, K. Freeman, Detecting subcanopy invasive plant species in tropical rainforest by integrating optical and microwave (InSAR/PolInSAR) remote sensing data, and a decision tree algorithm. *ISPRS J. Photogramm. Remote Sens.* **88**, 174–192 (2014). doi: 10.1016/j.isprsjprs.2013.12.007
48. A. Gérard, J. U. Ganzhorn, C. A. Kull, S. M. Carrière, Possible roles of introduced plants for native vertebrate conservation: The case of Madagascar. *Restor. Ecol.* **23**, 768–775 (2015). doi: 10.1111/rec.12246
49. A. Di Sacco *et al*., Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Glob. Change Biol.* **27**, 1328–1348 (2021). doi: 10.1111/gcb.15498; pmid: 33494123
50. C. M. M. DeSisto *et al*., An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar. *Biol. Invasions* **22**, 2845–2858 (2020). doi: 10.1007/s10530-020-02293-7
51. S. M. Goodman, V. Soarimalala, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 1737–1769.
52. J. P. Benstead, M. L. J. Stiassny, P. N. Loiselle, K. J. Riseng, N. Raminosoa, in *Global Perspectives on River Conservation: Science, Policy, and Practice*, P. J. Boon, B. R. Davies, G. E. Petts, Eds. (Wiley, 2000), pp. 205–231.
53. P. N. Reinthal, M. L. J. Stiassny, The freshwater fishes of Madagascar: A study of an endangered fauna with recommendations for a conservation strategy. *Conserv. Biol.* **5**, 231–243 (1991). doi: 10.1111/j.1523-1739.1991.tb00128.x
54. B. M. Marshall *et al*., Widespread vulnerability of Malagasy predators to the toxins of an introduced toad. *Curr. Biol.* **28**, R654–R655 (2018). doi: 10.1016/j.cub.2018.04.024; pmid: 29870701
55. M. C. Bletz *et al*., Widespread presence of the pathogenic fungus *Batrachochytrium dendrobatidis* in wild amphibian communities in Madagascar. *Sci. Rep.* **5**, 8633 (2015). doi: 10.1038/srep08633; pmid: 25719857
56. J. L. Brown, A. D. Yoder, Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecol. Evol.* **5**, 1131–1142 (2015). doi: 10.1002/ece3.1418; pmid: 25859320
57. J. C. Ingram, T. P. Dawson, Climate change impacts and vegetation response on the island of Madagascar. *Phil. Trans. R. Soc. A* **363**, 55–59 (2005). doi: 10.1098/rsta.2004.1476; pmid: 15598621
58. J.-N. Wan *et al*., Modeling impacts of climate change on the potential distribution of six endemic baobab species in Madagascar. *Plant Divers.* **43**, 117–124 (2020). doi: 10.1016/j.pld.2020.07.001; pmid: 33997544
59. S. R. Weiskopf, J. A. Cushing, T. L. Morelli, B. J. E. Myers, Climate change risks and adaptation options for Madagascar. *Ecol. Soc.* **26**, 36 (2021). doi: 10.5751/ES-12816-260436
60. J. Busch *et al*., Climate change and the cost of conserving species in Madagascar. *Conserv. Biol.* **26**, 408–419 (2012). doi: 10.1111/j.1523-1739.2012.01838.x; pmid: 22497442
61. G. Chomicki, M. Weber, A. Antonelli, J. Bascompte, E. T. Kiers, The impact of mutualisms on species richness. *Trends Ecol. Evol.* **34**, 698–711 (2019). doi: 10.1016/j.tree.2019.03.003; pmid: 31003875
62. L. P. Koh *et al*., Species coextinctions and the biodiversity crisis. *Science* **305**, 1632–1634 (2004). doi: 10.1126/science.1101101; pmid: 15361627
63. M. L. Moir *et al*., Current constraints and future directions in estimating coextinction. *Conserv. Biol.* **24**, 682–690 (2010). doi: 10.1111/j.1523-1739.2009.01398.x; pmid: 20067486
64. R. K. Colwell, R. R. Dunn, N. C. Harris, Coextinction and persistence of dependent species in a changing world. *Annu. Rev. Ecol. Evol. Syst.* **43**, 183–203 (2012). doi: 10.1146/annurev-ecolsys-110411-160304
65. D. M. Hansen, M. Galetti, Ecology. The forgotten megafauna. *Science* **324**, 42–43 (2009). doi: 10.1126/science.1172393; pmid: 19342573
66. C. A. Kull, in *Conservation and Environmental Management in Madagascar*, I. R. Scales, Ed. (Routledge, 2014), pp. 146–171.
67. C. J. Gardner *et al*., The rapid expansion of Madagascar's protected area system. *Biol. Conserv.* **220**, 29–36 (2018). doi: 10.1016/j.biocon.2018.02.011
68. J. P. G. Jones, O. S. Rakotonarivo, J. H. Razafimanahaka, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 2130–2140.
69. S. M. Goodman, H. M. Rakotondratsimba, J. C. Ranivo Rakotoson, in *The New Natural History of Madagascar*, S. M. Goodman, Ed. (Princeton Univ. Press, 2022), pp. 2091–2107.
70. M. Virah-Sawmy, C. J. Gardner, A. N. Ratsifandrihamanana, in *Conservation and Environmental Management in Madagascar*, I. R. Scales, Ed. (Routledge, 2014), pp. 216–252.
71. S. M. Goodman, M. J. Raherilalao, S. Wohlhauser, *The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota* (Association Vahatra, 2018).
72. Protected Planet, The World Database on Protected Areas (2020); https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA.
73. Key Biodiversity Areas Partnership, World Database of Key Biodiversity Areas (2021); https://www.keybiodiversityareas.org/kba-data/request.

