Edinburgh Research Explorer

Madagascar's extraordinary biodiversity: Threats and opportunities

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Science
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1 **Title:** Madagascar's extraordinary biodiversity: Threats and

2 opportunities

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97   **Abstract:**

98   Madagascar's unique biota is heavily impacted by human activity and under intense threat. Here,

99   we review the current state of knowledge on the conservation status of Madagascar's terrestrial

100 and freshwater biodiversity by presenting data and analyses on documented and predicted species-

101 level conservation status, the most prevalent and relevant threats, *ex situ* collections and programs,

102 and the coverage and comprehensiveness of protected areas. The existing terrestrial protected area

103   network in Madagascar covers 10.4% of its land area and includes at least part of the range of the

104   majority of described native species of vertebrates with known distributions (97.1% of freshwater

105   fishes, amphibians, reptiles, birds and mammals combined) and plants (67.7%). The overall figures

106   are higher for threatened species (97.7% of threatened vertebrates and 79.6% of threatened plants

107   occurring within at least one protected area). IUCN Red List assessments and Bayesian neural

108   network analyses for plants identify overexploitation of biological resources and unsustainable

109   agriculture as the most prominent threats to biodiversity. We highlight five opportunities for action

110   at multiple levels to ensure that conservation and ecological restoration objectives, programs and

111   activities take account of complex underlying and interacting factors and produce tangible benefits

112   for the biodiversity and people of Madagascar.

113

114   **One Sentence Summary:** Current knowledge on Madagascar's biodiversity and its decline

115   indicates an urgent need for inclusive actions.

116 **Main text:**

117 Madagascar's biota, the result of millions of years of evolution in relative isolation, is both unique

118 and under threat. At the same time as the scientific description of new species is accelerating (*1*),

119 so is the overall rate of extinction (*2*), and many species may be disappearing before they are even

120 documented. In this review, we aim to consolidate information on the conservation status of some

121 of the main elements of Madagascar's biodiversity, evaluate the many and varied threats faced by

122 species assessed under the criteria for the International Union for Conservation of Nature (IUCN)

123 Red List of Threatened Species, and provide some perspectives on future opportunities to ensure

124 the future of this hyperdiverse and unique biota.

125

126 **Threats to Madagascar's biodiversity**

127 Madagascar's biodiversity is in decline, with some groups more threatened than others (Fig. 1). In

128 our review of threatened species, we follow the IUCN Red List data (*3*) and threat categories (*4*),

129 unless otherwise specified. Threatened species are those listed as Critically Endangered (CR),

130 Endangered (EN) or Vulnerable (VU). At one extreme, 22% (35 species) of assessed birds are

131 threatened, while, at the other end of the scale, approximately 73% (66 species) of freshwater

132 fishes and 75% (173 species) of magnoliid plants are threatened. Trees are particularly important

133 in terms of their broad ecological functions and human uses, and 63% of the 3,118 assessed tree

134 species in Madagascar are threatened (*5*). Humans have impacted the environment since arrival on

135 Madagascar, not only in recent years. To avoid a shifting baseline effect, it is necessary to view

136 changes in light of human settlement beginning hundreds or even thousands of years ago (*1*). For

137 example, despite the relatively low proportion of bird species currently threatened with extinction,

138   Madagascar has already lost at least 14 species (7% of all species) that were present when humans

139   first settled the island (Fig. 1). The rate of anthropogenic extinction is even higher in mammals,

140   with 23 species (10%) extirpated since first human settlement. Vertebrate extinctions include the

141   loss of lineages representing millions of years of evolution – e.g., the sloth-, koala- and monkey-

142   lemurs (families Palaeopropithecidae, Megaladapidae, and Archaeolemuridae) and two species of

143   hippopotamus (family Hippopotamidae). The extinction of four species of elephant birds (order

144   Aepyornithiformes) represents the global loss of a functionally unique clade (*6, 7*). Extinctions,

145   especially those of megafauna such as these, have broad scale implications for ecosystem

146   functioning (*6-8*).

147   In total, 13 endemic animal species are listed as Extinct (EX), defined as extinctions after 1500

148   AD, and an additional 33 are listed as Extinct Prehistorically [EP], defined as anthropogenic

149   extinctions prior to 1500 AD (see (*9*) for a full list of documented anthropogenic extinctions before

150   1500 AD). A further nine have been categorized as Critically Endangered (Possibly Extinct) –

151   CR(PE). For plants, no species has been assessed as Extinct, and only one species (*Aloe silicicola*)

152   is categorized as Extinct in the Wild (EW). A further 118 plant species are listed by IUCN as

153   CR(PE) (111 spp.) or Critically Endangered (Possibly Extinct in the Wild) – CR(PEW) (7 spp.).

154   Of those currently listed as CR(PE), five species are present in *ex situ* living collections, and their

155   status should therefore be updated to CR(PEW) (*3, 10*).

156   Malagasy species feature prominently among animal groups that have been considered by the

157   EDGE of Existence program (*11-13*), which ranks species according to their evolutionary

158   distinctiveness and the level of threat they face (EDGE = Evolutionary Distinct and Globally

159   Endangered). Almost one in five species of amphibians (18 spp.), reptiles (17 spp.), and mammals

160   (17 spp.) in the top 100 EDGE species of each group are found in Madagascar (*13*). Yet only one

161   in 20 (4 spp.) of the top 100 EDGE species of birds are found on the island.

162   Given the narrow geographic range of many Malagasy species (e.g., (*14*)), numerous undetected

163   anthropogenic extinctions are likely to have taken place (*15*), such as CR *Aloe* species, which may

164   have become extinct in the wild since they were last recorded. This may be especially pronounced

165   in groups with high levels of micro-endemism, for example freshwater fishes and amphibians (*16*).

166   Ascertaining extinction events is difficult due to sampling biases, insufficient taxonomic

167   knowledge regarding the morphological features of extant species, and the challenges of

168   comparisons with fossil and subfossil remnants in certain groups, such as frogs (e.g., (*17*)).

169

170   *Reliability of species conservation assessments*

171   Conservation assessments rely on taxonomic classification, and different opinions on species

172   limits and numbers may influence the proportion of threatened species (e.g., (*18*)). This proportion

173   may also be biased by an over-assessment of well-known and widespread taxa, or, alternatively,

174   range-restricted species that are more likely to be threatened. To investigate indications of bias,

175   we calculated the fraction of threatened species across different plant groups based on two sets of

176   species: taxa with full threat-status assessments in the Red List compiled by the IUCN and their

177   partners (*19*); and those estimated with a Bayesian neural network approach (Fig. 1; (*9, 20*)), which

178   inferred the threat status for all remaining species. Using this method, we predicted the threat status

179   of 8,821 species with an estimated test accuracy of >65%. All taxa with a full threat-status

180   assessment were included, although some assessments may be out of date and could underestimate

181   threat levels.

182   The neural network approach combined with current IUCN assessments revealed a similar fraction

183   of species inferred to be threatened across most taxonomic groups (Fig. 1). Large deviations from

184   the proportion of threatened species in the current IUCN assessments occur in the ferns and

185   lycophytes, and to a lesser extent the magnoliids. The neural network results combined with the

186   known IUCN categories predicted a far higher proportion of threatened ferns and lycophytes (146

187   of 306 spp; 47.7% [95%CI: 38.5-56.7%]) than reflected in published IUCN assessments (1 of 33

188   spp; 3.0%), suggesting a bias towards assessing more common species. In the magnoliids, the

189   combined results predict a lower proportion of threatened species (211 of 294 spp; 71.8% [95%CI:

190   68.0-75.9%]) compared to published IUCN assessments alone (173 of 225 spp; 76.9%),

191   suggesting a bias towards assessing rare species in that group.

