



Anthropogenic landscape change and amphibian diversity in tropical montane biodiversity hotspots: insights from satellite remote sensing in the Madagascar highlands

Antonio T. Monteiro^{1,2} · Sophia Rosa³ · Franco Andreone⁴ · Serge Ndriantsoa⁵ · Tsanta Rakotonanahary⁵ · Jeff Dawson⁶ · Falitiana C. E. Rabemananjara⁷ · Nirhy H. C. Rabibisoa⁸ · Richard Lucas⁹ · Angelica Crottini^{10,11,12}

Received: 24 July 2022 / Accepted: 6 November 2023
© The Author(s) 2023

Abstract

The magnitude of anthropogenic landscape change in tropical montane biodiversity hotspots and its relationship with biodiversity is a global issue that remains ‘locked-in’ in the broad narrative of tropical change in Africa. Over a montane biodiversity hotspot of Madagascar highlands (Ankaratra Massif), we conducted analysis on land cover change with Landsat satellite sensor data to identify the magnitude of change (1995–2016) and on the habitat change–amphibian diversity relationship to understand links with biodiversity. The results evidenced that 17.8% of the biodiversity hotspot experienced change in land cover in only 20 years. That pressured the already threatened forests, particularly since 2005. Of the total forest area in 1995 (2062.7 ha), 21.5% was cleared by 2016 (1618.3 ha). Changes in forest cover followed a bidirectional pattern. While in the period 1995–2005, forests expanded at a rate of 2.0% year⁻¹ (from 2062.7 to 2524.8 ha), the area declined between 2005 and 2016 at a rate of -4.1% year⁻¹, fourfold the rate reported nationally for Madagascar (-1.1% year⁻¹). Forest-to-shrubland transitions emerged as being of increasing concern to forest integrity. We identified a significant link between habitat change and amphibian diversity, but only for species richness. Counter to expectations, no significant relationship was found between species richness and deforestation rates, and between microendemism rates and any of the habitat change variables. Species richness responded to the spatiotemporal variability in vegetation dynamics represented by the standard deviation of the Normalized Differenced Vegetation Index (NDVI_std). Species richness was strongly negatively related to NDVI_std in the short-term ($R^2=0.91$, $p=0.003$) and long-term ($R^2=0.69$, $p=0.03$), increasing where the spatiotemporal variability in NDVI was lower. The magnitude of changes in this biodiversity hotspot suggests that region-specific assessments are necessary in the context of the tropical change narrative in Africa and should consider conservation policies tailored for local conditions. Reducing deforestation and land conversion rates through a management plan codesigned with local communities is urgent. Habitat change appears to impact on amphibian diversity by altering the functional attributes of the habitat and not just by reducing habitat extent. NDVI_std seems a relevant indirect metric for monitoring such change although other biophysical attributes obtained from satellite sensor data should be integrated and explored.

Extended author information available on the last page of the article

Keywords Land cover change · Forest loss · Remote sensing mapping · Amphibian diversity · Tropical montane cloud forest · Natural reserves

1 Introduction

Anthropogenic landscape change in tropical regions is one of the most concerning issues to nature and humanity (Appiah et al., 2009; Barbier, 2021; Roberts et al., 2021). Within this change narrative, there are, however, locally specific but concerning realities that remain relatively neglected. The tropical montane biodiversity hotspots of Africa is a noteworthy case (Soh et al., 2019; Yesuf et al., 2019). Biodiversity hotspots are priority conservation areas (Norman, 2003), but those located in montane regions have the peculiarity of being refuges for unique species assemblages with limited geographical ranges (He et al., 2023) where local communities make use of natural resources to survive and relieve poverty (Leite et al., 2018). The fragile balance between natural asset preservation and human community uptake is a main feature and biodiversity, a key for sustainable development and living (Blicharska et al., 2019), is being highly affected (He et al., 2023). For instance, the forests and endemic species occurring here are nowadays among the most threatened on Earth due to the combined effects of land cover/use change, climate change and population growth (Hu et al., 2021; Salinas et al., 2021). Notwithstanding the relevance of the African tropical montane biodiversity hotspots, they remain largely understudied (Barbier, 2021; Christmann & Menor, 2021) and landscape changes are ‘locked-in’ in assessments at country or continent level (Yesuf et al., 2019). Assessing the dynamics of landscape change in these systems and its links with biodiversity is therefore crucial for understanding anthropogenic pressure, mitigating the impacts in the sensitive biodiversity (He et al., 2023; Yesuf et al., 2019) and assisting the dialogue among stakeholders in view of more sustainable management strategies and development pathways (Vedeld et al., 2007).

Over the African montane biodiversity hotspots, satellite remote sensing has been one of the most common approaches to assess anthropogenic landscape change and its impacts for biodiversity (Barbier, 2021; Hamunyela et al., 2020; Kidane et al., 2012; Leite et al., 2018; Noroozi et al., 2018; Soh et al., 2019; Yesuf et al., 2019). The continuous tracking of such remote areas and the sensitivity of satellite sensors in relation to processes driving biodiversity (e.g., primary production dynamics) are among the main reasons (Kwok, 2018; Pettorelli et al., 2018). Supervised classification of Landsat satellite data has been the most common approach (Cronin et al., 2014; Kidane et al., 2012; Leite et al., 2018; Vieilledent et al., 2018), and machine learning classification techniques (i.e., random forest) are increasingly considered to assess landscape change (Koskikala et al., 2020). Most of the studies evidenced strong anthropogenic change activity in the African montane biodiversity hotspots. In the scarp forests of Angola, Leite et al. (2018) described an unsustainable overexploitation of forests that affects carbon dioxide emissions and biodiversity (Cáceres et al., 2014). A threat also found in the Afromontane areas of the Gulf of Guinea, where authors recommended more effective management and law enforcement to ensure conservation (Cronin et al., 2014). In eastern Tanzania, Hamunyela et al. (2020) showed that more than one-quarter of montane forests were lost in only 17 years. Here, the upward shift of deforestation and forest degradation emerged as a major threat for the persistence of the remaining blocks of forest. In Ethiopia, Kidane et al. (2012) described a shift from natural to more farming mountain landscapes, but Afromontane rainforests