74. P. Kullberg, E. Di Minin, A. Moilanen, Using key biodiversity areas to guide effective expansion of the global protected area network. *Glob. Ecol. Conserv.* **20**, e00768 (2019). doi: 10.1016/j.gecco.2019.e00768
75. J. Geldmann, A. Manica, N. D. Burgess, L. Coad, A. Balmford, A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 23209–23215 (2019). doi: 10.1073/pnas.1908221116; pmid: 31659036
76. J. Eklund, L. Coad, J. Geldmann, M. Cabeza, What constitutes a useful measure of protected area effectiveness? A case study of management inputs and protected area impacts in Madagascar. *Conserv. Sci. Pract.* **1**, e107 (2019). doi: 10.1111/csp2.107
77. J. Eklund *et al*., Contrasting spatial and temporal trends of protected area effectiveness in mitigating deforestation in Madagascar. *Biol. Conserv.* **203**, 290–297 (2016). doi: 10.1016/j.biocon.2016.09.033
78. Protected Planet, Management effectiveness (PAME) (2022); https://www.protectedplanet.net/en/thematic-areas/protected-areas-management-effectiveness-pame?tab=METT.
79. Species 360, Zoological Information Management Software (2021); https://zims.species360.org.
80. A. Miralles, M. Raymond, G. Lecointre, Empathy and compassion toward other species decrease with evolutionary divergence time. *Sci. Rep.* **9**, 19555 (2019). doi: 10.1038/s41598-019-56006-9; pmid: 31862944
81. J. R. Ali, M. Huber, Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653–656 (2010). doi: 10.1038/nature08706; pmid: 20090678
82. R. A. Griffiths, L. Pavajeau, Captive breeding, reintroduction, and the conservation of amphibians. *Conserv. Biol.* **22**, 852–861 (2008). doi: 10.1111/j.1523-1739.2008.00967.x; pmid: 18616746
83. T. Ziegler *et al*., Keeping and breeding of threatened endemic Malagasy freshwater fishes at Cologne Zoo (Germany): A contribution towards the advancement of a conservation breeding network. *Der Zoologische Garten* **88**, 123–155 (2020).
84. L. Leiss *et al*., Review of threatened Malagasy freshwater fishes in zoos and aquaria: The necessity of an ex situ conservation network—A call for action. *Zoo Biol.* **41**, 244–262 (2022). doi: 10.1002/zoo.21661; pmid: 34870879
85. P. V. Loiselle, in *The Natural History of Madagascar*, S. M. Goodman, J. P. Benstead, Eds. (Univ. Chicago Press, 2003), pp. 1569–1574.
86. K. Traylor-Holzer, K. Leus, O. Byers, in *The Ark and Beyond: The Evolution of Zoo and Aquarium Conservation*, B. A. Minteer, J. Maienschein, J. P. Collins, Eds. (Univ. Chicago Press, 2018), pp. 129–141.
87. A. Britt, B. R. Iambana, C. R. Welch, A. S. Katz, in *The Natural History of Madagascar*, S. M. Goodman, J. Benstead, Eds. (Univ. Chicago Press, 2003), pp. 1547–1552.
88. Secretariat of the Convention on Biological Diversity, Global Biodiversity Outlook 5 (2020); https://www.cbd.int/gbo5.
89. M. D. Barnes, L. Glew, C. Wyborn, I. D. Craigie, Prevent perverse outcomes from global protected area policy. *Nat. Ecol. Evol.* **2**, 759–762 (2018). doi: 10.1038/s41559-018-0501-y; pmid: 29556080
90. R. L. Pressey *et al*., The mismeasure of conservation. *Trends Ecol. Evol.* **36**, 808–821 (2021). doi: 10.1016/j.tree.2021.06.008; pmid: 34303527
91. Critical Ecosystem Partnership Fund, Indian House Crow Eradication and Invasive Species Surveillance in Madagascar (2021); https://www.cepf.net/grants/grantee-projects/indian-house-crow-eradication-and-invasive-species-surveillance-madagascar.
92. INSTAT, instat Madagascar (2022); https://www.instat.mg/.
93. J. P. G. Jones *et al*., Madagascar: Crime threatens biodiversity. *Science* **363**, 825–825 (2019). doi: 10.1126/science.aaw6402; pmid: 30792294
94. J. P. G. Jones *et al*., Last chance for Madagascar's biodiversity. *Nat. Sustain.* **2**, 350–352 (2019). doi: 10.1038/s41893-019-0288-0