192

193   *Genetic erosion*

194   The reduction of genetic diversity within species resulting from the extirpation of

195   subpopulations is a crucial, yet easily overlooked, facet of biodiversity loss that is often a precursor

196   to extinction. Genetic erosion has negative effects on the individual fitness, the health of

197   populations, and a species' ability to adapt to changing environments, reducing their resilience to

198   further change, and potentially incurring extinction debt (*21, 22*). In practice, genetic factors are

199   not directly incorporated into IUCN assessments, which are based on measures of the probability

200   of extinction due to population declines, restricted geographic ranges, and small population sizes

201   (*23*).

202   The reduction in population sizes of wild plants and animals, together with their fragmentation and

203   isolation, is generally expected to increase inbreeding and genetic load, reducing genetic diversity

204   and fitness over time (*22, 24*). The few studies of intraspecific diversity in Malagasy species to

205   date reveal that some species have maintained high genetic diversity in spite of habitat

206   fragmentation (e.g., (*25, 26*)), whereas others have relatively low diversity, possibly as a result of

207   anthropogenic effects (e.g., (*25, 27-29*)). Results differ even within species, such as in the palm

208   *Beccariophoenix madagascariensis*, in which only some populations show strong signals of

209   inbreeding, reflected by an excess of homozygotes (*30*). It is important to note that under some

210   circumstances, population decline may outstrip the speed with which genetic diversity is eroded

211   due to inbreeding. Estimates of heterozygosity may therefore not indicate the true genetic health

212   and long-term prospects of populations when considered in isolation (*31, 32*).

213   A more powerful, although less explored, approach is to use coalescence-based demographic

214   modeling, which uses genome-wide data to estimate the longer-term trends in population size,

215   providing more information than metrics of contemporary genetic diversity alone (*25, 33*). In

216   *Cheirogaleus* dwarf lemurs, genomic analysis suggests that four species have experienced

217   population size declines in the last 50,000 years, with one decline (*C.* cf. *medius*) starting as long

218   as 300,000 years ago – all clearly in pre-human times and resulting in lower genetic diversity (*29*).

219   In contrast, another genomic study shows that five out of ten analyzed plant species with varying

220   extinction risk have experienced substantial population declines since human colonization of

221   Madagascar (*25*). In the golden-crowned sifaka (*Propithecus tattersalli*) (*26*), mouse lemurs

222   (*Microcebus* spp.) (*28*), *Mantella* frogs (*34*), and the Milne-Edwards' sportive lemur (*Lepilemur*

223   *edwardsi*) (*35*) demographic declines also appear to have taken place after the arrival of humans

224   on the island (although the inherent uncertainties of mutation rates in the microsatellite data used

225   makes the timing of these declines less certain).

226 The risks of inbreeding and increased genetic load may represent substantial and likely

227 underestimated longer-term threats to the survival of Malagasy species. This is especially relevant

228 considering the high level of fragmentation of native habitats in some vegetation types, such as the

229 humid forests, and is worthy of further investigation.

230

Predicting future extinction: direct drivers of loss

232 Identifying direct threats is part of the IUCN Red List Assessment process, and even species that

233 are not explicitly threatened (i.e., those that are Least Concern [LC], Near Threatened [NT], or

234 Data Deficient [DD]) can still have threats listed. Here we discuss these threats and how they apply

235 to all species. Our analysis of IUCN assessments indicates that overexploitation and agriculture

236 are the most frequently listed threats to Malagasy fauna (excluding invertebrates) and flora (Fig.

237 2), mirroring global findings (*36*). Overexploitation is unsustainable biological resource use as

238 defined by the IUCN (*37*), including hunting and collecting for subsistence use or

239 national/international trade. Overexploitation is linked in some cases to illegal harvesting – for

240 example, the illegal logging of rosewood for trade (*Dalbergia* spp.) – which is banned under the

241 Convention on International Trade in Endangered Species of Wild Fauna and Flora since 2013 and

242 under Malagasy law since 2010.

243 We estimated that 62.1% of vertebrates and 87.1% of plants are threatened by overexploitation

244 and that 56.8% of vertebrates and 87.8% of plants are threatened by agriculture. These two major

245 threats, almost equal in magnitude (Fig. 2), have different modes of impact – overexploitation is

246 more targeted and tends to occur over relatively restricted areas compared to the broad effects of

247 land clearance for agriculture.

248   Agriculture, and to a lesser extent overexploitation, are also the primary causes of deforestation in

249   Madagascar. Approximately 44% of the land area covered by native forest in 1953 was deforested

250   by 2014 (*38*). The rate of deforestation has steadily increased, reaching 99.0 kha/yr between 2010

251   and 2014 (*38*), and according to Global Forest Watch remains very high at 72.9 kha/yr (2014–

252   2020) (*39*). Deforestation in Madagascar reflects global patterns (*40*) and is primarily driven by

253   the small-scale but widespread practice of swidden agriculture (also known as shifting cultivation;

254   in Madagascar referred to as *tavy* for rice cultivation in humid and subhumid areas, and *hatsake*

255   for cassava and maize in dry and subarid areas). Additionally, cash crop production, particularly

256   maize and peanut, has become a major driver of deforestation (*41*), alongside the production of

257   products for international markets, such as forest-derived vanilla (*42*). The most frequent threats

258   listed for plants and vertebrates suggest that this trend of increasing deforestation rates will

259   continue, with forest loss and degradation a consequence of clearance of land for agriculture,

260   potentially associated with small-scale fire activity (*43*) and overexploitation through selective

261   logging and highly targeted activities such as the collection of palm hearts. Additionally, natural

262   system modifications (threats from actions that convert or degrade habitat, e.g., anthropogenic fire

263   in forests or changes in water management; Fig. 2), adds to deforestation and threatens 23.2% of

264   vertebrates and is estimated to threaten 68.9% of plants. Some predictions indicate that in the

265   absence of an effective strategy against deforestation, 38–93% of forest present in 2000 will be no

266   longer present in 2050 (*41*).

267   For vertebrates, the greatest threat after overexploitation and agriculture is 'invasive and

268   problematic species and emerging infectious diseases' (referred to as invasives/diseases in Fig. 2),

269   which impacts 27% of all species (360 spp.; Fig. 2). This category includes non-native invasive

270   species, as well as problematic native species and diseases of any origin. Changes in habitat due

271 to the spread of non-native plant species can have a large effect, and one study reports that of a

272 total of 546 naturalized non-native plants in Madagascar, 101 have been found to display invasive

273 characteristics (*44*). Many non-native plants, such as the Mexican yellow pine (*Pinus patula*) in

274 terrestrial systems (*45*)*,* and common water hyacinth (*Pontederia crassipes*) in freshwater systems

275 (*46*), are aggressively invasive and transformative in semi-natural habitats, and are clearly

276 impacting native fauna and flora. Even within reserves and protected areas, the issue can be

277 pronounced. For example, three species of invasive/problematic plants – strawberry guava

278 (*Psidium cattleyanum*), Molucca raspberry (*Rubus moluccanus*), and wild cardamom (*Aframomum*

279 *angustifolium*) – together occupy 17.6% of the Betampona Nature Reserve (*47*) and are also

280 widespread in Ranomafana National Park and other protected areas.

281 Not all impacts are negative, however, and there is some evidence to suggest that, due to their

282 potential for faster growth, some non-native plants are better able to combat the rapid

283 fragmentation of native vegetation, and may be beneficial for endemic vertebrates, providing

284 refuge, food, and vegetation corridors, while also improving human livelihoods (*48*). The potential

285 for such species to become invasive or readily burn must however be fully considered before

286 embarking on any planting initiatives (*49*). In addition, effects must be considered at different

287 scales. For examples, the presence of strawberry guava has been reported to locally increase

288 species richness in frugivores, but as they are primary dispersers of the seed this further contributes

289 to the spread and to associated changes in floral and faunal community structure and reduction in

290 taxonomic richness (*50*).

