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ARTICLE

THIRTY YEARS OF DEFORESTATION WITHIN THE ENTIRE RANGES OF NINE ENDANGERED LEMUR SPECIES IN NORTHWESTERN MADAGASCAR

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Abstract. Forest loss is a main driver of biodiversity decline, particularly in tropical regions. In this study, we investigate the degree of deforestation in the entire ranges of nine highly threatened lemur species in northwestern Madagascar. Landsat satellite images were acquired from four different years (1990, 2000, 2011, 2020), classified into forest/non-forest, and changes quantified. Forest cover has declined from 17.5% to 9.3% within the last 30 years. This decline varied across four protected areas (PAs) investigated: the forest cover of Ankarafantsika National Park (ANP) declined only moderately over time (from 76.3% to 67.4%), while it declined drastically in other PAs (e.g., from 54.9% to 18.9%, Bongolava Forest Corridor). Two lemur taxa are most affected (*Lepilemur otto*, *Microcebus bongolavensis*) by this development. For two other species (*L. ahmansoni*, *L. aeeclis*), most of the remaining forest is concentrated in two coastal PAs (in total 627.2 and 477.9 km^2, respectively), while those species occurring inside ANP (5 taxa) experienced rather stable forest coverage until 2020. A reversal of these deforestation trends and active reforestation measures are desperately needed and can be initiated following an outlined workflow of site selection, tree species selection, nursing of saplings, preparation of sites and follow-up care.

Keywords: Protected area, forest restoration*, Avahi, Eulemur, Lepilemur, Microcebus, Propithecus*

INTRODUCTION

The global decline in forest cover is a major conservation concern. Most widespread drivers of this development are wildfires, forestry and agricultural expansion, either as a subsistence strategy or for economic benefits (Curtis et al. 2018). The latter is particularly relevant in tropical forested ecosystems, with more than 90% of deforestation being devoted to agriculture-driven changes in land use (Pendrill et al. 2022). Forest cover change in the tropical biodiversity hotspot of Madagascar (Myers et al. 2000) has long been. However, understanding forest change and the processes that created today's species' distributions, past extinctions and the anthropogenic role in this process is pivotal. Contrary to a long-held hypothesis of an entirely forest-covered Madagascar before human arrival (e.g., Gade 1996, see Kull 2000), evidence is accumulating that most parts of Madagascar, especially the central highlands, were more likely characterized by a grass-woodland mosaic, with more or less forest cover depending on paleoclimatic conditions and the amount of precipitation (Crowley et al. 2021, Joseph et al. 2020, Solofondranohatra et al. 2018). Following this hypothesis, the increasing aridity (except in the eastern rainforests) since the end of the African Humid Period at around 5.5k years before present (DeMenocal et al.

2000) was one of the major drivers for the late Holocene decline in forest cover and subsequent demographic changes for a variety of forest-dwelling species (Gasse & van Campo 2001, Teixeira et al. 2021a,b, Salmona et al. 2017, Quéméré et al. 2012). These natural processes were accompanied by habitat fragmentation effects triggered by an expanding human population and a shift of livelihood activities towards cattle herding and agriculture within the last 1-2k years (Godfrey et al. 2019, Vorontsova et al. 2016).

It is possible to monitor changes in forest cover since the middle of the 20th century consistently across the island by means of remote sensing data. Starting with aerial photographs from the 1950s (Harper et al. 2007, Scales 2011), and continuing with Landsat satellite images from the 1970s onwards (Vieilledent et al. 2018), the degree of human-induced forest cover change in recent times can be assessed. Deforestation between 1973 and 2014 contributed to a decrease in forest cover in the dry deciduous forests of western Madagascar of 41.5% (44,350 to 25,960 km²) with the period since 1990 accounting for almost half of this decline (19.5% decline 1990-2014). This has led to increasing fragmentation as indicated by decreasing mean distances to forest edges (1.5km in 1973 to 300m in 2014) and about 46% of core forest being located less than 100m away from the edge (Vieilledent et al. 2018). This has unmistakable consequences for people and wildlife that depend on forest-derived ecosystem services. Consistent with paleontological records and the assembly of extant species, most wildlife in Madagascar was and is adapted to a forest-dwelling lifestyle, requiring a certain degree of tree coverage (Goodman & Benstead 2005). The lemurs of Madagascar are a striking example of the consequences of forest cover change (i.e. loss) with 98% of all the known 100+ species being listed as threatened with extinction by the IUCN (*www.iucnredlist.org*). Negative effects of forest fragmentation have been documented in a variety of ecological and genetic studies for different lemur species (e.g., Andriatsitohaina et al. 2019, Craul et al. 2009, Salmona et al. 2017, Quéméré et al. 2012).