95. United Nations World Food Programme, "Southern Madagascar faces drought-driven hunger, threatening millions" (2020); https://www.wfp.org/news/southern-madagascar-faces-drought-driven-hunger-threatening-millions.
96. S. E. Vollset *et al*., Fertility, mortality, migration, and population scenarios for 195 countries and territories from 2017 to 2100: A forecasting analysis for the Global Burden of Disease Study. *Lancet* **396**, 1285–1306 (2020). doi: 10.1016/S0140-6736(20)30677-2; pmid: 32679112
97. T. T. Gatiso *et al*., Effectiveness of protected areas influenced by socio-economic context. *Nat. Sustain.* **5**, 861–868 (2022). doi: 10.1038/s41893-022-00932-6
98. World Bank, "Madagascar—Third Environment Program Support Project. Independent Evaluation Group, Project Performance Assessment Report 158221" (World Bank, 2021).
99. I. R. Scales, The future of conservation and development in Madagascar: Time for a new paradigm? *Madag. Conserv. Dev.* **9**, 5–12 (2014). doi: 10.4314/mcd.v9i1.2
100. S. Díaz *et al*., Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* **366**, eaax3100 (2019). doi: 10.1126/science.aax3100; pmid: 31831642
101. F. C. Bolam *et al*., How many bird and mammal extinctions has recent conservation action prevented? *Conserv. Lett.* **14**, e12762 (2021). doi: 10.1111/conl.12762
102. L. M. Gardiner, D. Rabehevitra, R. Letsara, A. Shapcott, *Tahina spectabilis*: An exciting new discovery in Madagascar ten years on. *Palms* **61**, 69–82 (2017).
103. Durrell Wildlife Conservation Trust, Durrell Index: Ploughshare Tortoise (2022); https://www.durrell.org/conservation/species/ploughshare-tortoise/.
104. Ministere de l'Enseignement Supérieur et de la Recherche Scientifique, "La Stratégie Nationale de la Recherche Scientifique à Madagascar" (2013); http://www.recherches.gov.mg/IMG/pdf/strategie_nationale_de_la_recherche.pdf.
105. E. Razanatsoa *et al*., Fostering local involvement for biodiversity conservation in tropical regions: Lessons from Madagascar during the COVID-19 pandemic. *Biotropica* **53**, 994–1003 (2021). doi: 10.1111/btp.12967; pmid: 34219750
106. Convention on Biological Diversity, "First draft of the post-2020 global biodiversity framework" (UN Environment Programme, 2020); https://www.cbd.int/doc/c/abb5/591f/2e46096d3f0330b08ce87a45/wg2020-03-03-en.pdf.
107. P. O. Waeber, L. Wilmé, J.-R. Mercier, C. Camara, P. P. Lowry II, How effective have thirty years of internationally driven conservation and development efforts been in Madagascar? *PLOS ONE* **11**, e0161115 (2016). doi: 10.1371/journal.pone.0161115; pmid: 27532499
108. J. Börner, D. Schulz, S. Wunder, A. Pfaff, The effectiveness of forest conservation policies and programs. *Annu. Rev. Resour. Econ.* **12**, 45–64 (2020). doi: 10.1146/annurev-resource-110119-025703
109. N. Seddon *et al*., Getting the message right on nature-based solutions to climate change. *Glob. Change Biol.* **27**, 1518–1546 (2021). doi: 10.1111/gcb.15513; pmid: 33522071
110. 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
111. C. Funk *et al*., Warming of the Indian Ocean threatens eastern and southern African food security but could be mitigated by agricultural development. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 11081–11086 (2008). doi: 10.1073/pnas.0708196105; pmid: 18685101
112. J. Eklund *et al*., Elevated fires during COVID-19 lockdown and the vulnerability of protected areas. *Nat. Sustain.* **5**, 603–609 (2022). doi: 10.1038/s41893-022-00884-x
113. H. S. Grantham *et al*., Diminishing return on investment for biodiversity data in conservation planning. *Conserv. Lett.* **1**, 190–198 (2008). doi: 10.1111/j.1755-263X.2008.00029.x
114. J. Liu, F. Slik, S. Zheng, D. B. Lindenmayer, Undescribed species have higher extinction risk than known species. *Conserv. Lett.* **15**, 12876 (2022). doi: 10.1111/conl.12876
115. IUCN, Motion 116 - Building Madagascar's capacity to counter the threat from invasive species (2020); https://www.iucncongress2020.org/motion/116.
