Projecting forest cover in Madagascar's protected areas to 2050 and its implications for lemur conservation

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Abstract Predicting future conservation needs can help inform conservation management but is subject to uncertainty. We measured deforestation rates during 2015–2017 for 114 protected areas in Madagascar, linked deforestation to the status of protection according to IUCN categories I–VI, used recent deforestation rates to extrapolate forest cover over 2017–2050 and linked the size of forest blocks to the projected persistence of lemur subpopulations. In the six IUCN categories for protected areas in Madagascar the median size of forest blocks is 9–37 km² and median annual deforestation rates range from 0.02% in the single IUCN category III site to 0.19% in category II and 1.95% in category VI sites. In 2017, 40% of all forest blocks within protected areas were < 10 km², and this is projected to increase to 45% in 2050. Apart from these small forest fragments, the modal site of forest blocks was 160–320 km² in 2017, and this is projected to decrease to 80–160 km² in 2050. The range of > 50% of all lemur species exclusively contains forest blocks of < 10 km². The modal size of forest blocks > 10 km² is predicted to remain at 120 km² until 2050. Although uncertainty remains, these analyses provide hope that forest blocks within the protected areas of Madagascar will remain large enough to maintain lemur subpopulations for most species until 2050. This should allow sufficient time for the implementation of effective conservation measures.

Keywords Biodiversity, deforestation, forest change, IUCN protected area category, lemur, Madagascar, primate conservation, viable population

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Introduction

To counteract future biodiversity loss, Madagascar has quadrupled the area of its protected area system since 2003. Although this increase is remarkable, it remains uncertain whether current conservation efforts will be able to save the unique biodiversity of Madagascar (Gardner et al., 2018). Conservation assessments of terrestrial ecosystems mostly distinguish between forest and non-forest areas. This binary typology of forest vs non-forest is overly simplistic for classifying Malagasy terrestrial vegetation (e.g. Lowry et al., 1997; Moat & Smith, 2007), but the majority of the endemic vertebrate fauna of Madagascar is forest dependent, and the dichotomous classification of forest vs non-forest is often used as a proxy for conservation measures (Goodman et al., 2018; Rafanoharana et al., 2023). Although the original protected areas belonging to IUCN categories I–III seem to have provided reasonable protection over the last few decades (Goodman et al., 2018), most of the protected areas added recently are of IUCN categories IV–VI. Categories V and VI assign governance responsibilities to communities and allow multiple uses of the areas, such as supposedly sustainable extraction of natural resources to secure traditional livelihoods (Table 1). As this is a new approach for Madagascar, the protected areas under the responsibility of communities and/or NGOs often lack crucial resources and capacities and thus seem to be less effective for biodiversity conservation than protected areas of IUCN categories I–III (Gardner et al., 2018; Rafanoharana et al., 2021; Stoudmann et al., 2023). Thus, it is unclear what role these new protected areas could have in species conservation and how the biodiversity of Madagascar will be affected by ongoing deforestation (Vieilledent et al., 2018).

Given that a large proportion of the biodiversity of Madagascar remains unknown, species-based conservation management is mostly based on conspicuous taxa, such as higher plants or vertebrates, which can also be considered umbrella species (Kremen et al., 2008; Miller & Morgan, 2011; Vieilledent et al., 2013; Jenkins et al., 2014; Schwitzer et al., 2014; Tagliari et al., 2021). Because of their close relatedness to people and their precarious conservation situation, primates in general and lemurs of Madagascar in particular are regularly assessed (Schwitzer et al., 2014;

TABLE 1 The protected area categories system advocated by IUCN since 1994 (Phillips, 2004).

Category	Function (official name)
I	Strict protection (a, Strict nature reserve; b, Wilderness area
II	Ecosystem conservation & protection (National park)
III	Conservation of natural features (Natural monument or feature)
IV	Conservation through active management (Habitat/ species management area)
V	Landscape/seascape conservation & recreation (Protected landscape or seascape)
VI	Sustainable use (Protected areas with sustainable use of natural resources)

Estrada et al., 2017). Although assessing the current status of species is difficult, projecting the fate of species into the future adds another level of uncertainty. For lemurs this projection has been attempted in the context of overall deforestation, fragmentation and climate change (Brown & Yoder, 2015; Morelli et al., 2020; Vieilledent et al., 2021; Steffens et al., 2022).