In this study, we provide a detailed analysis of the forest cover changes within the entire ranges of nine threatened lemur species in northwestern Madagascar over the last 30 years to highlight the urgent need to protect certain key habitats from further deforestation effectively in order to prevent the extinction of these and other co-occurring species. We end our study with a practical guide for lemur-focused forest restoration that was derived from an ongoing restoration project in Ankarafantsika National Park.

METHODS

Study region

The study region has an area of 69,290.35 km² and comprises the last remaining larger forest complex of northwestern Madagascar (ANP - Ankarafantsika National Park) and four adjacent inter-river systems (IRSs) covered by cloud-free areas of two neighboring Landsat satellite images available from four different years (1990-2020, Fig. 1). We thereby covered the entire ranges of nine partly sympatric, forest-dwelling lemur species (Table 1). A further eight species also occur in this region, with their ranges extending beyond it but are nevertheless negatively impacted by forest cover loss (i.e., *Cheirogaleus medius, Daubentonia madagascariensis, Eulemur fulvus, E. rufus, Hapalemur griseus, M. murinus, M. myoxinus, Propithecus coronatus*). Four protected areas are located in the region. These are Antrema NPA (new protected area), Ankarafantsika NP (National Park), Bongolava FC (forest corridor) and the Mahavavy-Kinkony wetlands NPA. The region is primarily characterized by dry deciduous forests, open grassland vegetation and agricultural activities (Gade 1996, Koechlin 1972). Several large rivers open into the Indian Ocean but traverse northwestern Madagascar and have their headwaters in the central highlands defining different inter-river systems (Fig. 1). These major rivers are considered as distributional boundaries for a variety of species (e.g., Craul et al. 2007, Olivieri et al. 2007).

Forest cover mapping

Georeferenced and terrain corrected satellite images were retrieved from the U.S. Geological Survey (*www.earthexplorer.usgs.gov*) for four different periods: 1990/91, 2000, 2011 and 2020 (Table S1). No radiometric or solar correction was applied, as satellite images were analyzed separately (i.e. we did not create mosaic images) and no derived indices were calculated. Different optical bands were combined to yield raster stacks of 30 m x 30 m spatial resolution (Table S1). We classified the satellite images applying a supervised maximum likelihood algorithm based on sets of training areas for each land cover class (Table S2). These were *a priori* defined as forest (= dense and broad-leafed vegetation with a nearly closed canopy), open soil (= almost barren land with only marginal grass coverage including dry agricultural fields (due to season)), grassland (= dense grass coverage with interspersed trees) and water (= open water bodies like lakes, rivers and the Indian Ocean). Land cover classes were *a posteriori* summarized as forest and non-forest to increase the accuracy of the classification. Areas for training of the algorithm were selected based on our own experiences from the region