116. Madagascar Protected Areas, Protected Areas of Madagascar (2022); https://protectedareas.mg/.
117. L. P. Koh, S. A. Wich, Dawn of drone ecology: Low-cost autonomous aerial vehicles for conservation. *Trop. Conserv. Sci.* **5**, 121–132 (2012). doi: 10.1177/194008291200500202
118. S. L. Maxwell *et al*., Area-based conservation in the twenty-first century. *Nature* **586**, 217–227 (2020). doi: 10.1038/s41586-020-2773-z; pmid: 33028996
119. R. E. Golden Kroner *et al*., The uncertain future of protected lands and waters. *Science* **364**, 881–886 (2019). doi: 10.1126/science.aau5525; pmid: 31147519
120. I. J. Bateman, G. M. Mace, The natural capital framework for sustainably efficient and equitable decision making. *Nat. Sustain.* **3**, 776–783 (2020). doi: 10.1038/s41893-020-0552-3
121. C. Birkinshaw, P. P. Lowry II, J. Raharimampionona, J. Aronson, Supporting Target 4 of the Global Strategy for Plant Conservation by integrating ecological restoration into Missouri Botanical Garden's conservation program in Madagascar. *Ann. Mo. Bot. Gard.* **99**, 139–146 (2013). doi: 10.3417/2012002
122. J. Aronson, A. F. Clewell, J. N. Blignaut, S. J. Milton, Ecological restoration: A new frontier for nature conservation and economics. *J. Nat. Conserv.* **14**, 135–139 (2006). doi: 10.1016/j.jnc.2006.05.005
123. L. Robson, "The history of PHE in Madagascar: Looking back over the last 25 years and forward to the next chapter" (Blue Ventures for the Madagascar PHE Network, 2014); https://phemadagascar.org/wp-content/uploads/2014/10/History-of-PHE-in-Madagascar-Robson-2014.pdf.
124. S. Naeem, R. Chazdon, J. E. Duffy, C. Prager, B. Worm, Biodiversity and human well-being: An essential link for sustainable development. *Proc. R. Soc. B* **283**, 20162091 (2016). doi: 10.1098/rspb.2016.2091; pmid: 27928039
125. M. Poudyal *et al*., Who bears the cost of forest conservation? *PeerJ* **6**, e5106 (2018). doi: 10.7717/peerj.5106; pmid: 30002962
126. S. Faurby *et al*., PHYLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology* **99**, 2626 (2018). doi: 10.1002/ecy.2443; pmid: 29989146
127. N. Dudley, Ed., "Guidelines for applying protected area management categories including IUCN WCPA best practice guidance on recognising protected areas and assigning management categories and governance types" (IUCN, Gland, 2013).
128. C. Amante, B. W. Eakins, "ETOPO1 1 Arc-minute global relief model: Procedures, data sources and analysis" (National Oceanic and Atmospheric Administration, NOAA Technical Memorandum NESDIS NGDC-24, 2009); https://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/docs/ETOPO1.pdf.
129. UNEP-WCMC, WorldFish Centre, WRI, TNC, "Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project," version 4.1 (2021); https://doi.org/10.34892/t2wk-5t34.
130. Center for International Earth Science Information Network (CIESIN), Columbia University, "Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11" (NASA Socioeconomic Data and Applications Center, 2018); https://doi.org/10.7927/H49C6VHW.
131. L. Giglio, C. Justice, L. Boschetti, D. Roy, MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006, data set (NASA EOSDIS Land Processes DAAC, 2015); https://doi.org/10.5067/MODIS/MCD64A1.006.
132. G. J. Huffman *et al*., The TRMM Multisatellite Precipitation Analysis (TMPA): Quasi-Global, Multiyear, Combined-Sensor Precipitation Estimates at Fine Scales. *J. Hydrometeorol.* **8**, 38–55 (2007). doi: 10.1175/JHM560.1
133. G. Vieilledent *et al*., Output data from: Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in Madagascar, V2, CIRAD Dataverse (2018); https://doi.org/10.18167/DVN1/AUBRRC.
134. J. Moat, P. Smith, *Atlas of the Vegetation of Madagascar (Atlas de la Végétation de Madagascar)* (Royal Botanic Gardens, Kew, 2007).