Here we use an analysis of the extent of forest areas and deforestation rates of all protected areas of Madagascar during 2015–2017 as a proxy for a formal assessment of lemur populations and to project their development within protected areas for 2017–2050. Specifically, we seek to answer the following questions: (1) How did forest cover change in the protected areas of Madagascar during 2015–2017? (2) Did the forest cover change differently in protected areas of different IUCN categories? (3) Was the change in forest cover related to the size of the forest? From the answers to these three questions we project the size of forest blocks for 2017–2050, assuming that the current deforestation rate of each protected area will remain constant. (4) Taking the size of forest blocks as a proxy for the relative number of individuals per forest block, we ask: how do conservation assessments based on the reduction of the size of subpopulations change when based on projections of the total size of protected areas in 2050 and of the forest areas when considering distinct forest blocks within protected areas?

Methods

Estimating forest cover

The approach used to assess forest cover has been described previously (Rafanoharana et al., 2021) and is summarized here only briefly. Within a larger project to estimate forest change for all of the protected areas of Madagascar, we analysed 114 terrestrial protected areas, considering humid forest, dry western forest and south-western dry and spiny forests and thickets. We obtained the raw shapefile data from the protected area management system of the Ministry of Environment and Sustainable Development of Madagascar based on the legal document of creation. From our long-term historical dataset covering 1990–2017 we used time series forest cover data for the years 2015 and 2017 (based on those from Vieilledent et al., 2018), which were the result of a combination of the 2000 forest cover map and annual tree cover loss maps at 30-m spatial resolution. We restricted the analyses to these 2 years because most of the new protected areas of IUCN categories IV and V were formally established only in 2015. The forest data used here have some biases because the remote sensing tools currently applied tend to underestimate forest cover in dry forest and overestimate it in humid forest (Rafanoharana et al., 2023). Therefore, the data for the dry forests used here should be regarded as minimum values, and forest cover changes are likely to be higher.

Almost 20% of the protected areas (22/111) comprise several forest blocks; a block is defined as any non-contiguous shape within a protected area. These blocks are separated by a non-forest matrix, and thus the forested part of a protected area is smaller than the total surface of the area.

We did not consider the protected areas of Bemaraha, Beza-Mahafaly and Zahamena because the delimitation of blocks was unclear at the time of analysis. These sites experienced little deforestation during 2015–2017 (Bemaraha: 95,909 to 95,534 ha; Beza-Mahafaly: 521.26 to 521.16 ha; Zahamena: 69,008 to 68,792 ha). Their exclusion does not change the general conclusions of the analyses.

Areas (either the protected area as a whole or the exact size of the different non-contiguous forest blocks within any given protected area) were assigned to size classes of 0–9.99 km^2, 10–19.99 km^2, 20–39.99 km^2, 40–79.99 km^2, etc., doubling from one class to the next to ≥ 2,559 km^2 (Fig. 1). We assume that all forest areas provide suitable habitat for all lemurs occurring in the region. This is improbable, and so this approach overestimates the area inhabited by lemurs.

Projecting forest loss during 2017–2050

Forest loss until 2050 was estimated using the per cent of annual forest loss during 2015–2017 for each protected area separately. To check whether this period is representative of long-term deforestation rates we compared the annual rate during 2015–2017 with the deforestation rates over 5-year intervals during the previous 25 years. We included only the IUCN category I–III areas. We did not consider protected areas that changed in size during 1990–2015. The median annual deforestation rate for the remaining 45 areas (all of IUCN categories I–III) was 0.06% during