have remained relatively stable. Much less is known regarding the impacts of landscape change in biodiversity. The existing knowledge is reduced, a gap also highlighted by Soh et al. (2019). Habitat loss was identified as the major concern for biodiversity hotspots in the short term, particularly in the tropical Africa due to demographic pressure and demand for agricultural land (Habel et al., 2019). Anthropogenic land-use change and habitat degradation were both associated to a decline in bats population over the Ethiopian highlands (Razgour et al., 2021) and frog species richness in western Cameroon (Hirschfeld et al., 2016). Nonetheless, recent studies points to biotic resistance when anthropogenic landscape changes are less severe (Soh et al., 2019). This reinforces the role of a planned given-take relationship between community needs and natural assets (Topp-Jørgensen et al., 2005), where local landscape change assessments are of relevance, given also the underestimation of forest loss in global derived products (Hamunyela et al., 2020).

The highlands of Madagascar are thought to be one of the most threatened biodiversity hotspots in the world regarding anthropogenic landscape change and its impacts in biodiversity (Hirschfeld et al., 2016; Myers et al., 2000). Approximately 44% of the primary forest cover was lost between 1953 and 2014 (Vieilledent et al., 2018). Among the major causes are the illicit charcoal exploitation and logging, uncontrolled slash-and-burn agriculture, and introduction and exploitation of invasive productive forest species (i.e., pinewood plantations; Kull, 2008). The montane vegetation that flourished in the highlands of Madagascar's during the climatic oscillations of the Pleistocene (Burney, 1996) is nowadays restricted to the highest summits. These summits are however exposed to degradation (Crowley, 2000a, 2000b) and with no ample areas to provide space for further upward shift of their unique biodiversity. In this context, amphibians are one of the most exposed biodiversity assets. Amphibians in Madagascar stand out in terms of species diversity (with 4.5% of worldwide described amphibian diversity hosted here), endemism (100% of its described amphibian species are endemic to this island, Zimkus et al., 2017) and threat (over half of the described Malagasy amphibian species are currently listed in threatened categories of the IUCN red listing Andreone et al., 2005; IUCN, 2019). The amphibians of montane forests often show striking patterns of microendemism (Raxworthy & Nussbaum, 1996), and they are increasingly threatened by habitat degradation and fragmentation, and upslope displacement due to global warming (Hirschfeld et al., 2016).

The present study centers on the Madagascar highlands at Ankaratra Massif, a montane biodiversity hotspot that remained understudied in the previous studies (Yesuf et al., 2019) and 'lock in' in national (Vieilledent et al., 2018) and global assessments (Hu et al., 2021). Here, we assessed anthropogenic landscape change during 20 years and evaluated the link between amphibian diversity and habitat change. The main goal was to extend the existing knowledge for montane biodiversity hotspots within the tropical change narrative in Africa (Yesuf et al., 2019) and to assist the strategic conservation plan aiming a more sustainable coexistence between natural assets and human community uptake in the Ankaratra Massif. In specific, (a) land cover changes between 1995 and 2016 were reconstructed using classification of Landsat satellite imagery with a random forest machine learning approach; (b) error-adjusted change estimates were used to analyze landscape change dynamics with emphasis on forest dynamics (10-year time step); and (c) linear regression models evaluated the relationship of amphibian species richness and microendemism rate in relation to habitat change in 100 m circular buffers. Together, these steps address two major questions: (1) How and at which rate landscape change in montane biodiversity hotspots? (2) How does amphibian diversity respond to habitat change? Based on literature, we hypothesized considerable anthropogenic activity at expenses of forest areas that affects negatively amphibian diversity by altering the habitat conditions. We conclude

by discussing the results at the lens of the tropical change narrative in montane biodiversity hotspots and by providing insights for the sustainable conservation in the Ankaratra Massif.

2 Materials and methods

2.1 Study area

The study area covers 245 km² and encloses the Natural Resource Reserve of Ankaratra-Manjakatampo (19°20'0S, 47°16'0E, Figure 1) officialized in April 2015 (decree-law 2015–711, Madagascar official journal). It is located in the Central Highlands, which is the most densely populated Malagasy region (CEPF, 2014) and a major watershed that divides the rivers flowing into the Mozambique channel from those flowing into the Indian Ocean (Vences et al., 2002). The Ankaratra Massif is an extinct volcano range with a north–south orientation and the third highest peak of Madagascar with elevation ranging from 1533 to 2643 m above sea level (Vences et al., 2002). The climate is shaped by a cold and dry season in the austral winter and a warm and wet season in the austral summer. Mean temperatures range from 11.9° to 17.9 C, while mean annual precipitation amounts to 2012 mm that falls mainly between November and April (Ranarilalantiana et al., 2022). The landscape is mainly covered by an extensive grassland area, heathland and remnants of savannah approximately above the 2000 m. Forest instability and deforestation is a main concern (Jenkins, 1987), and forest cover is nowadays reduced. The remnants of the Tropical Montane Cloud Forest (TMCF) are mainly located along the eastern slopes (Ranarilalantiana