ACKNOWLEDGMENTS

C. Cowell (RBG Kew) provided information on Management Effectiveness Tracking Tool assessments and monitoring and K. Freeman (Madagascar Fauna and Flora Group) provided information on invasive vertebrates. A. Rauhaus (Cologne Zoo) as well as J. Kamphausen and L. Leiss (both of the University of Cologne) supported the zoo database analyses. I. Voet illustrated the graphical abstract. J. P. G. Jones (Bangor University) contributed to discussions that shaped and improved the analyses and text. We thank J. Aronson (Missouri Botanical Garden), D. Ashley (UK Ambassador to Madagascar and Comoros), 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 full draft of the manuscript as well as 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 & Wallenberg Data Driven Life Science Program, grant no. 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 no. 2017-04980. F.B. was supported by Fundação para a Ciência e a Tecnologia, grant no. 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 Plant.ID, a European Union's Horizon 2020 research and innovation program under grant agreement no. 765000. J.D.C. was supported by the Swiss National Science Foundation, grant nos. P400PB_186733 and P4P4PB_199187. A.C. was supported by Portuguese National Funds through the Foundation for Science and Technology, FCT, grant no. 2020.00823.CEECIND and project PTDC/BIA-EVL/31254/2017. G.D. was supported by Vinnova, grant no. 2019-02717. D.E. was supported by the Swedish Research Council, grant no. 2016-00796, and the Swedish Foundation for Strategic Research, grant no. FFL15-0196. S.F. was supported by the Swedish Research Council, grant no. 2017-03862. B.L.F. was supported by the National Science Foundation, grant no. DEB-1655076. P.d.L.F. was supported by the MEMOVA project, EU Operational Programme Research, Development and Education, grant no. CZ.02.2.69/0.0/0.0/18_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. no. NE/L002485/1). P.M.-M. was funded by the Czech Science Foundation, grant no. 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 no. NE/R001081/1. L.N.P. was supported by a Swiss National Science Foundation Early Postdoc Mobility Grant, grant no. 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 and an ANID National Scholarship (grant no. 21181931); and the Institute of Ecology and Biodiversity (project ANID FB210006). E.R. was supported by the NRF/SASSCAL (Southern African Science Service Centre), grant no. 118589, and the NRF/African Origins Platform, grant no. 117666. F.S. was supported by European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement, grant no. 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 Techne Arts and Humanities Research Council Doctoral Training Partnership. P.W. was supported by the Darwin Initiative, grant nos. 22-005 and EIDPO049. **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 three sections, with corresponding working groups, each making full use of the expertise and direct in-country experience of the 25 Malagasy coauthors. The sections were organized, written, and led by A.L.P., H.Ral., J.S.B., M.S.V., M.T.R., R.J.S., S.F., and T.R. Formal analyses were carried out by A.R., A.Z., D.E., D.S., H.F., J.S.B., L.N.P., M.C.H., M.Ri., M.S.V., R.S.C.C., S.F., T.A., and W.T. Visualizations and figures were done by D.E., F.S., H.F., H.Raz., J.S.B., L.N.P., and R.S.C.C. This paper and its sister manuscript on evolution, distribution, and use (*1*) 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 coauthors 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.-E., P.d.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.-E., O.M.G., P.d.L.F., P.M.-M., P.W., R.A., R.H., R.S.C.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 coauthors were involved in the writing, revision, and editing of the text. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** All data are 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.science.org/about/science-licenses-journal-article-reuse