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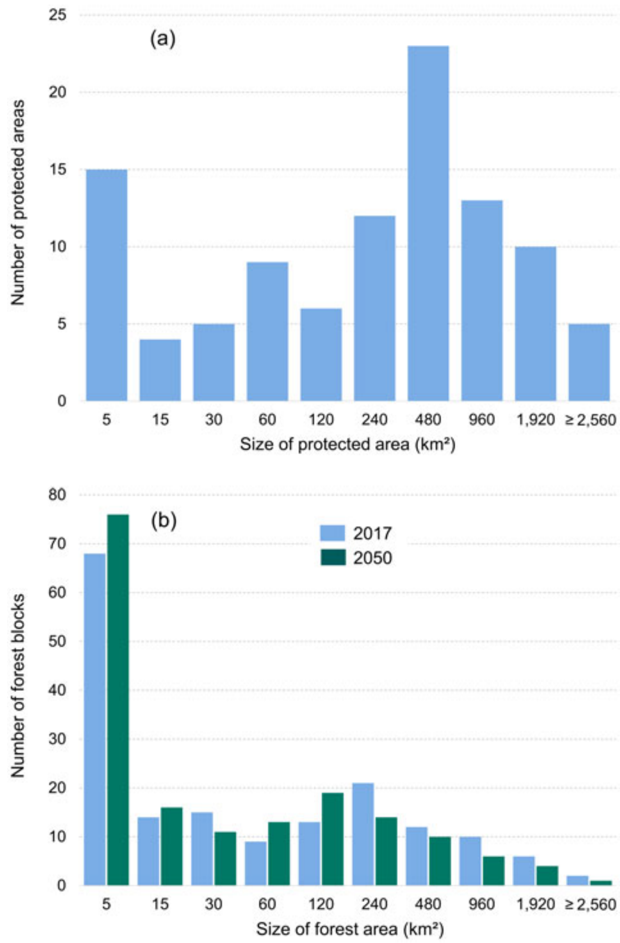

FIG. 1 Size distribution of protected areas in Madagascar (a) as a whole and (b) as forest blocks in 2017 and projected to 2050 based on current deforestation rates (Table 2). Size classes double from one class to the next. Values on the x-axes are the midpoints in each category (e.g. 5 km^2 represents blocks of 0–9.99 km^2, 15 km^2 represents blocks of 10–19.99 km^2, etc.).

1990–2000, 0.03% during 2000–2005, 0.04% during 2005–2010, 0.14% during 2010–2015 and 0.18% during 2015–2017. Thus, the deforestation rate during 2015–2017 was higher than in previous years. The trends in deforestation rates in the protected areas over time match the deforestation trends for all of the forests of Madagascar (including forest outside protected areas), although our deforestation rates within IUCN category I–III protected areas were approximately an order of magnitude lower than the deforestation rates reported for Madagascar as a whole (Vieilledent et al., 2018). For the projections of future degradation, we assumed the deforestation rates during 2015–2017 remain constant for each protected area until 2050. If the deforestation rates during 2015–2017 were exceptionally high, their application to the projection might overestimate future deforestation rates. If deforestation rates increase over time, as indicated by the trend for 2000–2017, the application of constant deforestation rates until 2050 would underestimate forest loss. We then calculated the forest loss of each protected area for the 33 years of 2017–2050 using compound computation of interest as follows: Forest size in 2050 = Forest size in 2017 × ((100 – mean of annual forest loss in per cent)/100)^{33}.

Lemur subpopulations

As of 2018, 107 lemur species are recognized on the IUCN Red List. This number is likely to change because of revisions, the use of new taxonomic methods and/or new discoveries (Tattersall & Cuozzo, 2018; Hending et al., 2022; Poelstra et al., 2022), but the principal conclusions of our analyses should remain valid. We took the occurrence of lemur species from the Noe4D biodiversity database (Wilmé et al., 2006; Waeber et al., 2020), supplemented by Goodman et al. (2018). Given the localized occurrence of some lemur species (Wilmé et al., 2006, 2012; Mittermeier et al., 2010), we did not consider species to be present in any given protected area on the basis of their geographical range but only when they had been reported to occur in the protected area. Lemur occurrences are not available for individual forest blocks but rather for the protected area as a whole. Although it is unlikely that all lemur species listed as occurring within any given protected area occur in all of its forest blocks, in the absence of more detailed data we assume this. This results in an overestimate of the number of lemur subpopulations.