291 Non-native vertebrates have also had marked and diverse impacts, which we also here illustrate

292 with some examples. Introduced rats (*Rattus rattus*; present since at least the 14th century) are

293 now ubiquitous, even in remote areas, and there is evidence that their presence is associated with

294   declines in native small mammals (*51*). In freshwater habitats, competition and predation by exotic

295   fish species is considered a major factor in the decline of native freshwater fish (*52*), which have

296   been completely replaced by non-native species across much of the Central Highlands and western

297   areas (*53*). While not yet listed in current assessments, the recent invasion of the toxic Asian

298   common toad (*Duttaphrynus melanostictus*), along with the predicted vulnerability of most native

299   vertebrates to its toxins (*54*), is expected to represent a new threat to many nocturnal carnivores.

300   The effects of other introduced and naturalized animals on native biodiversity are not well studied;

301   this includes widely occurring species such as dogs (*Canis familiaris*), cats (*Felis catus*), the

302   common myna (*Acridotheres tristis*), and the marbled crayfish (*Procambarus virginalis*). The

303   threat of emerging infectious diseases is primarily driven by the occurrence of the chytrid fungus

304   *Batrachochytrium dendrobatidis*, widely documented across Madagascar over the last decade and

305   a potential threat to all amphibians, although no mass mortalities associated with chytridiomycosis

306   have been reported in the country (*55*). Species often face multiple threats at the same time,

307   although the impact of each threat can vary between species (Fig. 2).

308   Among vertebrates, amphibians have the highest number of IUCN-identified threats per species

309   (Fig. 2A), with a mean of 4.8 threats per species, followed by mammals (mean 2.5 threats/species),

310   and reptiles (mean 2.2 threats/species). For plants (Fig. 2B), magnoliids have the most threats per

311   species (mean 2.9 threats/species), followed by rosids (mean 2.8 threats/species), and other

312   eudicots (mean 2.8 threats/species). Although there might be some variation in the perception and

313   documentation of threats between the specialists carrying out assessments, all follow the same

314   protocols (*4*).

315   The number and relative impact of these threats may change in coming decades. The impact of

316   climate change on Malagasy biodiversity remains understudied and it is not currently indicated in

317   IUCN assessments as a major threat. However, this impact is expected to increase in the future

318   (*56-59*), and could potentially result in synergistic negative effects with unsustainable agriculture

319   associated with land clearance, invasive alien species, and inappropriate management of fire

320   regimes that can increase future fire risk (*43, 56, 57, 60*). Extinctions in one group could also have

321   effects on others that depend on them, such as in cases of strong plant–animal mutualisms (*61, 62*).

322   Although coextinction is hard to quantify, with substantial knowledge and data gaps (*63*), models

323   suggest that the effects of extinction can be amplified as a result of the interactions between species

324   within and between trophic levels, with the potential to lead to secondary and even cascading

325   extinctions (*64, 65*).
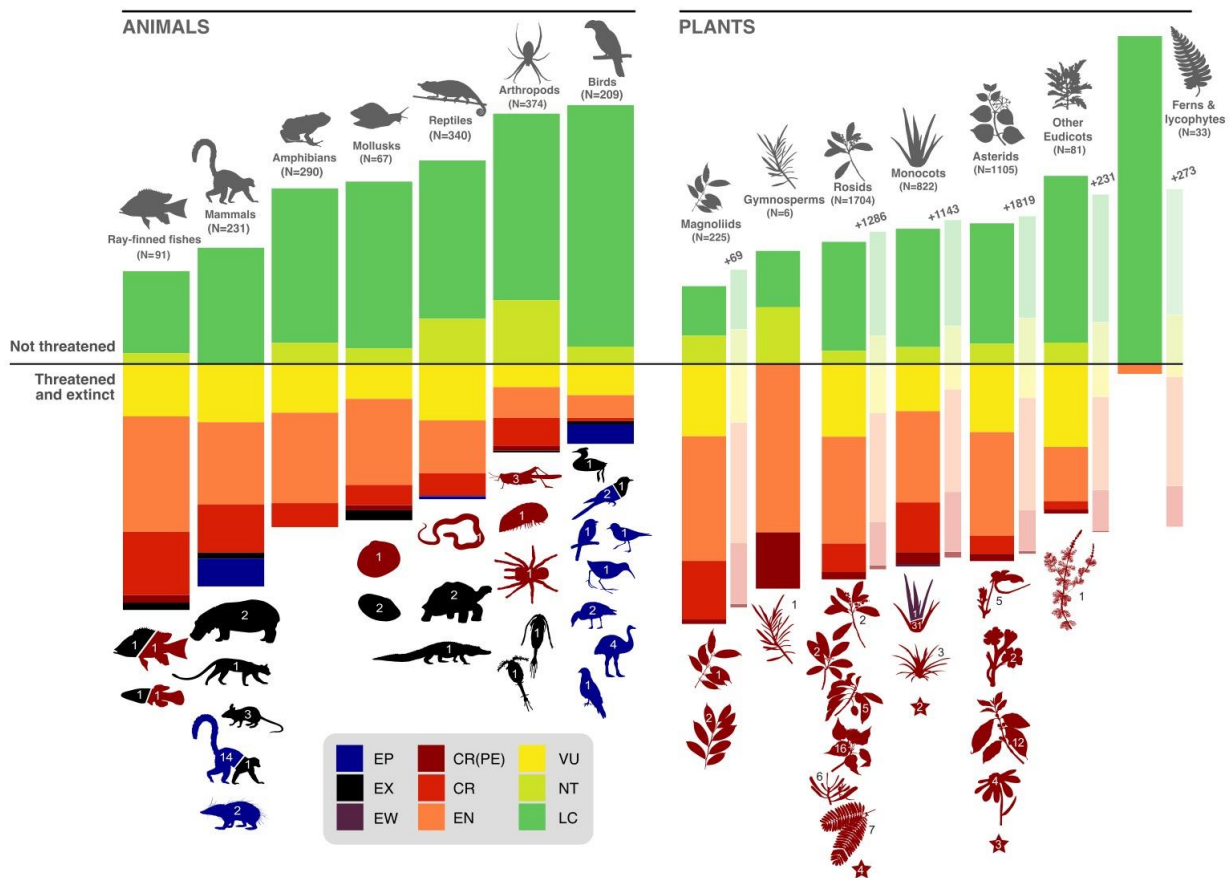
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328 **Fig. 1. Madagascar's threatened and lost biodiversity.** IUCN Red List assessment categories

329 of major groups of plants and animals from Madagascar. Assessment categories and coloration

330 follow the standards used by the IUCN Red List. Category distributions for animal groups

331 include ray-finned fishes, (Actinopterygii, freshwater species only, N=91), mammals

332 (Mammalia, N=231 species), amphibians (Amphibia, N=296), mollusks (Mollusca, N=67),

333 reptiles (Reptilia, N=340), arthropods (Arthropoda, N=374), and birds (Aves, N=209). Category

334 distributions for plants, indicated with saturated, wider bars, include magnoliids (N=225),

335 gymnosperms (N=6), rosids (N=1,704), monocots (N=822), asterids (N=1,105 species), other

336 eudicots (N=81), and ferns & lycophytes (N=33). Thinner, unsaturated bars indicate the relative

337 proportion of plant taxa in each threat category for IUCN Red List assessments combined with

338 the taxa where the threat category was predicted in a Bayesian neural network analysis: asterids

339 (N=2,924 species), rosids (N=2,990), other eudicots (N=312), magnoliids (N=294), monocots

340 (N=1,965), and ferns & lycophytes (N=306). The number indicated above each bar with "+" is

341 the number of taxa for which the threat category was predicted using the neural network analysis.