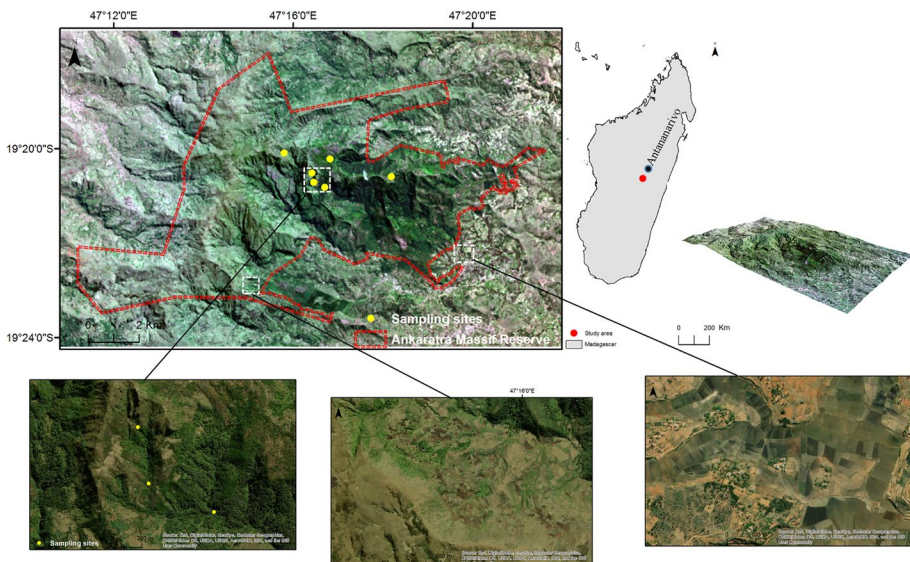


Fig. 1 Overview of the study area in the highlands of Madagascar at Ankaratra Massif with a true color composite of Landsat 8 from April 30th, 2016 and sampling points used for the amphibian survey between 2011 and 2013 overlapping. Characterization of main landscape features using very high-resolution imagery from google archive. Lower left: forest cover; center: typical slash-and-burn agriculture mosaic; lower right: the crop land areas at lower elevations

et al., 2022). Reforested areas-based non-native pine (*Pinus* spp.) and cypress (*Cupressus* spp. ~13%) are also present (Rabemananjara et al., 2011). Agriculture and farming are very important for the survival of local communities, with rice, potatoes, and maize being the major crops. Cattle and fish breeding are also relevant (Andrianarivelo et al., 2021). Cultivation land is usually close to scattered human settlements at lower elevations.

Amphibians, including some microendemic species, is a key feature of Ankaratra Massif (Vences et al., 2002). Fifteen species of amphibians are currently known from here and the fragmented TCMF is home to three microendemic species: Williams' bright-eyed frog (*Boophis williamsi*), the Madagascar frog (*Mantidactylus pauliani*) and *Mantidactylus* sp. Ca19 (Glaw & Vences, 2007; Vences et al., 2002). *Boophis williamsi* and *M. pauliani* are probably two of the most threatened species of amphibians in Madagascar (Group,). In 2010, a local organization (Vondrona Ivon'ny Fampandrosoana; VIF) jointly with the IUCN SSC Amphibian Specialist Group Madagascar (ASG), the Amphibian Survival Alliance, Global Wildlife Conservation and Rainforest Trust (Rabemananjara et al., 2012), started a conservation program to guide the establishment of a protected area in Ankaratra, which was officialized in April 2015.

2.2 Overview

Anthropogenic landscape change and its links with amphibian diversity in montane tropical biodiversity hotspots was assessed in four main steps: First, existing amphibian diversity and Landsat satellite data were assembled. Second, classification of satellite sensor data with the machine learning classifier random forests classifier was performed to create land cover maps (1995, 2005, 2011, 2012, 2013, and 2016). Third, land cover change analysis was conducted using error-adjusted change estimates obtained from post-classification comparison of land cover maps (1995–2005, 2005–2016) followed by accuracy assessment according to the good practices protocol of Olofsson (2014). Fourth, linear regression models evaluated the link between amphibian diversity metrics recorded in field surveys ($n=6$) and anthropogenic landscape change using as proxy the deforestation rates and spatiotemporal variability in the NDVI (NDVI_std) in the immediate surroundings (100 m buffers) in the long-term (1995–2013) and short-term (2011–2013) scale of analysis. Amphibians were selected as a model of understanding for the responses of biodiversity to anthropogenic landscape change, because they are one of the most sensitive groups to habitat modification (Becker et al., 2007) and a key biodiversity feature of the study area (Vences et al., 2002).

2.3 Data collection

2.3.1 Amphibian diversity

To characterize amphibian diversity, we relied on field data collected twice a year for three consecutive years (2011–2013) in the study area (Rabemananjara et al., 2012, see Fig. 1 and Online Resource 1 and 2). Ankaratra Massif is a remote mountain area of difficult access and surveying has been always challenging. The repeated surveying has the advantage of delivering more consistent snapshots of patterns with respect to the common single or short-time assessments (Muluvhahotho et al., 2021). The surveys were carried out in the wet and dry season at six high-altitude streams ($n=6$, Fig. 1), except for one plot that was only surveyed in 2013. At each site, a 100 m transect, with varied widths

according to the stream structure, was established. Each transect was surveyed twice during each field visit, with both diurnal and nocturnal visits. Data on species encountered at each site are available in SI Appendix 1. Using these data, two diversity metrics were derived: species richness (SR) defined as the number of species encountered during the surveys and microendemism rate (ME) defined as the ratio between the total number of individuals of the three microendemic species (*Boophis williamsi*, *Mantidactylus pauliani* and *Mantidactylus* sp. Ca19) over the total number of surveyed individuals.

2.3.2 Landsat satellite data

Five satellite scenes from the Landsat 5 and 8 platforms (20th March 1995, 18th May 2005, 22nd July 2011, 22nd April 2013, and 30th April 2016) were downloaded from the USGS Earth Explorer (<https://earthexplorer.usgs.gov>) as surface reflectance, geometrically corrected and stored in Geotiff format. They were selected based on the following criteria: (i) cloud-free scenes taken in the (ii) late wet-early dry season, and (iii) in all years of the analysis (anniversary-date scenes), in order to optimize mapping and change detection and to reduce errors related to seasonal differences (Panuju et al., 2020). To allow the multi-temporal comparison between scenes, a radiometric normalization was applied to Landsat 5 data using the pseudo-invariant features technique (PIFs; Schott et al., 1988). For each scene, three ancillary satellite derivatives were additionally computed: Soil Adjusted Vegetation Index (SAVI; Huete, 1988), Normalized Difference Vegetation Index (NDVI; Huang et al., 2021).