We did not consider taxa that were not identified to species. This approach eliminated some representatives of the genera *Avahi*, *Cheirogaleus*, *Hapalemur*, *Lepilemur*, *Microcebus*, *Mirza* and *Phaner* from some sites. We did not include *Hapalemur alaotrensis* in the analyses as this species is restricted to reed habitat.

We excluded protected areas without lemurs or for which inventories are not available. These are Ambohidray (1,241 ha, no information on lemur occurrences), Ampanangandehibe-Behasina (580 ha, no forest), Andreba (39 ha, no forest), Ibity (6,137 ha, no forest), Mahialambo (304 ha, no forest), Maningozy (5,973 ha, 773 ha of forest in 2017), Manjakatompo Ankaratra (8,131 ha, 815 ha of forest in 2017, no lemur species recorded by the Mission zoologique Franco-Anglo-Américaine in 1929 or during a biodiversity inventory in 1996; Goodman et al., 1996).

Results

Forest cover and loss during 2015–2017

In 2017 the 102 protected areas considered ranged from 0.97 to 4,194.12 km^2, with a median size of 236.29 km^2 and an interquartile range of 43.25–750.49 km^2. Most protected areas were 320–640 km^2 (Fig. 1). At this time there were 170 forest blocks within the protected areas (Fig. 1). The

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TABLE 2 Number and size of forest blocks and total forest area in 2017, and deforestation per year during 2015–2017 in the protected areas of Madagascar (Fig. 1), by IUCN category, and projections of per cent forest loss during 2017–2050 and total forest area in 2050.

IUCN category	Number of forest blocks in 2017	Size of forest blocks in 2017[1] (km^2)	Total forest area in 2017 (km^2)	Deforestation per year during 2015–2017[1] (%)	Projected forest loss during 2017–2050 (%)	Projected total forest area in 2050 (km^2)
I	2	13.62/868.00	881.62	0.00/1.29	0/34.63	13.62/564.78
II	48	5.37–52.56–422.77	16,319.55	0.04–0.19–0.56	15.97	13,712.58
III	1	37.45	37.45	0.02	0.76	37.16
IV	26	7.09–28.21–16.61	2,667.44	0.03–0.44–1.41	21.31	2,099.10
V	66	2.37–20.48–54.38	10,236.33	0.14–0.95–2.74	39.16	6,228.18
VI	27	4.81–9.13–86.34	6,331.56	0.55–1.95–3.18	28.73	4,512.67
I–VI combined	170	4.57–21.92–172.27	36,473.94	0.07–0.52–1.96	25.51	27,168.10

[1]Values are medians and quartiles (Q_{25}–median–Q_{75}).

median size of these blocks was 21.92 km^2, with an interquartile range of 4.57–172.27 km^2.

With a median area of 37.45 km^2, IUCN categories I–III protected areas were larger than the IUCN categories IV–VI protected areas, whose median areas were 9.13–28.21 km^2 (Table 2). The former comprised 47.3% of the whole protected forest area.

The annual deforestation rate during 2015–2017 ranged between no measurable change to a decrease of 13.57% per year (Table 2). It differed significantly depending on IUCN category, with protected areas of IUCN categories IV–VI having higher deforestation rates than those of IUCN category II (Kruskal–Wallis ANOVA without protected areas of categories I and III, removed because of small sample size: $H = 19.07$, $P < 0.001$, $df = 3$). Annual deforestation in IUCN category II protected areas differed significantly from those in IUCN categories V and VI (Mann–Whitney U: $P \leq 0.01$, Bonferroni corrected). IUCN category I protected areas are Betampona and Tsaratanana, and the IUCN category III protected area is Alandraza-Analavelo.