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adf1466
Materials and Methods
Fig. S1
Tables S1 to S8
References (*135*–*194*)

Submitted 8 September 2021; accepted 7 November 2022
10.1126/science.adf1466

Science

Madagascar’s extraordinary biodiversity: Threats and opportunities

Hélène RalimananaAllison L. PerrigoRhian J. SmithJames S. BorrellSøren FaurbyMamy Tiana RajaonahTianjanahary RandriamboavonjyMaria S. VorontsovaRobert S. C. CookeLeanne N. PhelpsFerran SayolNiels AndelaTobias AndermannAndotiana M. AndriamanoheraSylvie AndriambololoneraSteven P. BachmanChristine D. BaconWilliam J. BakerFrancesco BelluardoChris BirkinshawStuart CableNataly A. CanalesJuan D. CarrilloRosie CleggColin ClubbeAngelica CrottiniGabriel DamascoSonia DhandaDaniel EdlerHarith FarooqPaola de Lima FerreiraBrian L. FisherFélix ForestLauren M. GardinerSteven M. GoodmanOlwen M. GraceThaís B. GuedesJan HackelMarie C. HennigesRowena HillCaroline E. R. LehmannPorter P. Lowry IILovanomenjanahary MarlinePável Matos-MaravíJustin MoatBeatriz NevesMatheus G. C. NogueiraRenske E. OnsteinAlexander S. T. PapadopulosOscar A. Perez-EscobarPeter B. PhillipsonSamuel PirononNatalia A. S. PrzelomskaMarina RabarimanarivoDavid RabehevitraJeannie RaharimampiononaFano RajaonaryLandy R. RajaovelonaMijoro RakotoarinivoAmédée A. RakotoarisoaSolofo E. RakotoarisoaHerizo N. RakotomalalaFranck RakotonasoloBerthe A. RalaiveloarisoaMyriam Ramirez-HerranzJean Emmanuel N. RandriamamonjyVonona RandrianasoloAndriambolantsoa RasoloheryAnitry N. RatsifandrihamananaNoro RavololomananaVelosoa RazafiniaryHenintsoa RazanajatovoEstelle RazanatsoaMalin RiversDaniele SilvestroWeston TestoMaria F. Torres JiménezKim WalkerBarnaby E. WalkerPaul WilkinJenny WilliamsThomas ZieglerAlexander ZizkaAlexandre Antonelli

Science, 378 (6623), eadf1466. • DOI: 10.1126/science.adf1466

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

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.