2.4 Mapping of land cover

To assess anthropogenic change over the montane biodiversity hotspot of Ankaratra Mas-sif, land cover was mapped in 1995, 2005, 2011, 2013 and 2016. Supervised land cover classifications were performed using the Landsat data collected and the machine learning classifier random forests (RF), which is a particularly effective classifier (Breiman, 2001). For each date, a land cover map composed by five classes was created (shrubland, grassland, crop, barren land and forest, Fig. 2). Shrubland described the areas dominated by shrubs or short trees, usually resulting from succession after forest cutting. Grasslands were the open areas occupied by grass plants or pastures, usually used for livestock grazing. Cropland defined the cultivated areas mainly of irrigated rice and increasingly upland rice. Barren land is eroded land usually caused by land degradation. Forests were areas entirely covered by trees. Due to insufficient knowledge in the historical extent of non-native plantation areas, we did not discriminate between natural tree cover and non-native tree plantations. Non-native types are mainly plantations of *Pinus* spp. and *Cupressus* spp. (Rahantaliou et al., 2011). For each class a set of training areas (forest, $n=24$; shrubland, $n=16$; grassland, $n=16$; barren land, $n=6$; cropland, $n=16$) were manually collected using the very high-resolution (VHR) satellite images archived in Google Earth and visual inspection of Landsat scenes using the existing expertise. These training areas were used as input in all classifications performed ($n=5$). In each classification, the input data was composed by the spectral bands of Landsat and the derivatives SAVI, NDVI ($n=8$). All operations were performed in python using the packages scikit-learn, gdal and numpy (contributors, 2020; Pedregosa, 2011).

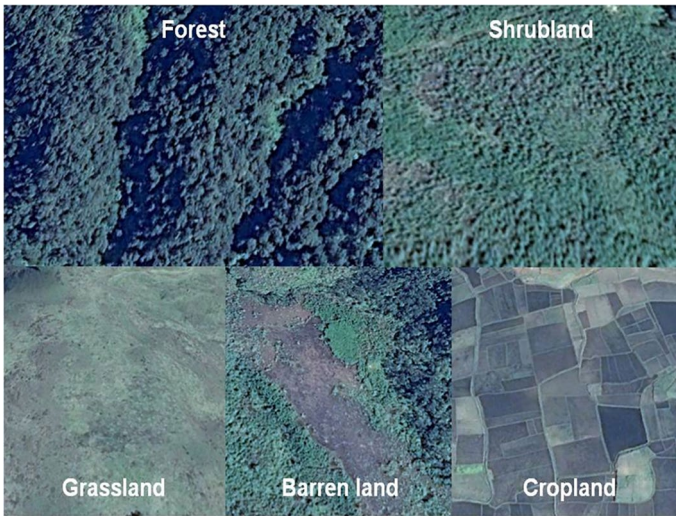


Fig. 2 Visual illustration of training areas defined for each land cover class during mapping between 1995 and 2016

2.5 Change analysis and accuracy assessment

Change analysis were performed to characterize land cover change over the Ankaratra massif. That combined post-classification comparison of maps with accuracy assessment according to the good practices protocol of Olofsson's (Olofsson et al., 2014). In specific, the post-classification comparison of maps identified the spatial changes in land cover between 1995–2005 and 2005–2016. For each time period, a change map with six classes was obtained: shrubland, grassland, forest, crop, forest loss and forest gain. Next, an accuracy assessment was undertaken according to the error matrix technique of Olofsson's et al. (2014) created error-adjusted change estimates. These estimates correct the mapped areas for the omission and commission errors found during the confrontation of mapped and reference class. To obtain the error-adjusted change estimates, we first applied a stratified random sampling over the change maps (i.e., 2005–2016) to create validation sites for each class (1995–2005, $n=253$; 2005–2016, $n=317$). The concordance between mapped and reference class was then verified using as source data the available high-resolution images in Google Earth. For each class, the sample size was determined as in Cochran (1963) and is provided in Online Resource 3. Using this information, error matrices were built, accuracy characterized, and error-adjusted area estimates with standard error and confidence interval (0.95) generated.

2.6 Analysis on the link between anthropogenic landscape change and amphibian diversity

The relationship between habitat change and amphibian diversity was analyzed through linear regression models. It was hypothesized that landscape change can affect amphibian diversity not only by reducing habitat area (i.e., habitat loss), but also by altering relevant functional

characteristics (i.e., habitat primary productivity, Riemann et al., 2017). It was also assumed that changes in the near surroundings of survey transects would be the most relevant to amphibian communities (Becker & Zamudio, 2011), and that historical habitat stability in endemic low-dispersal taxa may have an important role in biodiversity patterns (Graham et al., 2006). According to that, habitat change was measured by the predictor variables deforestation rate (% year⁻¹) and spatiotemporal variability of vegetation, represented by the standard deviation of NDVI (NDVI_std). Both variables are measured inside a 100 m circular buffer centered in each survey transect in the short-term (2011–2013, Online resource 4) and long-term time scales (1995–2013, Fig. 3). Deforestation is a main cause of habitat change in the survey plots and large deforestation rates are expected to present less amphibian diversity (Decena et al., 2020; Schneider-Maunoury et al., 2016). The NDVI is a satellite indirect proxy to primary productivity in ecosystems (Rocchini et al., 2016) and the NDVI along space and time can be used as a proxy for the stability of vegetation dynamics (Bonthoux et al., 2018; Nieto et al., 2015). Survey plots with less variation in the NDVI (lower NDVI_std) are expected to be associated with less spatial and temporal habitat instability favoring amphibian diversity. Deforestation rate in the long-term represents the averaged value inside the buffer plot in the time period 1995–2005, 2005–2011 and 2011–2013. Deforestation rate was estimated following Puyravaud (Eq. 1, 2003). In Eq. 1, r is the annual deforestation rate (in %/yr⁻¹), A_2 and A_1 are the forest cover at time 2 and time 1, and t_2-t_1 is the time interval (in years) between the two dates. For the extraction of forest cover inside each buffer plot, we used GIS analysis with the land cover layers of the years (1995, 2005, 2011, 2013). Species richness and microendemism rate were the response variables for biodiversity. All statistical analyses were performed in R version 4.1.2.