Deforestation rate was not related to the size of the forest blocks within the protected areas (Spearman's correlation: $r_s = 0.12$, $P > 0.05$, $N = 170$).

Projecting forest loss to 2050

Assuming constant deforestation rates in all protected areas, the protected forest is projected to decrease by 9,306 km^2 during 2017–2050 (c. 25% of the total forest area). The decrease in IUCN categories I–III protected areas is projected to be 16.88% during 2017–2050, and 21.31–39.16% in the other IUCN categories.

In 2017, 68 (40%) of the 170 forest blocks were < 10 km^2. Apart from these smallest blocks, the largest number of forest blocks were 160–320 km^2 (Fig. 1). By 2050, these figures are projected to have changed to 76 (45%) forest blocks < 10 km^2, with the mode projected to be 80–160 km^2.

Perspectives for lemur species

Two lemur species are not known to occur in any protected area. *Microcebus boraha* is restricted to Île Sainte Marie, an island off the east coast of Madagascar that lacks any protected areas (Reuter et al., 2020). The distribution of *Lepilemur grewcockorum* falls between Bongolava Reserve, 30 km south-south-east of the reported occurrence of this species, and the Réserve Spéciale Bora, 57 km to the north-east (Louis et al., 2020). The remaining 105 of the 107 recognized lemur species are recorded in at least one protected area, although the representation of IUCN categories for protected areas varies widely between species (Supplementary Table 1). Thirty species are known only from a single protected area, and > 50% of them occur in no more than four protected areas (Fig. 2). On average, by 2050 the forested area currently inhabited by lemurs is projected to decrease by 19% (Supplementary Table 2).

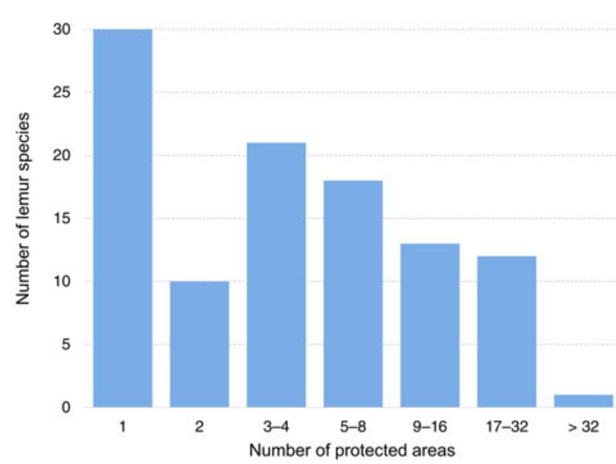

FIG. 2 Occurrence of lemur species in the protected areas of Madagascar as of 2017. The numbers on the x-axis represent the number of protected areas where any given lemur species has been recorded (e.g. 30 species are known from a single protected area and 10 species from two areas).

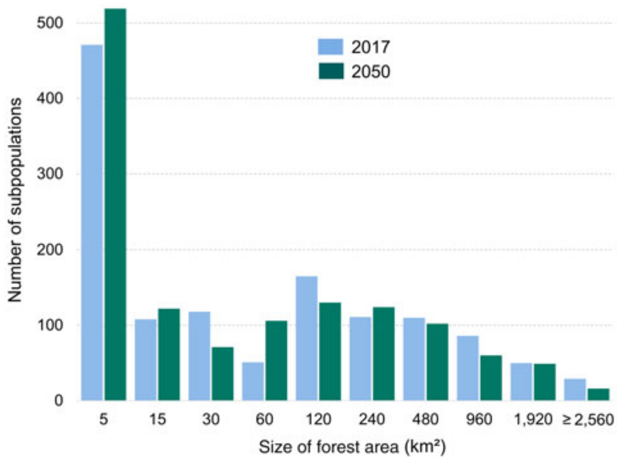

FIG. 3 Lemur subpopulations occurring in different-sized forest blocks in Madagascar in 2017 and 2050, assuming the same deforestation rates as recorded during 2015–2017. Size classes double from one class to the next. Values on the x-axis are the midpoints in each category (e.g. 5 km² represents blocks of 0–9.99 km², 15 km² represents blocks of 10–19.99 km², etc.).