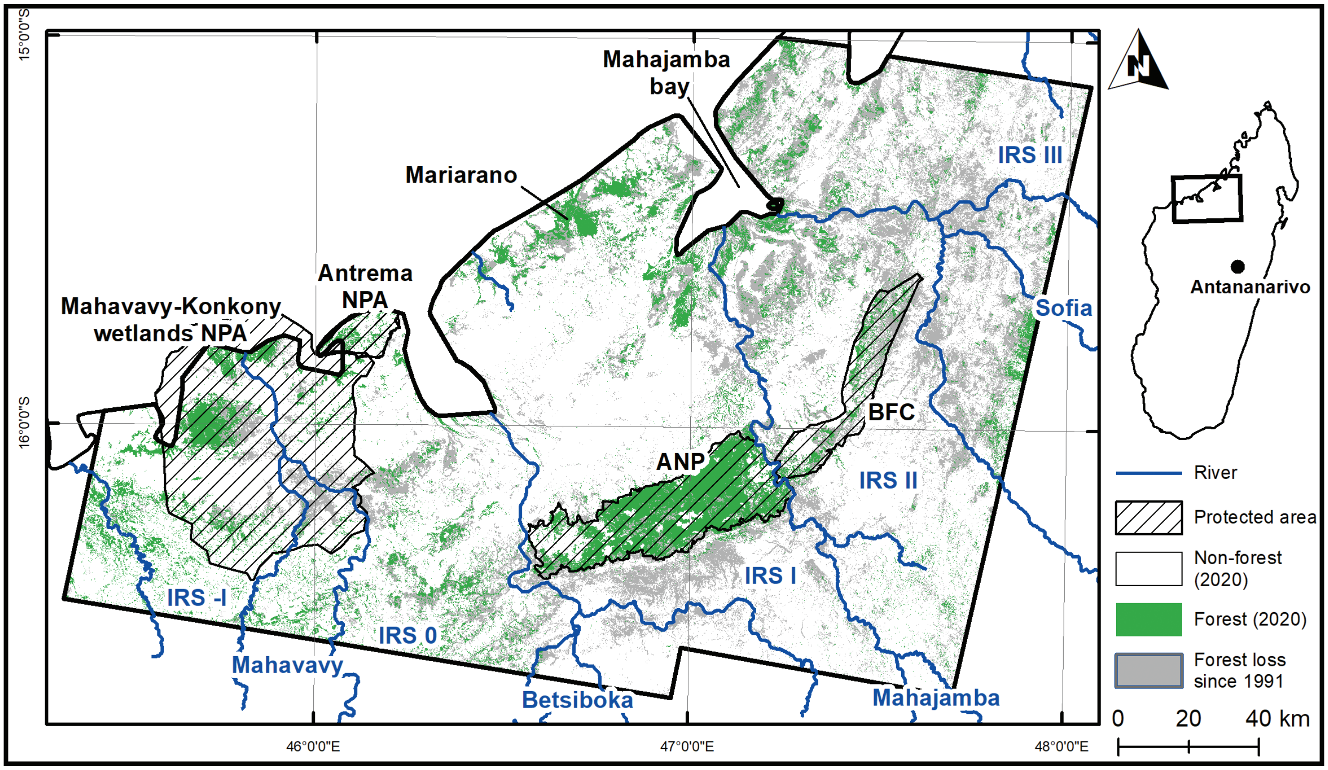

Figure 1. Forest cover in 2020 and forest loss since 1991 in northwestern Madagascar. Protected areas and inter-river systems (IRS) are marked for orientation. ANP = Ankarafantsika National Park, BFC = Bongolava Forest Corridor, NPA = New Protected Area.

and from published records (Andriatsitohaina et al. 2019, Rakotondravony & Radespiel 2009). Annual rate of forest cover change (i.e. mean annual deforestation or afforestation) was calculated following Formula 7 of Puyravaud (2003).

Accuracy assessment was conducted using 500 random points across the study region in a stratified sampling scheme (i.e. proportional number of points according to land cover class) for each time interval. Ground truthing was based on visual interpretation of actual land cover (forest or non-forest) as displayed in the Landsat images at each random point based on experiences from previous projects (Schüßler et al. 2018, 2020). User's and producer's accuracy (commission and omission rate, respectively) and the overall accuracy were calculated according to guidelines by Olofsson et al. (2014). All analyses were conducted in ArcMap (ArcGIS Desktop 10.6.1, ESRI, Redlands, USA). The forest cover maps for the different time stages are freely available and can be downloaded at: *https://doi.org/10.25625/2U5U5J*

Table 1. Lemur species with their entire ranges within the study region and their IUCN conservation states (Mittermeier et al. 2010, www.iucnredlist.org). IRS = Inter-river system as defined by Craul et al. (2007), see Figure 1, CR = Critically Endangered, EN = Endangered, VU = Vulnerable.

Lemur species		IUCN status	Distribution in IRS
Avahi occidentalis	Western wooly lemur	VU	I, II
Eulemur mongoz	Mongoose lemur	CR	–I, 0, I, II
Lepilemur aeeclis	Antafia sportive lemur	EN	0
Lepilemur ahmansoni	Tsiombikibo sportive lemur	CR	-I
Lepilemur edwardsi	Milne-Edwards sportive lemur	EN	I
Lepilemur otto	Ambodimahadibo sportive lemur	EN	II
Microcebus bongolavensis	Bongolava mouse lemur	EN	II
Microcebus ravelobensis	Golden-brown mouse lemur	VU	I
Propithecus coquereli	Coquerel's sifaka	CR	I-III

RESULTS

Overall accuracies for the four time periods 1990/91, 2000, 2011 and 2020 were 92.2%, 91.4%, 93.0% and 96.0%, respectively. User's and Producer's accuracies did not fall below 71.4% and 83.3% across all time stages, respectively (Table S3).