$$r = \left(\frac{1}{t_2 - t_1} \right) \ln \left(\frac{A_2}{A_1} \right) \times 100 \quad (1)$$

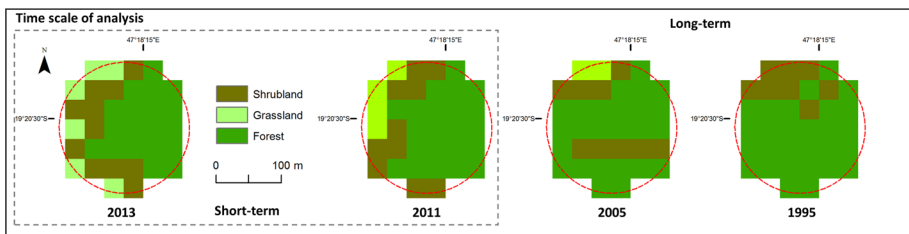


Fig. 3 Analytical framework used to assess the relationship between amphibian diversity–habitat change in the 100 m circular buffer surrounding the survey plots

3 Results

3.1 The land cover changes in the montane biodiversity hotspot of Ankaratra Massif

This study used error-adjusted change estimates to reconstruct the land cover dynamics in the Ankaratra Massif and understand how and at which rate landscape change in tropical montane biodiversity hotspots. The error-adjusted change estimates correct the mapped areas for the omission and commission errors found during the accuracy assessment (Fig. 4). The accuracy assessment based on the stratified estimators shows that land change maps were in general accurate. Overall accuracies varied between 0.82 and 0.86 (Tables 1 and 2). However, some classes registered low to moderate accuracy, thus supporting the decision of using error-adjusted change estimates to reconstruct the land cover dynamics. For the period 1995–2005, user’s accuracy was in the range 0.54–0.89. The lowest values were registered by the challenging classes of forest loss (0.64) and forest gain (0.57). All the remaining classes presented values >0.80, including the stable forest class (0.94). Most producer’s accuracy values were also >0.80, except for the class shrubland (0.55) and stable forest (0.66). This accuracy pattern also prevailed in the period 2005–2016, except for the stable forest (0.86) and forest loss (0.89) classes that increased producer’s and user’s accuracy, respectively. To what concern the importance of variables

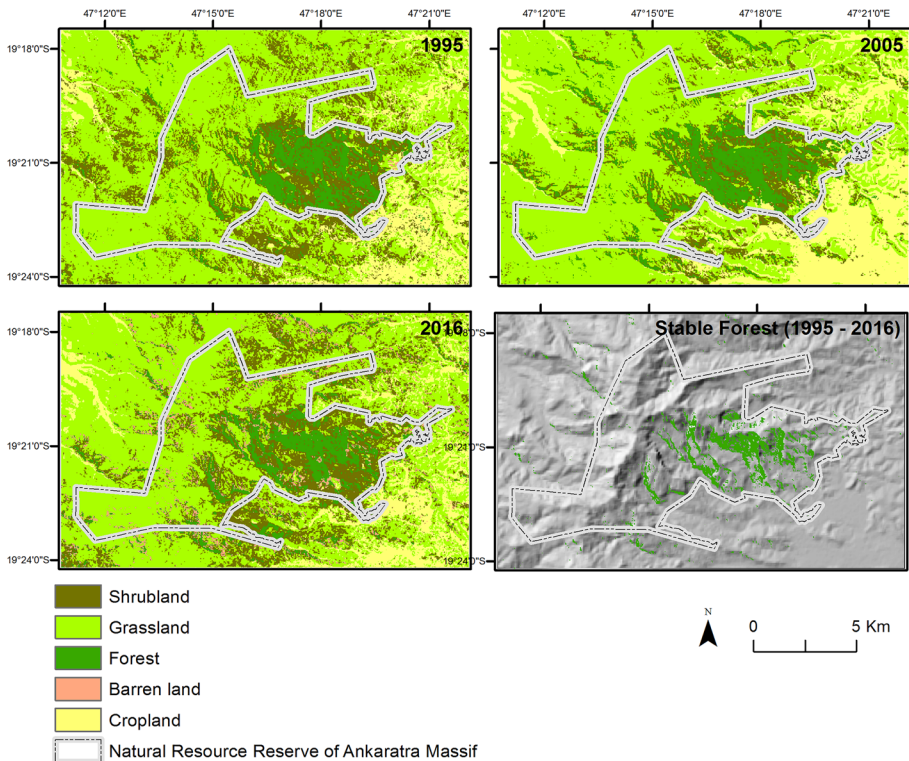


Fig. 4 Maps of land cover and stable forest area between 1995 and 2016 in the Ankaratra Massif

Table 1 Error matrix of land cover change maps for the two periods of analysis (1995–2005 and 2005–2016) based on the good practices protocol of Olofsson

1995–2005										
Reference										
Class	Shrubland	Grassland	Stable Forest	Cropland	Forest Loss	Forest Gain	Total	w_i	User's (%)	Producer's (%)
Predicted	24	3	0	0	0	0	27	0.11	0.89	0.55
	18	131	1	5	0	0	155	0.61	0.85	0.96
	0	1	15	0	0	0	16	0.06	0.94	0.66
	1	0	0	36	0	0	37	0.15	0.97	0.91
	0	0	3	0	7	1	11	0.04	0.64	1.00
	0	1	2	0	0	4	7	0.03	0.57	0.94
	43	136	21	41	7	5	253	1.00		
									Overall Accuracy	0.86
2005–2016										
Reference										
Class	Shrubland	Grassland	Stable Forest	Cropland	Forest Loss	Forest Gain	Total	w_i	User's (%)	Producer's (%)
Predicted	24	4	0	0	2	0	30	0.18	0.80	0.53
	15	162	2	16	2	0	197	0.57	0.82	0.95
	1	0	21	0	1	0	23	0.06	0.91	0.86
	1	4	0	35	1	0	41	0.13	0.85	0.51
	2	0	0	0	17	0	19	0.05	0.89	0.84
	0	2	1	0	1	3	7	0.02	0.43	1.00
	43	172	24	51	24	3	317	1.00		
									Overall Accuracy	0.82