Lemur subpopulations in protected areas of different sizes

If all lemur species were present in all forest blocks of any given protected area (which is unlikely), the protected areas would be home to 1,299 subpopulations of the various lemur species (Supplementary Table 3). Of these 1,299 mostly isolated subpopulations, 471 (36.3%) would occur in forest blocks < 10 km² (Fig. 3).

Change in protected forest areas for lemur subpopulations until 2050

The projection of the 2015–2017 deforestation rates to 2050 is restricted to analysis at the level of forest blocks. The number of lemur subpopulations in forest blocks of the smallest size of up to 10 km² would increase by c. 10% (from 471 to 519). The mode remains at 80–160 km². According to this analysis, the sizes of lemur subpopulations would be reduced, but in 2050 most species would still remain within the size classes of forest blocks they occupied in 2017 (Supplementary Table 3).

Discussion

Application of the forest analysis to lemur occurrences illustrates the importance of obtaining more detailed information regarding the actual situation of protected areas for conservation evaluations. If the total size of protected areas was used to estimate the size of lemur subpopulations, most species would be assumed to occur in areas of 320–640 km². However, when one considers the forested areas and fragmentation of forest areas, the majority of forest blocks within protected areas are < 10 km². Any species occurring in only one of these forest blocks would be categorized as Critically Endangered according to the B2 criterion of the IUCN Red List threat categories (area of occupancy < 10 km²; IUCN, 2001). When not considering these smallest forest fragments, the mode of forest blocks is predicted to decline from 320–640 km² for protected areas as a whole to 80–160 km². As these isolated forest blocks comprise the actual forests within the protected areas, they reflect a decline in area for continuous subpopulations to c. 25% of their size in 2017. This reduction in size is relevant not only for subpopulations but also for communities as a whole. Species–area relationships predict a continuous decline in species numbers with decreasing area of suitable habitat (MacArthur & Wilson, 1967). The slope of this relationship varies widely amongst taxa and ecosystems (Brown & Lomolino, 1998), and, apart from analyses on national and continental scales (Brown, 1995; Cowlishaw, 1999), most studies address this issue using forest fragments of much smaller size and thus do not allow predictions of the viability of lemur subpopulations in relation to the size of larger forest blocks (Harcourt, 2002; Fahrig, 2017; Kling et al., 2020; Strier, 2021). However, a fourfold difference in size from a mean area of c. 480 to c. 120 km² would be associated with a change in community processes and substantial extinction debt (i.e. a delayed extinction of species until the number of species associated with a certain area is reached again according to the species–area relationships deriving from the biogeography of the island; MacArthur & Wilson, 1967). In the long term, the reduction in size of the forest blocks would result in a reduction of individuals per subpopulation, possibly with subsequent extinction and finally reduced species numbers per forest block. As data on the viability of different-sized lemur populations are lacking (Ganzhorn et al., 2000), the predicted reduced forest block size adds a new conceptional dimension and challenge to conservation planning (Kuussaari et al., 2009; Laurance et al., 2012).

Although lemur subpopulations suffer significantly from large-scale forest destruction and hunting (Schwitzer et al., 2014; Randriamady et al., 2021; Borgerson et al., 2022; Kappeler et al., 2022), fragmentation effects do not yet seem to be significant at the scale of forest blocks > 10 km² (Steffens et al., 2022). Even the species with the largest body mass and thus the lowest population densities and numbers of individuals seem to maintain viable populations in relatively small forest blocks if human pressure is controlled (Jolly et al., 2002). Although genetic deficits because of genetic erosion or inbreeding could become relevant (Montero et al., 2019), most of these forest blocks are projected to persist up to and beyond 2050, providing a time buffer of more than one human generation for establishing effective conservation measures.