Forest cover change

The overall trend of forest cover change was negative, with a decline from 17.52% in 1991 to 9.26% in 2020. This pattern was, however, inverted between 2000 and 2011 with a slight increase in forest cover (Table 2). This observation can be exemplified in areas at the northern border of ANP, where regenerating vegetation in 2000 was not classified as forest, but gained comparable reflectance values as forests by 2011 (Fig. 2, Fig. S1). Mean annual rates of forest change were 2.54% deforestation (1991-2000), 1.11% afforestation (2000-2011) and 1.89% deforestation (2011-2020). Within the four protected areas, trends were different: in Ankarafantsika NP, forest cover fluctuated over time, with regenerating forests until 2011 and a decline towards 2020 (Fig. 2). In Antrema NPA, we have observed an increase in forest cover since 1991, while in Bongolava FC, we documented the strongest and most pronounced deforestation from >54% in 1991 to <19% forest coverage in 2020. In Mahavavy-Kinkony wetlands NPA, forest cover was rather stable but declined sharply towards 2020 (Table 2). This primarily happened in the southeastern part of the protected area, where riparian forests were converted into agricultural fields (Fig. 2).

Impact on lemur populations

Of the nine lemur species, those taxa occurring in IRS I (*A. occidentalis*, *E. mongoz*, *L. edwardsi*, *M. ravelobensis*, *P. coquereli*) have the highest proportion of forested habitats still available within their ranges (1,535.2 km² in IRS I). These are located in Ankarafantsika NP and along the coast around the village of Mariarano (Fig. 1). Apart from smaller forest patches on the southwestern stretch of the Mahajamba bay, these two forested areas have become increasingly disconnected from each other since 1991. For species with their entire distribution confined to IRS II (*L. otto*, *M. bongolavensis*), only very few small forest fragments remain in 2020 totaling 552.7 km² (6.3% of IRS II, Table 3). These are partly located inside Bongolava FC where forest cover has decreased by 36% since 1991 (Table 2) and along Mahajamba Bay (Fig. 1). IRS 0 containing the range of *L. aeeclis,* harbors the last remaining forests with a total size of 477.9 km² (9.3% of IRS 0) along the coast within the two protected areas and in a few unprotected stretches further inland. This also applies to IRS -I and the range of *L. ahmansoni* with a total amount of forest cover of 627.2 km² (15.5% of IRS –I, Table 3). However, further small forest patches can be found west of Mahavavy-Kinkony wetlands NPA (Fig 1).

DISCUSSION

Forest cover change

Deforestation has been an ongoing trend in Madagascar for many decades (Vieilledent et al. 2018) and has received substantial and increasing attention, particularly with respect to declines in the dry deciduous forests of western Madagascar (Waeber et al. 2015). Compared with the numbers for the entire western part of Madagascar (i.e. dry deciduous forests), mean annual deforestation rates were markedly higher and comparable in the first and third study decade (1991-2000, 2011-2020) within the study region. Between 2000-2011, however, a net-recovery of forest cover was documented, a trend not recorded by a larger scale dataset (i.e., Vieilledent et al. 2018) or observations from the Menabe region of western Madagascar (Scales 2011). For example, a significant recovery of forest was observed at the northern border of Ankarafantsika

Table 2. Forest cover in km² (and percentages in brackets) in the study region and inside the four protected areas between 1991-2020.

	Size [km²]	1991	2000	2011	2020	Protected since
Study region	69,290.35	12,141.19 (17.5%)	7,169.66 (10.4%)	9,485.31 (13.7%)	6,417.95 (9.3%)	-
Ankarafantsika NP	1,351.24	1,031.59 (76.3%)	914.88 (67.7%)	1,020.91 (75.6%)	911.34 (67.4%)	1927
Antrema NPA	190.46	29.34 (15.4%)	35.61 (18.7%)	45.70 (24.0%)	43.91 (23.1%)	2010
Bongolava FC	607.00	333.13 (54.9%)	258.63 (42.6%)	186.63 (30.7%)	114.40 (18.9%)	2015
Mahavavy-Kinkony wetlands NPA	2,995.84	651.99 (21.8%)	874.19 (29.1%)	873.54 (29.1%)	427.87 (14.3%)	2007