342 IUCN Red List Assessment categories include Least Concern (LC) and Near Threatened (NT),

343 together making up the "not threatened" category; while Vulnerable (VU); Endangered (EN);

344 Critically Endangered (CR); Critically Endangered, Possibly Extinct (CR(PE)); Extinct in the

345 Wild (EW); Extinct (EX; i.e., extinct after 1500 CE), and Extinct Prehistorically (EP; sensu (*66*),

346 i.e., extinct before 1500 CE but with dated records within the last 130,000 years) make up the

347 group "threatened and extinct." Silhouettes below the bars depict taxonomic orders with EP, EX,

348 EW, and CR(PE) species, with the number of species in each category per order. For some plant

349 groups, additional orders with single CR(PE) species are indicated with a star. Depicted orders

350 are, from left to right and top to bottom: Perciformes, Cyprinodontiformes, Cetartiodactyla,

351 Carnivora, Rodentia, Primates, Afrosoricida, Venerida, Unionoida, Perciformes,

352   Cyprinodontiformes, Squamata, Testudines, Crocodilia, Orthoptera, Spirobolida, Araneae,

353   Calanoida, Cyclopoida, Podicipediformes, Cuculiformes, Coraciiformes, Charadriiformes,

354   Gruiformes, Anseriformes, Aepyornithiformes, Accipitriformes, Laurales, Magnoliales, Pinales,

355   Oxalidales, Sapindales, Myrtales, Malvales, Malpighiales, Fabales, Asparagales, Poales,

356   Ericales, Boraginales, Gentianales, Asterales, Saxifragales.

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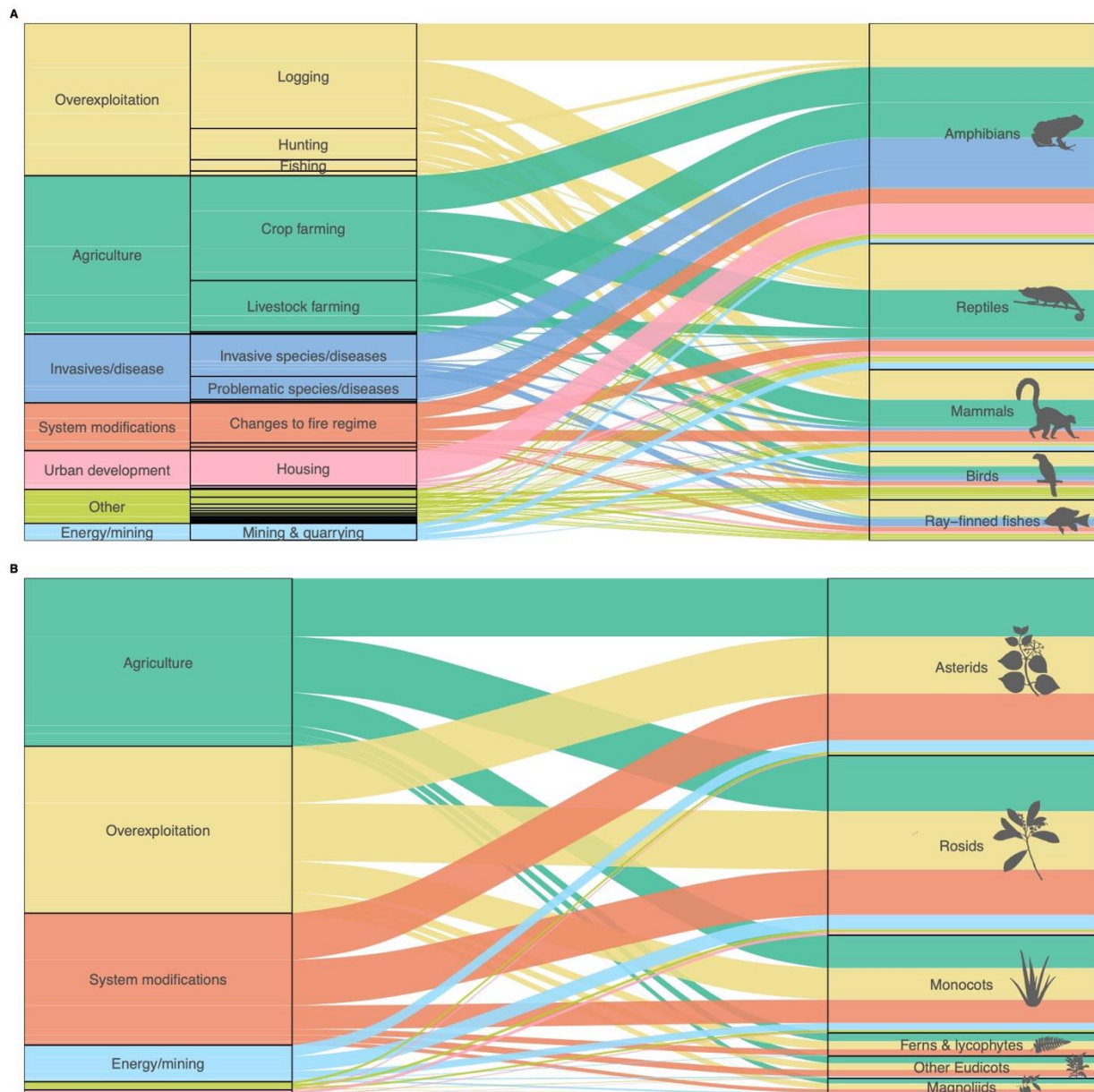
358

359   **Fig. 2. Threats to Malagasy biodiversity.** Alluvial plots showing threats, as defined by the IUCN,

360   and their associations with major groups of terrestrial and freshwater (A) vertebrates (1,332 species

361   with IUCN assessments, of which 993 species have at least one listed threat) and (B) plants (9,268

362   species with IUCN assessments or predictions, all of which have at least one listed threat; includes

363   gymnosperms [6 species], which could not be visualized). Widths of the boxes/lines reflect the

364   number of species impacted by each threat. Threats for vertebrates are further divided into sub-

365   threats, whereas only the highest threat classification was available for assessed plants. The

366   estimates for plants include predictions for unassessed species based on a Bayesian neural network

367   analysis (*9*). The color scheme is consistent across panels. The "Other" threat class includes

368   Pollution, Climate change, Transportation, and Human disturbance, plus Invasives/diseases for

369   plants. Some threat classes have been renamed for brevity/clarity, including the IUCN category

370   "biological resource use", which is labeled "overexploitation" here and in the text, for brevity and

371   in line with IPBES terminology (*36*).

372

373   **Conservation efforts and effectiveness**

374   *Protected Areas*

375   Protected areas (PAs) are the central political and scientific accomplishment of Madagascar's

376   conservation strategy. The network has been continuously developed since the first PA was

377   established in 1927 (*67-71*). Our data compilation shows that the network now encompasses 10.4%

378   of the land area of Madagascar, having grown by more than a third over the last two decades (Fig.

379   3). This recent and extensive designation of new PAs was carried out via a multi-stakeholder

380   consultative process, in combination with data and literature analyses, through the Durban Vision

381 initiative conceived in 2003. In addition to preserving diverse ecosystems and landscapes, the

382 focus has been on species groups for which sufficient diversity and distribution data were

383 available, primarily vertebrates (including birds, mammals, amphibians, and reptiles), and some

384 plant groups. Despite the production of considerable new data since the Durban Vision began (e.g.,

385 many newly described species; (*1*), the network designed during that process remains highly

386 taxonomically comprehensive. From a global perspective, the PA network also excels at capturing

387 the vast majority of Madagascar's many EDGE species: 14 out of 18 amphibians, 15 out of 17

388 reptiles, 16 out of 17 mammals, and all four birds (*13*).