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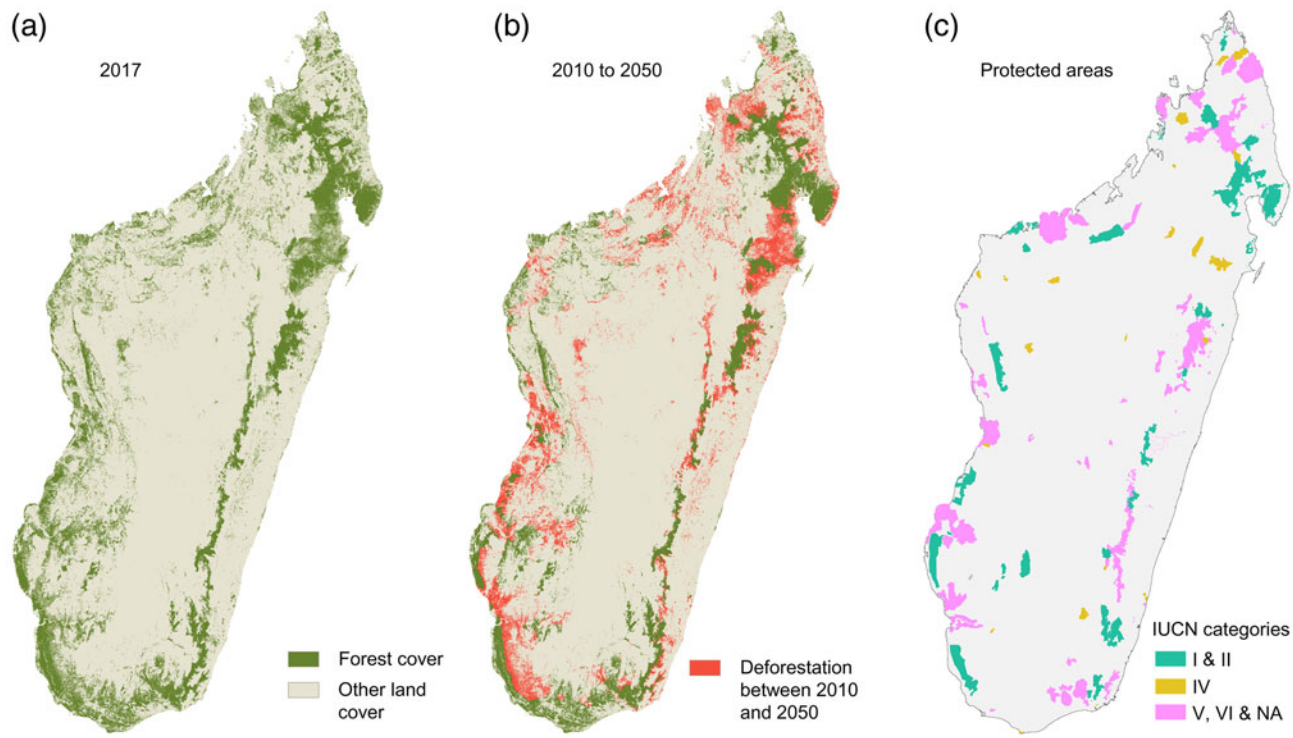

FIG. 4 (a) Forest cover in Madagascar in 2017, (b) projection of deforestation (from Vieilledent et al., 2021) assuming a constant deforestation rate of 100,000 ha/year (corresponding to 1.2% on the basis of the forest cover of 2010) from 2010 to 2050, and (c) the locations of protected areas, by IUCN category (Table 1). NA, not assigned to an IUCN category. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

Although the present analysis provides some hope for the persistence of the forest ecosystems of Madagascar within the protected area system, our analyses are based on the assumption that deforestation rates would not change for the next few decades. If the trend of increasing deforestation rates continues as it did during 2000–2017, we would expect an annual deforestation rate of c. 0.7% in 2050 even in the IUCN category I–IV protected areas (trends could not be calculated for the IUCN categories V and VI protected areas because they were established only in 2015 and long-term deforestation rates were not available). In addition to these possible assumption errors, there is substantial error in defining forest vs non-forest pixels when applying standard remote sensing methods, especially for dry and spiny forests (Rafanoharana et al., 2023). It remains unknown whether these trends in deforestation rates would persist once the information derived from remote sensing has been adapted. Using a similar approach, Vieilledent et al. (2020) applied a constant annual deforestation rate of 100,000 ha during 2010–2050 (corresponding to 1.2% on the basis of the forest cover in 2010) for all of the forests of Madagascar in relation to protection status and environmental and socio-economic factors (Fig. 4). At the time of their analyses, IUCN categories V and VI protected areas had not yet been established, and thus their effect could not have been considered.