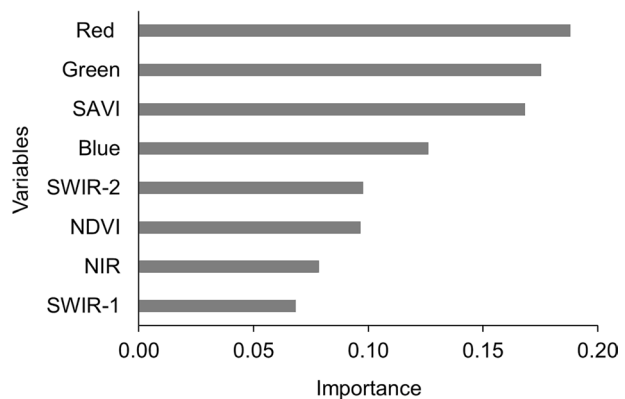
Table 2 Summary statistics for the variables considered to assess the links between habitat change and amphibian diversity in the biodiversity hotspot of Ankaratra Massif ($n=6$)

Time scale	Short-term (2013–2011)				Long-term (1995–2011)			
	Min	Mean	Max	SD	Min	Mean	Max	SD
Deforestation rate (% year ⁻¹)	-99.0	-38.3	-4.2	42.9	-33.2	-5.3	5.2	12.7
NDVI_std	0.03	0.05	0.09	0.03	0.03	0.04	0.08	0.01
Species richness	3	5	7	2	-	-	-	-
Microendemism rate (%)	17.4	62.7	94.5	28.0	-	-	-	-

during the classification, the Gini scores indicated the red (0.19) and green (0.18) bands of Landsat data and the vegetation index SAVI (0.17) as the most relevant (Fig. 5).

Regarding the land cover dynamics, the study period was shaped by extensive changes. A total of 4372.9 ± 594.6 ha, corresponding to 17.8% of the study area, experienced a change in land cover between 1995 and 2016, which pressured the already threatened forests, particularly in the second decade (Fig. 6a–b). The analysis showed that few remains from the tropical montane cloud forest landscape once described. In 2016, open areas covered by grasslands ($12,576.1 \pm 858.3$ ha) and cropland (3770.4 ± 465.6 ha) occupied the majority of landscape (66.8%, -5.2% relative to 1995). Grassland cover has remained relatively stable mainly by the transition of cropland into grassland areas (-0.01%, Fig. 6b). Cropland presents a dichotomous profile. It has expanded at a rate of 5.8% year⁻¹ in the period 1995–2005 (from 3114.3 to 4950.7 ha) and shrank by 2.8% between 2005 and 2016 (from 4950.7 to 3770.4 ha). Afforested areas were dominated by shrub formations that have been expanding in the last 20 years (+3.4% relative to 1995). Across the afforested areas a major concern is forest cover. Of the total forest area of the year 1995 (2062.7 ha), 21.5% was cleared by the 2016 (1618.3 ha). Forest cover changes presented though a bi-directional pattern. While in the period 1995–2005, forest had expanded at a rate of 2.0% year⁻¹ (from 2062.7 to 2524.8 ha), in the period of 2005–2016, a strong rate of reduction affected forest (-4.1% year⁻¹). Of the forest area present in 2016 (1618.3 ha), only a small fraction of forest remained spatially stable since 1995 (895 ha, Fig. 4). This may represent the last piece of tropical montane cloud forest in the Ankaratra montane biodiversity hotspot.

Fig. 5 Importance of predictor variables used in the random forests classification of land cover in the Ankaratra Massif, Madagascar. Variables are arranged by their importance for the classification, which was measured as the Gini importance or mean decrease impurity



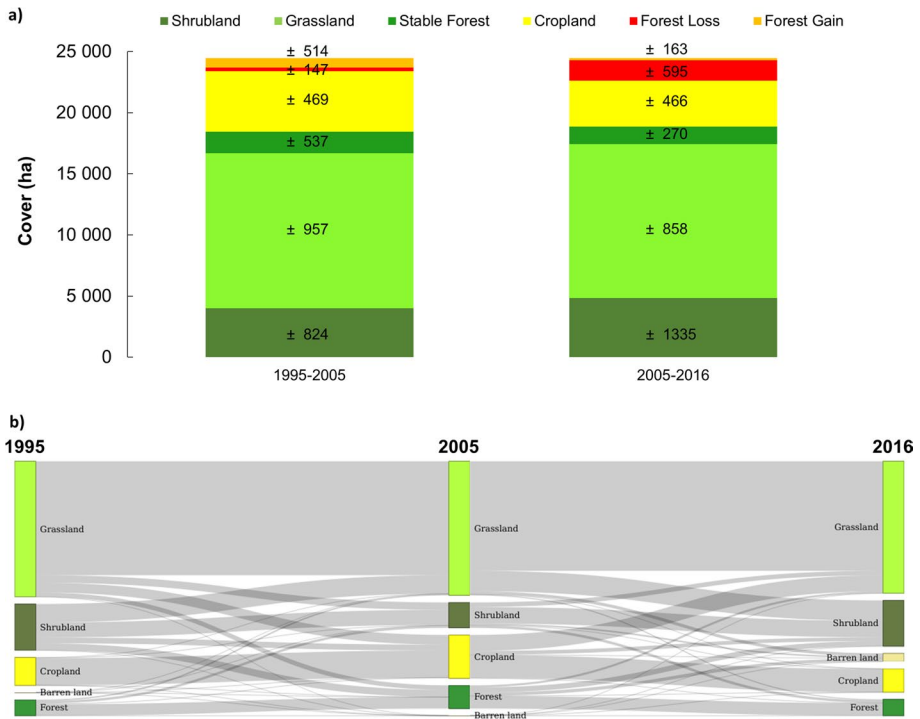


Fig. 6 **a** Land cover change areas with confidence interval for the period of 1995–2005 and 2005–2016. Errors bars are 95% confidence intervals based on standard errors estimated from the error matrix. **b** Sankey diagram of the land cover transitions from the year 1995 to 2016 using the land cover data