389 As of November 2020, there were 110 terrestrial PAs with permanent protected status in

390 Madagascar, covering 61,300 km^2 across the country (Fig. 3) (*70, 72, 73*). Eleven of these are

391 "orphan PAs" – sites abandoned by their former managers with responsibility reverting to the

392 Ministry of Environment and Sustainable Development (*70*). An additional 89 sites (15,200 km^2),

393 predominantly comprising Key Biodiversity Areas (KBAs), are not under formal protection (*70,*

394 *72, 74, 75*).

395 The long-term security and effective management of Madagascar's PAs is therefore crucial to

396 addressing the country's biodiversity challenges. Providing evidence of their effectiveness and co-

397 benefits, such as ecosystem service provision, will be critical to securing ongoing support and

398 management from local communities, as well as from local and national governments. However,

399 measuring PA effectiveness is challenging (e.g., at avoiding deforestation, or providing alternative

400 livelihoods) while accounting for numerous covariates (*76*), particularly in Madagascar with

401 comparatively little long-term biodiversity monitoring data (*77*). Recent counterfactual analyses

402 (*78*) have sought to address this question by identifying protected and non-protected sites that are

403 similar across multiple social and environmental variables, and then comparing indicators of

404   conservation effectiveness, such as deforestation rate. These analyses indicate that PAs have a

405   small, but significant, effect at reducing deforestation (*9*).

406   We show that since 1990, human impacts have measurably increased across all terrestrial PAs

407   (Table S8 (*9*)), a trend documented worldwide (*76*). Human activity by local communities inside

408   PAs is not necessarily detrimental to biodiversity, and land use and conservation are therefore not

409   mutually exclusive. Nevertheless, land conversion and unsustainable exploitation remain major

410   drivers of biodiversity loss. This suggests that protecting and realizing the potential of

411   Madagascar's comprehensive PA network will require the application of rigorous monitoring and

412   evaluation strategies, matched with extensive community collaboration, to understand co-benefits

413   and minimize detrimental human impacts.

414   Scores for deforestation and management effectiveness – for example, from the self-reported

415   Management Effectiveness Tracking Tool (*79*) – have been the main metrics used to monitor

416   effectiveness to date. However, these are not always reliable indicators of management

417   effectiveness (*77*). New and expanded capacity of variables such as remote-sensed fire and stable

418   night lights, with increased temporal resolution, offer promising new monitoring opportunities.

419   How fire is associated with land transformation in Madagascar has been discussed in the literature

420   but only recently quantitatively assessed (*43*), demonstrating that tree loss anomalies are highest

421   in environments where landscapes-scale fire (>21 ha) does not occur, and where the role of small-

422   scale fires (<21 ha) requires close and urgent investigation. We show that trends in anthropogenic

423   fire are variable, increasing in some areas of forest vegetation in the north, east, and west but

424   decreasing in grassland-woodland mosaic vegetation across central Madagascar (Fig. 4A, B).

425   Forest loss also reflects this pattern, primarily occurring in the humid forest biome in the east, but

426   also in dry forest and spiny forest in the west (Fig. 4C, D). Deforestation and land use conversion

427 remain key challenges to conservation in Madagascar, and improved remote-sensing will

428 accelerate monitoring and developing understanding on the effectiveness of PAs and other

429 conservation measures.

430

431 Ex situ *conservation and restoration*

432 Living plant collections in botanic gardens and seed banks represent invaluable sources of

433 taxonomic and genetic diversity for immediate conservation and research, and should continue to

434 support restoration efforts. Globally, 29.6% of all known native Malagasy plant species (23.1% of

435 endemic species and 23.1% of native threatened species) are held in botanic gardens, with 15.5%

436 held in Madagascar (*10*), where their cultivation is sometimes linked to educational programs and

437 community engagement, essential to raising awareness of biodiversity and conservation issues.

438 The Millennium Seed Bank Partnership in Madagascar, initiated in 1996, hosts collections of an

439 estimated 3,500 native Malagasy species, including members of four of the five endemic plant

440 families and all seven of the iconic baobab species (*Adansonia* spp.). The single Malagasy plant

441 species listed as Extinct in the Wild, *Aloe silicicola*, now only survives in one living collection

442 outside Madagascar.

443 For native terrestrial and freshwater vertebrates, 9% of amphibians, 17% of mammals, 20% of

444 reptiles, 21% of freshwater fishes, and 33% of birds are currently held in zoological collections

445 (18% overall) (*9, 80*). Many are part of active breeding programs: a subset of these (3% of

446 amphibians, 7% of reptiles, 11% of freshwater fishes, 13% of mammals, and 23% of birds) were

447 successfully bred during 2020 (*9*). Unsurprisingly, the species held in captive breeding facilities

448 are biased towards the more charismatic, well-known taxa (*81*). For example, among amphibians,

449   13 of the 34 species in zoos belong to the genus *Mantella,* a group of strikingly colored diurnal

450   frogs, even though *Mantella* contains only 4% of Madagascar's amphibian fauna. Freshwater

451   fishes, amphibians, and reptiles are highly suitable for targeted *ex situ* breeding and reintroduction

452   programs (*82-85*). For species in these groups and others with high levels of micro-endemism,

453   such conservation programs continue to represent a major safeguard against extinction (*86*). This

454   complies with the One Plan Approach to species conservation proposed by the IUCN SSC

455   Conservation Planning Specialist Group, which supports the development of conservation and

456   management plans for all populations of a species, even outside of their natural range (*87*). It

457   should be noted that the success of reintroduction relies also on the maintenance of natural habitat

458   and functional diversity at potential reintroduction sites, along with minimizing risks associated

459   with invasive species and infectious diseases. In addition, particularly for mammals, vulnerability

460   of captive-bred populations to predation can also jeopardize the success of reintroductions (*88*).

461   *Progress towards international conservation commitments*

462   Madagascar continues to make progress towards Convention on Biological Diversity targets, but

463   like most countries falls short of meeting them in full (*89*). Of particular relevance here is that

464   Madagascar did not formally meet Aichi Target 11 to protect at least 17% of its total land area

465   (Fig. 3) – as was the case for 48% of the parties reporting their progress (*89*). If areas designated

466   as important for biodiversity but not currently under formal protection were also given protection,

467   the total percentage of PA coverage would rise from the current 10.4% to 13% (Fig. 3B). However,

468   given that even the existing network is widely considered to be chronically under-resourced, this

469   action is not a priority for the near future (*90, 91*).

470   Target 4 of the Global Strategy for Plant Conservation seeks to protect 15% of each vegetation

471   type. This has been achieved for mangrove (currently at 29.4%), spiny forest (21.5%), humid forest

472   (18.5%), and tapia (17.9%), but not for dry forest (13.3%), subhumid forest (5.7%), and grassland-

473   woodland mosaic (1.8%) (Table S6 (*9*)). However, expansion of the areas of those vegetation types

474   under protection may not be feasible due to limited financial resources, the large degree of

475   fragmentation and geographical spread of habitats, and the long administrative process involved

476   in extending PAs or designating additional areas, as well as a lack of political will. It also may not

477   be desirable until it can be demonstrated that the existing PAs are well-resourced, achieving

478   conservation objectives and providing benefits to communities. Restoration within currently

479   protected areas may provide a longer-term pathway to meeting this goal, particularly where there

480   are rapidly realizable socio-economic benefits such as sustainable silk production from wild native

481   silkworms (*Borocera cajani*) associated with tapia (*Uapaca bojeri*) in the Itremo Massif PA and

482   Ambatofinandrahana KBA. Other targets are more difficult to assess due to lack of data. For

483   example, there is very little evidence to assess success in the control of invasive alien species, with

484   some exceptions such as the ongoing but promising house crow (*Corvus splendens*) eradication

485   (*92*).

486   Although most of the Aichi and GSPC targets were either not achieved or cannot be assessed, a

487   marked success is that Madagascar has comfortably achieved GSPC Target 7 (at least 75% of

488   known threatened plant species conserved *in situ*), with our analyses indicating this percentage is

489   currently at 80%.