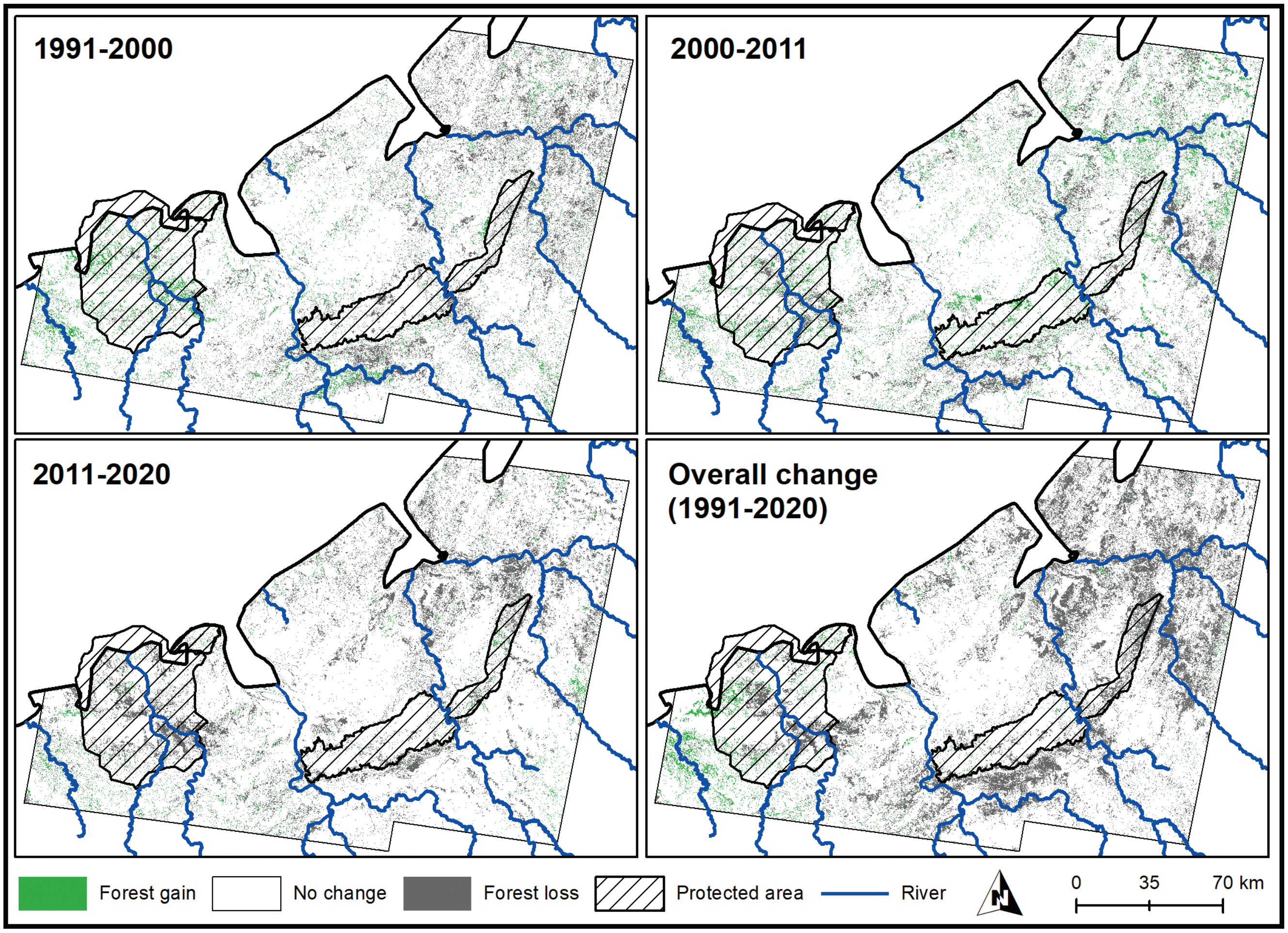

Figure 2. Forest gain and loss from 1991-2020. Protected area names and labels of inter-river systems are given in Figure 1.

NP, where a larger section of forest was lost by 2000 but appeared to have recovered by 2011. As detailed in supplementary figure S1, we attribute this loss to a wildfire which must have occurred in that area before 2000. Visual interpretation of the false-color composites of the satellite images indicated natural rejuvenation of previously burned places in comparison with surrounding areas. Apart from this region, significant forest recovery was observed and verified from raw satellite images in the Tsiombikibo forest in northwestern section of Mahavavy-Kinkony wetlands NPA and in northern parts of IRS II. We conclude, therefore, that the observed forest recovery was not an analytical artifact due to the slightly earlier sensing date of the Landsat images in 2011 (July instead of August/September 2000), but rather related to the process of forest recovery following fire.