3.2 The links between anthropogenic landscape change and amphibian diversity

Nine out of the fifteen species of amphibians known to occur on the Ankaratra Massif (Andreone et al., 2014; Rahantaliola et al., 2011; Vences et al., 2002) were repeatedly found during the three years of survey (2011–2012), which was directed at stream-dwelling species (Online Resource Tables 1 and 2). The species accumulation curve showed that the more the sampling sites are, the higher the probability of sampling all amphibian species present in the study area will be (Fig. 7a). However, the curve did not reach a plateau and it would be relevant to increase the number of sampling sites in future surveys. Regarding the number of microendemic species found, the curve reached the plateau state at site 3 (Fig. 7b), meaning that surveying as few as three sampling sites between the 6 analyzed in this study is enough if the sole objective of the survey is to encounter *B. williamsi* and *M. pauliani*. Mean species richness amounted to 5 species and ranged from minimum of 3 to a maximum of 7 species (Table 2). The mean microendemism rate ranged from 17.4 to 94.5%.

The habitat change metrics (100 m buffers around plots) used to assess the relationship between habitat change and amphibian diversity varied considerable among sites and time scale of analysis (Table 2). In the short-term period (2011–2013), mean deforestation rate amounted to remarkable $-38.3\% \text{ year}^{-1}$ in forest cover inside the plots indicating forest loss as the main pattern. Maximum and minimum deforestation rates amounted to -99.0 and

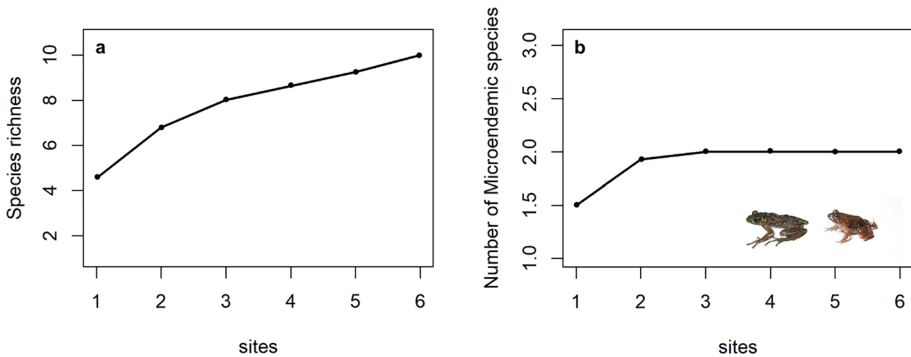


Fig. 7 Sample-based species accumulation curves. Species richness on the left and microendemic species on the right. Calculated using a random method, which subsamples the data without replacement, permutations = 100

$-4.2\% \text{ year}^{-1}$, respectively. When analyzed in the long-term period (1985–2013), the mean deforestation rate dropped drastically to $-5.3\% \text{ year}^{-1}$, but it still indicates forest loss as a the most prevalent feature. Similar pattern is present in the maximum ($-33.2\% \text{ year}^{-1}$) and minimum ($5.2\% \text{ year}^{-1}$) values. Minimum values indicate that forest cover has expanded in some sites between 1985 and 2013. To what concerns, NDVI_std, a proxy for spatiotemporal stability of vegetation dynamics, the values ranged from 0.03 (more spatial stable and homogeneous dynamics) to 0.09 (more spatially unstable and heterogeneous dynamics) in the short-term period. In the long-term, the values were just slightly lower for the maximum values (0.08).

The linear regression models identified a significant negative link between habitat change and amphibian diversity in the montane hotspot of the Ankaratra Massif (Fig. 8). This negative link occurred through the NDVI_std, a proxy for the spatiotemporal stability of vegetation dynamics usually associated to the functional attribute primary productivity in habitats. NDVI_std was strongly negatively related to species richness in the short-term ($R^2=0.91$, $p=0.003$) and long-term periods ($R^2=0.69$, $p=0.03$, Fig. 8c–d). Species richness increases where less spatiotemporal variability in NDVI has been registered in the short or long-term. Surprisingly, the linear model between species richness and deforestation rate was non-significant considering the short-term ($R^2=0.02$, $p=0.78$) or long-term periods ($R^2=0.48$, $p=0.12$, Fig. 8a–b). Thus, there was no significant effect of historical and recent deforestation rate on overall species richness. Counter to expectation, none of the models show a significant link of microendemism rate to the habitat change variables. Examination of the linear model intercept revealed no significant effect of short-term ($R^2=0.03$, $p=0.73$, Fig. 8a–b) or long-term ($R^2=0.001$, $p=0.86$) deforestation rates on the microendemism rate (Fig. 8e–g). No significant effects were also found for NDVI_stv in the short term ($R^2=0.10$, $p=0.54$, Fig. 8a–b) or long term ($R^2=0.001$, $p=0.86$).