490

491   *Realizing benefits of biodiversity for people*

492   The majority of Madagascar's over 28 million inhabitants live outside of, but often very close to,

493   PAs (*93*) (Figs. 3A; S1). These communities face challenges connected to widespread poverty,

494   which itself is related to degradation of natural capital in the landscape, limited access to formal

495   education and health care, crime, corruption, weak governance, and regulatory issues including

496   land tenure (*15, 94, 95*). For example, southern Madagascar is severely affected by food and water

497   insecurity, which catalyzes political and social instability, exacerbates economic insecurity, and

498   has led to large-scale migration within the country (*96*). This instability likewise hampers the

499   operations of local, national, and international conservation organizations, which could be

500   compounded further by adverse effects from climate change (*59*). As the human population in the

501   country is expected to reach 42–105 million by the end of this century, of which half will be under

502   15 years of age, and with the majority under the poverty threshold (*97*), the conservation success

503   of PAs will be inextricably linked to the effective provision of livelihoods, food security, and

504   natural capital – a situation echoed across all Malagasy ecosystems and the world over (*98*).

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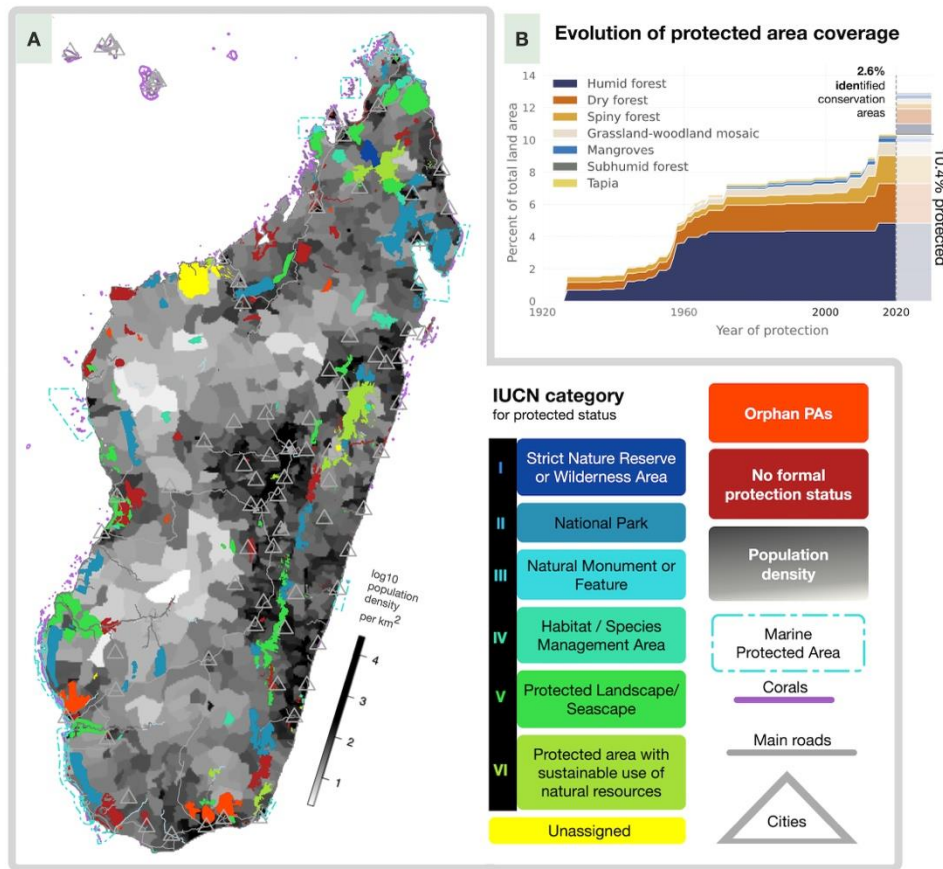
Fig. 3. Madagascar's terrestrial protected areas (PAs) in the context of human population density and changes in coverage of vegetation type over time. (A) PAs with IUCN protected status (*99*), "orphan" status, or no formal protection status (e.g., unprotected Key Biodiversity Areas [KBAs]), shown in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

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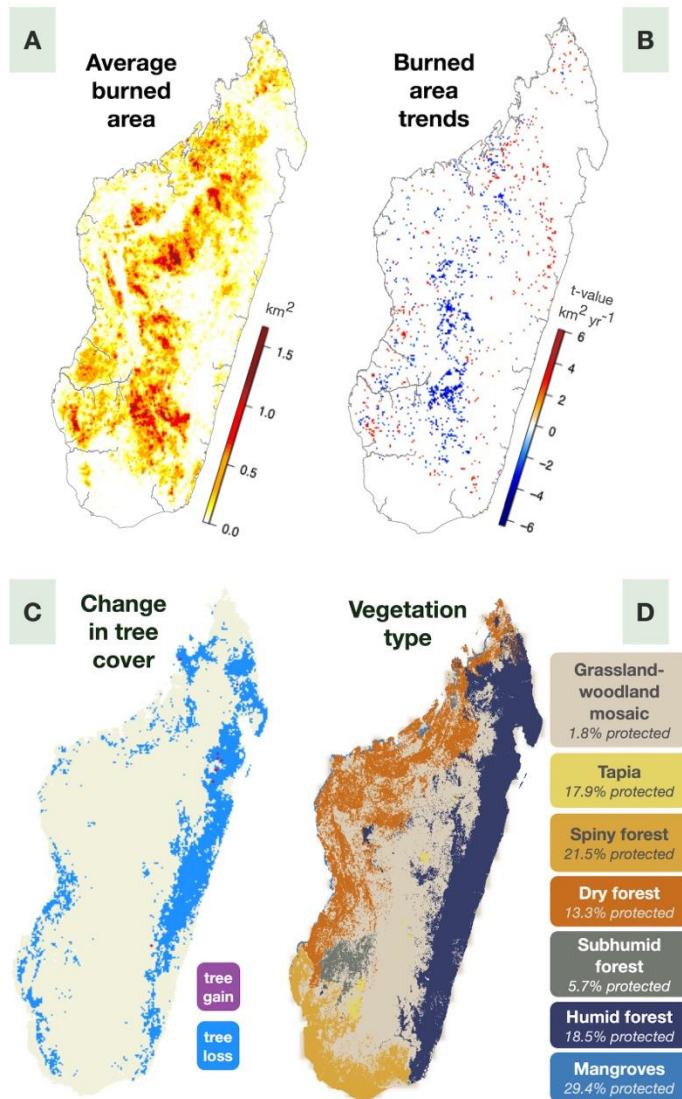
Fig 4. Recent changes and patterns in burned area and tree cover in Madagascar. (A)
Average burned area in the period 2003–2019. (B) Statistically significant trends in burned area
(MODIS) (*103*) from 2006–2016, not explained by precipitation change (TRMM) (*104*), dates
chosen for comparison with Goodman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

520   and simplified from Moat & Smith (*106*). The legend indicates the percentage of each vegetation

521   category currently covered by the protected area network.

522

523   **Looking back, moving forward**

524   Despite decades of research and applied conservation programs supported through substantial

525   financial investments (*95, 107*), Madagascar's remarkable biodiversity continues to face severe

526   challenges (Figs. 1, 2). It is reasonable to ask whether more of the same – even if better resourced

527   and underpinned with greater scientific understanding and technology – is likely to deliver a

528   tangible reversal in Madagascar's trajectory of biodiversity loss, or whether new approaches are

529   required to bring transformative change (*108*), including greater emphasis on monitoring

530   interventions and addressing underlying drivers through key leverage points. The responsibility

531   for averting humanitarian and biodiversity crises is a shared global challenge (*36, 109*), with

532   solutions needed at all societal levels – including via local communities, engagement of the private

533   sector, sound leadership and policy from regional and national government, steady international

534   support for conservation, and increased recognition of how historic and ongoing global and

535   national inequalities have contributed to the current situation. Scientific data and evidence will

536   continue to make a vital contribution, but it is crucial that this is done in an interdisciplinary

537   context, with open communication channels to relevant government departments and third sector

538   organizations.