Table 3. Forest cover change in km^2 (percentages in brackets) in the different inter-river systems (IRS) in relation to the ranges of the concerned lemur species. Species with their entire range confined to a single IRS are given in bold.

IRS	Size	1990/91	2000	2011	2020	Species concerned
-I	4,036.29	607.67 (15.1%)	895.58 (22.2%)	961.03 (23.8%)	627.18 (15.5%)	*E. mongoz*, ***L. ahmansoni***
0	5,166.39	1093.10 (21.2%)	1050.99 (20.3%)	947.38 (18.3%)	477.88 (9.3%)	*E. mongoz*, ***L. aeeclis***
I	11,064.88	2992.49 (27.0%)	2442.37 (22.1%)	2434.02 (22.0%)	1535.22 (13.9%)	*E. mongoz*, *A. occidentalis*, ***L. edwardsi***, ***M. ravelobensis***, *P. coquereli*
II	8,685.78	2715.74 (31.3%)	1849.17 (21.3%)	1477.11 (17.0%)	542.72 (6.3%)	*E. mongoz*, *A. occidentalis*, ***L. otto***, ***M. bongolavensis***. *P. coquereli*

Forest cover change inside the four protected areas followed different trends, only partly reflected by the changes in the overall study region. For Bongolava FC, we documented the strongest and steadiest decline. Ankarafantsika NP fluctuated around a high proportion of forest within its boundaries, while in Antrema NPA forest cover increased and stabilized over time. In Mahavavy-Kinkony wetlands NPA, forests first recovered in one section before a strong decline was observed in the south of this protected area due to agricultural expansion. Unfortunately, this area is one of those with highest densities of Critically Endangered *Propithecus coronatus* (Salmona et al. 2014). Differential change in forest cover in various protected areas is also mirrored by other studies from Madagascar (Eklund et al. 2016, Rafanoharana et al. 2021) highlighting the region-dependant challenges and differences in protected area management.

Although historic forest cover change in Madagascar was most likely triggered by climatic changes (Crowley et al. 2021, Joseph et al. 2020, Solofondranohatra et al. 2018), recent deforestation in the study region is mainly driven by human subsistence and some commercial activities like agricultural expansion, livestock grazing or forest exploitation for charcoal production (Dave et al. 2016, Gaydes-Combes et al. 2017, Jones et al. 2015, Steffens et al. 2020, this study). As in other regions of sub-Saharan Africa (Curtis et al. 2018), local land users in northwestern Madagascar and elsewhere are highly dependent on particular, forest-related ecosystem services to sustain their livelihoods but, increasingly, notice the decline in these services (Dave et al. 2016, Steffens et al. 2020). Our analysis provides remotely sensed evidence underpinning the experiences of residents from the region: forest cover and associated ecosystem services (i.e, the provision of raw materials or storm hazard mitigation) has been steadily declining for decades now (Dave et al. 2016, Steffens et al. 2020), with no indications for a trend reversal.

In fact, after the acquisition date of the latest satellite image used in our analyses (September 2020), and during the finalization of this article in December 2021, Ankarafantsika NP was hit hard by extensive fires. Forest loss equaled 6.66% of the park's surface or roughly 90 km^2 - within one year of time (Fig. 3). It is to be hoped that natural regeneration processes can be initiated and land degradation towards grasslands can be counteracted, to safeguard forest connectivity inside this key protected area of northwestern Madagascar.

Impact on lemur populations

For the majority of lemur species, the population-wide influence of habitat loss and fragmentation is not well investigated (Hending 2021, Irwin et al. 2010, Kling et al.