Apart from methodological uncertainties, the relatively low deforestation rates observed until 2017 could change as a result of stochastic events. Historically, deforestation rates have increased during times of political crisis (Zinner et al., 2014). A diversity of circumstances, such as the Covid-19 pandemic (Eklund et al., 2022), has the potential to change deforestation rates, although protected area management in Madagascar has shown a high capacity to counteract these expected negative impacts on protected areas (Andrianambinina et al., 2022). Nevertheless, there have been unusual records of forest destruction, such as the reported areas of forest burnt after periods with low rainfall in October 2022 at Baie de Baly (9,263 ha), Tsingy de Namoroka (785 ha), Zombitse Vohibasia (1,242 ha), Ankarafantsika (7,341 ha), Manongarivo (733 ha) and Sahamalaza (581 ha), although these primarily concerned degraded forests. It is also of note that the new protected areas of IUCN categories V and VI have 5–10 times higher deforestation rates than those of categories I–III. The reasons for this and possible countermeasures to be taken to improve the situation were outlined by Gardner et al. (2018).

Conclusion

Our analyses support the notion that the new protected areas in Madagascar belonging to IUCN categories V and

VI are not as effective for conserving subpopulations of lemur species as the previously existing protected areas. Many of these new protected areas are under multi-use management by local communities and NGOs, allowing sustainable extraction of natural resources. In many cases, socio-economic conditions, lack of knowledge or lack of resources for management prohibit sustainable utilization of these forests. The challenges of combining extractive resource management with conservation goals might be too complex to be left to local communities or NGOs with limited means (Gardner et al., 2018; Stoudmann et al., 2023). More positively, our results provide hope that sufficient forest will remain within protected areas for the next 25+ years to maintain the lemur species currently present there. However, although lemurs can be considered umbrella species for other forest-dependent taxa, conclusions based on lemur occurrences alone do not necessarily apply to the other higher taxa of Madagascar (Kremen et al., 2008).

For the future of the forests and lemurs of Madagascar, conservation initiatives outside protected areas need to be effective by 2050. Amongst these initiatives, agroforestry and ecological restoration concepts for the reforestation or rehabilitation of degraded land are promising (Holloway, 2003; Birkinshaw et al., 2013; Hending et al., 2018; Donati et al., 2021). These approaches could include planting tree species used by lemurs (Steffens, 2020), planting species of use for people and the endemic biota of Madagascar alike (Konersmann et al., 2022), complementary planting of native and introduced commercial species (Ganzhorn, 1987; Gérard et al., 2015; Lavialle et al., 2015) and stratified planting of multiple-use trees and crops that reduce pressure on forest resources (Manjaribe et al., 2013). These activities would extend suitable habitats for forest-dependent species (not only lemurs), improve habitat suitability and provide buffers and corridors between forest blocks (Waeber et al., 2020; Ralimanana et al., 2022).

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Author contributions Conceptualization: POW, LW, JUG; methodology: SCR, FODA, HAR, LW; validation: LW, JUG; analysis: SCR, FODA, HAR, LW, JUG; data curation: SCR, FODA; writing: LW, JUG; supervision and project administration: LW.

Conflicts of interest None.

Ethical standards The research abided by the *Oryx* guidelines on ethical standards and was approved by the Ethical Standards Committee of the Institute of Animal Cell and Systems Biology (Universität Hamburg, Germany).

Data availability No new data were created or analysed in this study. We reassessed publicly available data as described in the Methods section.

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