539

540   *Decades of progress in biodiversity science and conservation*

541   We now have a clearer and more detailed understanding than ever before of the past and present

542   diversity and distribution of Madagascar's biodiversity, and the threats it faces (*1*) (Fig. 1). The

543   underlying data are the product of decades of research – with an increasing number of Malagasy

544   biologists involved. This body of research and the evidence we have collated and presented here

545   makes a clear case for Madagascar as one of the world's foremost conservation priorities.

546   Despite multiple competing demands on land, the Malagasy government, in collaboration with a

547   broad group of conservation organizations and donors, has succeeded in designating 10.4% of the

548   country as terrestrial PAs in a network that is largely representative of Madagascar's diverse

549   biomes (Fig. 3, 4). Most terrestrial and freshwater vertebrate species with known distributions have

550   ranges that overlap with least one PA (94.7% of reptiles, 97.2% of amphibians, 98.1% of

551   mammals, 98.9% of freshwater fishes, 100% of birds, and 97.1% for all groups combined), as do

552   the majority of plants, but to a lesser extent (67.7%) (*9*). For threatened species with known

553   distributions, the percentages are similar for vertebrates (94.3% of reptiles, 99.3% of amphibians,

554   97.7% of mammals, 100% of freshwater fishes, 100% of birds, and 97.7% for all groups combined)

555   and markedly higher for plants (79.6%). Nonetheless, there are still many threatened species with

556   ranges that do not overlap with existing PA network, including one amphibian, three mammals,

557   seven reptiles, and 559 plants (*9*), and many more that have not yet been assessed but may be

558   threatened. The ranges of all birds overlapped with at least one PA; this was also true when we

559   filtered the analysis to only include resident and breeding areas (*9*).

560   Since the loss of Madagascar's terrestrial megafauna (here defined as vertebrates above 10 kg),

561   there have been few documented modern extinctions, but many species have perilously reduced

562   population sizes. The continued increase in new species descriptions suggests there may be

563   undocumented extinctions, especially in poorly studied taxa (*1*). Despite this, with limited

564 resources and/or capacity, Madagascar has made important progress towards achieving

565 international climate, biodiversity, and sustainable development goals, providing a foundation on

566 which to build in the coming decades.

567 Success stories for individual species highlight how positive collaborative efforts can avert

568 extinction. Examples include work on the Madagascar pochard (*Aythya innotata*) (*110*), which

569 shows a 30% probability that extinction was prevented due to conservation action, the success

570 story of the community-based protection of the tahina palm or dimaka (*Tahina spectabilis*) where

571 local communities were involved in propagation and population reinforcement (*111*), and the work

572 to prevent the extinction of the ploughshare tortoise (*Astrochelys yniphora*) through a captive

573 breeding program (*112*).

574 Other notable successes have come from Madagascar's "biodiversity conservation boom", which

575 started in the 1980s, including a growth in the number of students pursuing university-level

576 education in environmental sciences, biodiversity conservation and management, and related

577 fields, at both public and private universities. The result is an increasingly robust national capacity

578 for the conservation and management of biodiversity that extends to international conservation

579 organizations, which have been able to actively recruit Malagasy professionals to the highest

580 administrative and executive positions. Going beyond this, the gap in scientific leadership that

581 underpins conservation evidence is being incrementally filled by Malagasy biodiversity scientists.

582 Researchers from outside Madagascar are increasingly collaborating with Malagasy researchers

583 for mutual benefit. The requirement for international collaborators to provide financial and

584 technical support for Malagasy researchers and their research infrastructure via collaboration

585 protocols, set out in the national strategy for scientific research in Madagascar (*113*), reinforces

586 the importance of this.

587 As in many low-income countries, insufficient public funding means that the number of Malagasy

588 professionals is still insufficient to serve the country's needs, there are relatively few PhD positions

589 available to students, and those that are trained at higher levels often move away from academia

590 and into the private sector. Access to up-to-date biodiversity data has also been a limiting factor

591 (*15*). A further challenge is how to successfully engage multiple parts of society in conservation.

592 Efforts that are genuinely socially integrated have been shown to produce more effective and

593 resilient practices, policies, and decision-making, especially in the face of unstable environmental,

594 political, and health situations (*114*). The Madagascar Fauna and Flora Group, the Lemur

595 Conservation Foundation, Durrell Wildlife Conservation Trust, The Peregrine Fund Madagascar,

596 Madagascar Biodiversity Center, and Madagasikara Voakajy, as well as the work of the Royal

597 Botanic Gardens, Kew, and Missouri Botanical Garden, are all examples of successful

598 collaborations involving researchers, conservation partners and local communities to protect

599 biodiversity and empower local people.

600 *The future of biodiversity in Madagascar*

601 Meeting the Convention on Biological Diversity's Post-2020 Global Biodiversity Framework

602 2030 targets and milestones and achieving the 2050 goals (*115*) will be challenging – in

603 Madagascar and globally. Evaluating successes and failures over previous decades and learning

604 from these to prioritize effective conservation investment will be particularly important. To

605 embrace diverse views and promote inclusivity in the identification of future directions, we

606 discussed our results and current literature among our co-authors and consulted with Malagasy and

607 external researchers, conservation leaders, and politicians, to arrive at five main opportunities for

608 the future, which we now present.

609   1) Investment in conservation and restoration must be based on evidence, effectiveness, and future

610   challenges. Since the 1980s, billions of US dollars from international donors and conservation

611   organizations, in cooperation with the Malagasy government, have been dedicated to protecting

612   the country's biodiversity and creating today's network of PAs (*107, 116*). However, the

613   effectiveness of many interventions is poorly understood because impact evaluations are absent or

614   lacking rigor. Evaluating the effectiveness of conservation activities is challenging, but the subject

615   of increasingly sophisticated research efforts (*76, 78, 117*). Nevertheless, it is imperative

616   investments reinforce evidence-based and regularly evaluated interventions, requiring greater

617   collaboration and co-design between local communities, regional and national authorities,

618   researchers, the private sector, and other stakeholders. A particular opportunity is to frame these

619   evaluations around community-based conservation interventions that address challenges faced by

620   people and nature in unison. For example, nature-based solutions (*118*) for diversified, locally

621   adapted and sustainable agriculture can help address livelihood needs, while more efficient stoves

622   can substantially decrease the demand on charcoal from native forests for cooking and heating,

623   and further may reduce the health hazards of smoke inhalation. Such initiatives increase food and

624   energy security (*119*) while providing resilience to climate stochasticity (*120*). Similarly,

625   coordinated, community-based fire management and awareness raising can be used to help

626   mitigate risk to fire-sensitive forests. On-site management is especially important for fire

627   mitigation, as a study during the COVID 19 pandemic has shown (*121*). Fire management also

628   presents the opportunity to mitigate the impact of exotic species by targeting the removal of

629   flammable invasives (e.g., *Pinus*), and guide appropriate tree-planting initiatives to avoid fire-

630   prone plantations near areas of particular biological importance. Such measures can improve the

631   quality of grazing land for livestock, while reducing carbon emissions from fire and helping to

632   protect biodiverse habitats.

633

634   2) Expanded biodiversity monitoring is key to safeguarding Madagascar's most valuable natural

635   assets. Existing biodiversity data are sufficient to characterize major conservation challenges and

636   robustly support the orientation of conservation efforts in Madagascar. Calling for the collection

637   of additional data risks delivering diminished returns on investment for conservation planning

638   (*122*). Nevertheless, from collating the information for this review, we acknowledge a clear need

639   to address gaps in understudied ecosystems, taxa, and genetically distinct populations, noting that

640   many newly described species are already threatened (*123*) and in need of immediate protection.