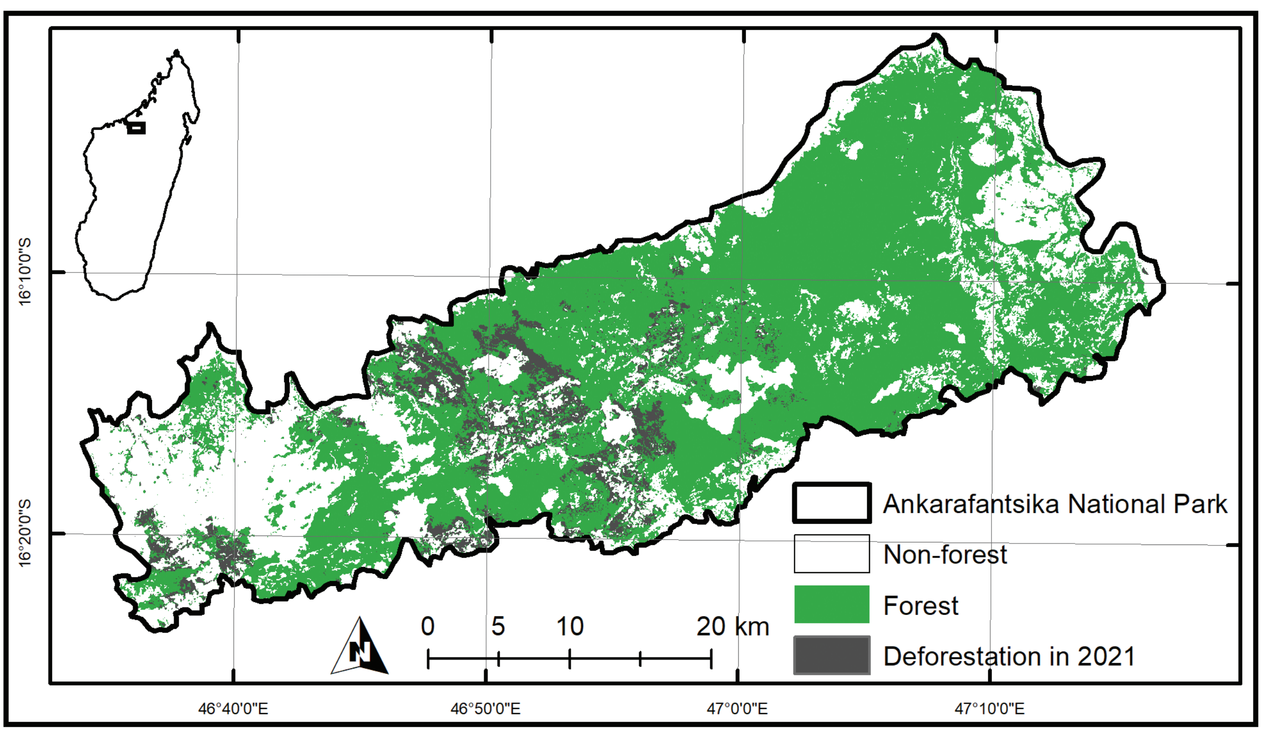

Figure 3. Forest burning inside Ankarafantsika NP between September 2020 and December 2021 as derived from Sentinel-2 satellite images acquired on 04-12-2021 (tiles: T38-LQH, T38-KPH).

2020). For those species having parts of their distributions inside Ankarafantsika NP (in IRS I), the proportion of available habitat was relatively stable in its extent until 2021. The impacts of the latest extensive fires have to be examined in the future. The previous stability in forest coverage was mirrored in the highest degree of genetic diversity for *P. coquereli* when compared with other species from this genus (Bailey et al. 2016). However, even in this rather stable region of northwestern Madagascar, local community members reported decreasing lemur populations and impairment in natural resources during their lifetimes (Steffens et al. 2020). The situation for species outside of IRS I is much more severe. Forest cover in the ranges of *L. aeeclis*, *L. ahmansoni*, *L. otto* and *M. bongolavensis* declined drastically leaving only very few, small refuges for these species today. It has to be noted, that our figures of extent of forest cover represent only the maximum size of available habitats, taking no account of habitat quality and the patchiness of the remaining forests.

Several studies on fragmentation effects give insights into the possible underlying patterns that can be linked to the changes in forest cover inferred by our analysis (e.g. Eppley et al. 2020). The lemur species of northwestern Madagascar are in general not equally distributed across forest fragments with notable absences, mainly of the larger bodied species or folivorous and arboreal nocturnal taxa (*Avahi* spp., *E. mongoz*, *Lepilemur* spp.) from some fragments (Olivieri et al. 2005). The area of a particular forest was found to be more important than fragment isolation in determining the species richness of lemurs (Steffens & Lehmann 2018, 2019). For example, *P. coquereli* and *L. edwardsi* did not occur in smaller fragments and did not form metapopulations across fragments (Steffens & Lehman 2018), whereas *A. occidentalis* and *E. mongoz* were not found in fragments around but in Ankarafantsika NP itself (Steffens & Lehman 2018, Steffens et al. 2020). Apart from this classical island biogeographic perspective (e.g., Diamond 1985), several species are negatively impacted by forest fragmentation, displaying lower genetic diversity or recent population collapses (*L. edwardsi*, Craul et al. 2009, *M. bongolavensis* and *M. ravelobensis*, Olivieri et al. 2008, *M. ravelobensis*, Radespiel et al. 2018, Andriatsitohaina et al. 2019, *P. coquereli*, Bailey et al. 2016) and possibly by molecular edge effects (e.g., lower genetic diversity in edge habitats in *M. ravelobensis*, Radespiel et al. 2018). Furthermore, whereas endemic species appear to be negatively impacted, non-native species like *Rattus rattus* benefit from increasing fragmentation (Andriatsitohaina et al. 2019). If the described trends cannot be reversed, local extirpations and genetic impoverishment of lemur species are to be expected.

Lemur-focused forest restoration – an experience-based guide

In order to prevent population extinctions and to reverse the ongoing loss of forest cover, restoration efforts are needed to maintain the ecosystem services upon which people and wildlife rely.

The non-governmental organization, Planet Madagascar, and its implementing partner the Planet Madagascar Association have been restoring forests around Ankarafantsika NP since 2017. Their main goal is to protect and to restore forest corridors for lemurs while providing opportunities for sustainable livelihoods for people that share these forests. Up to December 2020, Planet Madagascar had planted 66,937 seedlings into a plantation with a survivorship of 31.46% (21,061 seedlings) thereby restoring 100 ha of dry deciduous forest around Ankarafantsika NP. This has been done using their experience-based 6-step framework:

1. Plantation site selection is key to ensure restoration success. Planet Madagascar combined local knowledge with scientific data on the occupancy of lemurs, major threats to the forests within their management zone, and logistical considerations (e.g., proximity to communities and water) to determine which portion of the landscape should be restored. A restoration site is selected because (a) it contains forest fragments and adjacent continuous forest with high lemur species diversity (Steffens and Lehman 2018, 2019, Andriatsitohaina et al. 2019) and (b) because forests fragments are in close proximity (i.e., ~ 500 m) to allow reconnection via forest re-growth. In addition, it is important (c) to incorporate advantageous landscape features like natural depressions (i.e. low lying areas) where water retention capacity is naturally high.
2. Species selection is integral to ensuring recruitment. Plant species must be selected that are used by lemurs, are non-invasive (i.e. avoiding species such as *Tamarindus indica*) and that are abundant in nearby continuous forest (Supplementary Table S4). The selected species should grow relatively fast and be native to the area to ensure adaptability to the local climatic conditions.
3. Nursing of seedlings increases recruitment. This step involves three elements: (a) seed collection, (b) seed processing, and (c) nursery conditions.
    a) Fresh seeds must be collected from June to December (dry season) and planted immediately into a nursery. Storing of seeds is not advised as they can be preyed upon by insects or destroyed by mould. In 2017-2018 for example, Planet Madagascar lost more than 75% of seed that were stored from October to February.

b) Recruitment of seedlings can be increased when seeds are rinsed before planting. For example, Planet Madagascar compared recruitment of *Rhopalocarpus similis* and *Vitex* spp. seedlings that were treated by rinsing only and rinsing plus soaking in water for 24 hours. Rinsed seeds of both species had 31% and 95% higher recruitment than rinsed and soaked seeds, respectively.
c) Nurseries must be placed in areas with high quality soils and adjacent to permanent water supplies. Poor soil quality has negative impacts on recruitment and quality of saplings. Nurseries on good soils produced 4% more saplings, all of larger height and girth.

4. Planting of saplings from the nurseries to receiver areas must be done during the rainy season (December to late March in ANP).
5. Preparation of the plantation improves sapling survivorship. Planet Madagascar usually prepares the plantation area by clearing a firebreak around it, digging small holes for the saplings, clearing grass around each hole, and adding compost. Planting in proximity to shade trees or installation of artificial shade providers improves sapling survivorship. For example, saplings under shade had more than 70% greater survivorship than without shade. Additional measures to protect against damage from cattle (i.e. fencing) are recommended if financially feasible.
6. Continued monitoring of planted saplings is required to counteract unexpected events and prevent cattle from grazing on saplings. Fire is a common cause of failure for forest restoration projects (Elliott et al. 2013). Clearing plantations from encroaching grass during monitoring is important to maintain the fire breaks and to reduce competition for nutrients between grasses and saplings.

Future research should assess further other ways of improving reforestation methods, long-term survivorship of trees, and whether lemurs actually use these restored forests as habitat.

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