641   Monitoring is also crucial for the detection of new non-native and potentially invasive species, as

642   well as providing important data for the management of those that have already taken hold.

643   Increasing connections with international trading partners without concurrent improvements in

644   capacity for biosecurity increases Madagascar's vulnerability to such species (*124*), and strategies

645   to monitor and mitigate these risks while delivering near-term benefits are needed.

646   Although there are initiatives that provide broad overviews of conservation effectiveness (e.g.

647   (*117*)), many conservation interventions lack impact evaluations, in part due to a lack of robust,

648   long-term monitoring data for biodiversity and social outcomes. The major gap is a lack of capacity

649   for robust biodiversity monitoring. An example of the increasing value of data and coherency in

650   conservation efforts is the development of the Madagascar Protected Areas website (*125*), which

651   consolidates much of the information about Madagascar's extensive network of PAs. But as with

652   many initiatives, the key is in long-term financing and maintenance of these portals and ensuring

653   that data flows freely and openly to similar, global initiatives like Protected Planet (*73*).

654   Biological monitoring needs to be based on consistent, repeatable methodologies, with shared data.

655   This information provides the science-based evidence needed to leverage international funding

656   and government policy support. Monitoring is one area where new technologies will play a key

657   role, such as through the increasing availability of near real-time satellite images and small and

658   cost-effective unmanned aerial vehicles, which can increase visual access to remote areas (*126*).

659   Similarly, DNA-based biodiversity surveys, including environmental sampling, can greatly

660   improve the speed of site-inventories and identification of unknown and understudied taxa.

661   Advances in monitoring must be delivered with improved and centralized management. This

662   should include open-source and transdisciplinary data on biodiversity, social and conservation

663   governance and performance. These data should be in formats that are accessible and useful to

664   practitioners, to identify relevant baselines, and support evidence-based decisions for conservation

665   and restoration.

666   3) Improving the effectiveness of existing PAs is more important than creating new ones.

667   Madagascar has an extensive, evidence-based, and highly representative network of terrestrial PAs

668   (Fig. 3, 4). Madagascar's existing PAs already include at least partial ranges of a substantial

669   proportion of Malagasy taxa, including most Malagasy EDGE species. Focusing on improving

670   their quality and effectiveness will likely lead to positive biodiversity outcomes (*127*), further

671   increasing the already measurable impact that PAs have had on biodiversity. By strengthening

672   PAs, biodiversity can be conserved across ecosystem, species, and genetic levels, all of which are

673   integral in long-term conservation, as discussed above. Investment in restoration of degraded areas

674   within and beyond the existing network (see Opportunity 4 below) will provide multiple benefits

675   for biodiversity and people. This could help increase the resilience of habitats to future drivers of

676   biodiversity loss including climate change, while increasing potential ranges of many species in

677   parallel. Demonstrating the benefits of strengthened PAs to people is a likely prerequisite for

678   societal support to maintain and improve upon the existing network, while mitigating risk of future

679 downgrading, downsizing, or degazettement (legal removal of conservation status) (*128*).

680 Financial benefits that come with strengthened PAs must be distributed appropriately and

681 equitably within the country's political and social contexts, with the full inclusion of local

682 communities at all stages (*127, 129*).

683

684 4) Conservation and restoration should not focus solely on the PA network. Madagascar's PAs are

685 islands of natural capital in a landscape of degraded natural resources (*130*) and therefore provide

686 vital resources for communities living adjacent to them. Traditional "fortress conservation"

687 – seeking to protect areas by limiting access – is therefore both undesirable and unlikely to be

688 effective. To further reduce the detrimental human impacts that exist in all PAs (*107*) (Table S8

689 (*9*)), we argue for strategies to enhance the natural capital of the surrounding landscapes, to reduce

690 pressure on PAs as providers of basic resources, and to increase buffer zones for the species that

691 live in and around them. This could include increasing ecosystem provision, such as productive

692 soils, food, fibers, and other materials and services such as water flow regulation and carbon

693 capture. Such measures would serve to address some of the largest threats to species, including the

694 expansion of agriculture and overexploitation (Fig. 2).

695 In particular, ecological restoration could benefit people and biodiversity, particularly when

696 targeted to the 89.6% of the country that is not protected. It offers potential to provide new

697 livelihood opportunities that are far from, and independent of, the resources within PAs, further

698 reducing pressure on the system (*131*). Importantly, restoration should not only target those

699 ecosystems that traditionally receive the most conservation attention because they hold the greatest

700 biodiversity, for example forests. Other vegetation types such as grasslands, where most

701 agriculture takes place, are equally vital. Restoration should be carried out following best practice

702 and in places where people will benefit most, not necessarily only adjacent to PAs. Further,

703 restoration should include maximizing biodiversity recovery to meet multiple goals, using resilient

704 species, and working together with local communities (*49, 132*).

705 For the species and their inherent genetic diversity not covered by the PA network, particularly

706 those that are challenging to conserve, such as freshwater fishes and palms, *ex situ* conservation in

707 zoological and botanical gardens is a vital tool to support conservation and restoration. For plants,

708 efforts should especially focus on the 32.3% of plant species that fall outside of the PA network,

709 and the species that have cultural or economic value for people (e.g., crop wild relatives).

710 Promoting biobanking for animals and intensifying it for seeds, spores, and fungi will not only

711 support conservation but also contribute material and knowledge to restoration and research (*88*).

712

713 5) Conservation actions must address the root causes of biodiversity loss. Our analysis showed

714 that the most frequently listed threats to Madagascar's biodiversity come from overexploitation

715 and agriculture, predominantly a result of forest loss and potentially tied to increases in small-scale

716 anthropogenic fire in forests (Fig. 4A, B; see also (*43*)), significantly affecting humid forest areas

717 in the east and dry forest and spiny forest in the west (Fig. 4C, D). This trend is likely to continue

718 unless the root causes of this forest loss are addressed. Conservationists and their funders must

719 recognize that food, social security, health, and well-being are the utmost priorities for rural

720 communities, and that PAs will always be vulnerable when surrounded by impoverished people

721 living in landscapes with eroded natural capital (*133*). Politicians and economists must recognize

722 that sustainable and equitable development in Madagascar is inextricably linked to, and dependent

723 on, the maintenance of ecosystem function and the goods and services they provide. Initiatives that

724 address these issues by working with local communities to identify tailored solutions in health,

725 education, and green entrepreneurship are increasingly successful and should be expanded, but

726 generally lack data and evidence from monitoring (see Opportunity 2). Promising approaches

727 include voluntary savings and loans; inclusive, sustainable agricultural development schemes that

728 promote stable land ownership and build – rather than destroy – natural capital and the ecosystem

729 services it provides; implementation of conservation interventions, including research and

730 monitoring; and PA management that maximizes local employment (*107, 132*). Such efforts will

731 facilitate improved livelihoods for many, while reducing pressure on the PAs themselves, bringing

732 tangible benefits to communities, and contributing to sustainable management (*107, 134*).

733

734 **Conclusions**

735 The alarming status of Madagascar's biodiversity is the result of multifaceted, unsustainable

736 practices including historic and contemporary exploitation. In the eyes of much of the world,

737 Madagascar's biodiversity is a unique global asset that needs "saving"; in the daily lives of many

738 of the Malagasy people, it is a rapidly diminishing source of the most basic needs for subsistence.

739 Achieving a sustainable future that benefits people and biodiversity is possible by building on, and

740 expanding, integrated, inclusive conservation efforts. Biodiversity is the greatest opportunity and

741 most valuable asset for Madagascar's future development.

742

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1446

1447   **Supplementary Materials**

1448   Materials and Methods

1449   Figure S1

1450   Tables S1–S8

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