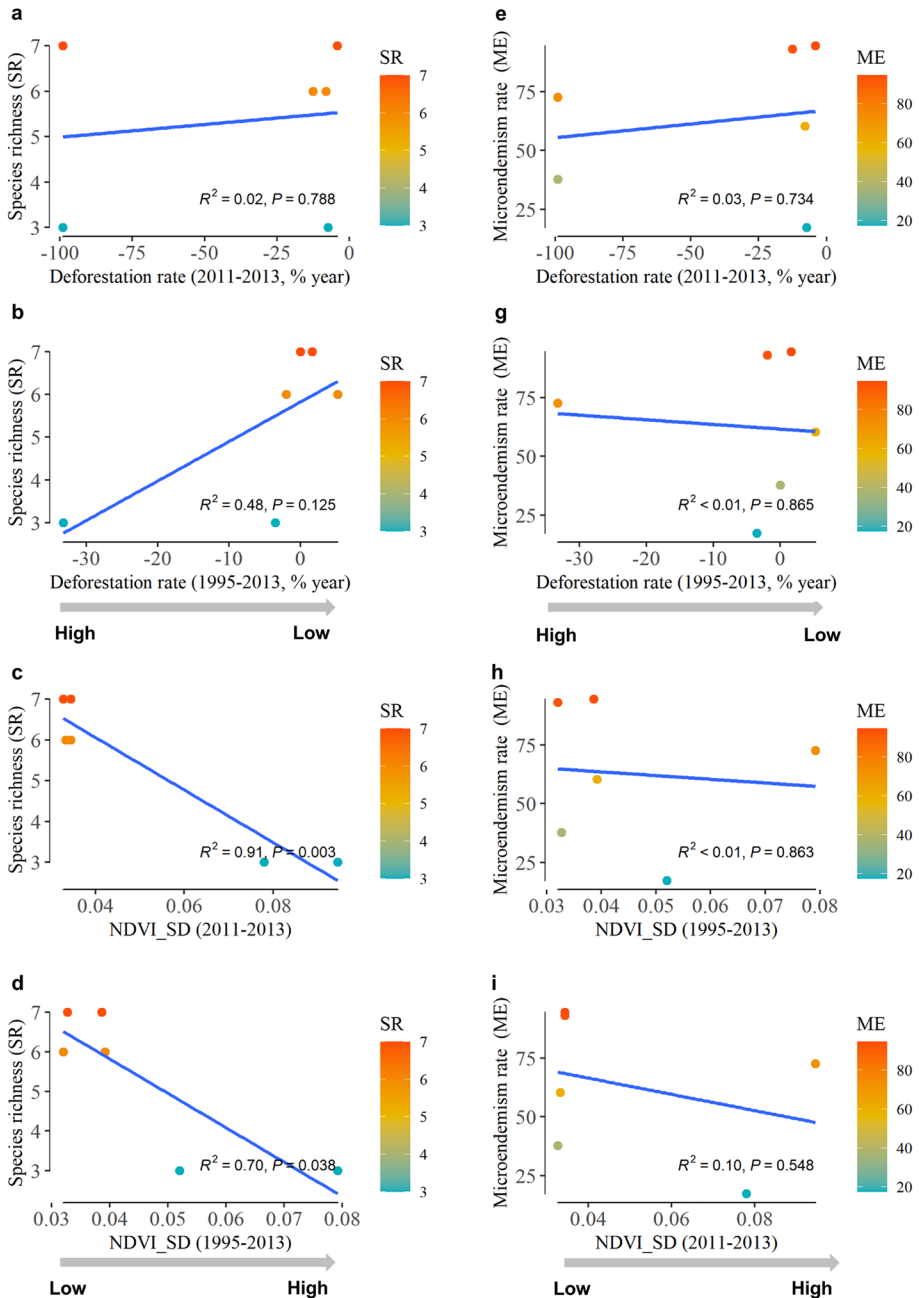


Fig. 8 Relationship between habitat change predictors (annual deforestation rate, % Year⁻¹; standard deviation of NDVI; NDVI_stdv) and measurements of amphibian richness and microendemism rate in the Ankaratra montane biodiversity hotspot. Relationship in the short-term (**a, c, e, g**) and long-term scale of analysis (**b, d, f, i**)

4 Discussion

4.1 Anthropogenic instability shaped the past 20 years of the Ankaratra montane biodiversity hotspot

This study used land cover analysis with error-adjusted area estimates based on Landsat satellite data to expand the knowledge existing for landscape change in African tropical montane biodiversity hotspots and cover the gap affecting the Ankaratra Massif that remained understudied in the previous studies (Yesuf et al., 2019) and ‘lock in’ in national (Vieilledent et al., 2018) and global assessments (Hu et al., 2021). The use of error-adjusted land cover estimates follows the best practices to discuss land cover change, particularly in tropical regions and when some uncertainty in map cover areas may exist (i.e., forest gain, Olofsson et al., 2014). The overall accuracy levels registered were in line with previous studies in montane contexts (Kidane et al., 2012; Los et al., 2021; Zhang et al., 2020) and as in other studies highlighted the difficulties in mapping forest changing classes (Leite et al., 2018). A time-series mapping approach (He et al., 2023) based on data cube technology can help to overcome such issues in future studies (Hamunyela et al., 2020). A standardized taxonomy and framework can be also valuable for better describing and understanding land cover change in African tropical montane biodiversity hotspots (Lucas et al., 2022).

Large landscape instability is a characteristic that prevailed in the analysis over the Ankaratra Massif. The rate of land cover change was almost two-fold the reported for biodiversity hotspots at global level (from 5 to 10% of the total hotspot area, Hu et al., 2021). The tropical montane cloud forest system once described (Kull, 2008) is closer to an agrosilvo-pastoral system in the recent times (1995–2016). The shift from a natural assembled into more anthropogenic-oriented landscape has been also found in other African montane biodiversity hotspots like the scarp forests of Angola (Leite et al., 2018), Bioko mountains in the Gulf of Guinea (Cronin et al., 2014), or in Eastern Arc Mountains of Tanzania (Hamunyela et al., 2020) and Bale mountains in Ethiopia (Cronin et al., 2014). It is also in line with the narrative that anthropogenic landscape change is modifying tropical montane systems globally (Crausbay et al., 2015; Soh et al., 2019), including island montane biodiversity hotspots as the one analyzed in the present study.

Among the changes, those associated with cropland and forest cover can have particular implications for montane biodiversity hotspots. Grasslands, covering approximately 60% of the study area, was the most stable land cover type in areal terms across the period of analysis. This class dominates the higher altitude plains (above 2000 m a.s.l.) and is likely to occur naturally (Vorontsova et al., 2016). Contrary to studies in other African montane biodiversity hotspots, agricultural area unexpectedly reduced between 1995 and 2016 (Kidane et al., 2012; Leite et al., 2018). This decline may be explained by an intensification of farming in the lowlands for rice and potato production, the reduction of cropping in highlands and the effects of the arsons that occurred between 2010 and 2015 (Falitiana Rabemananjara, personal communication). This reduction differs also from the agricultural narrative in drought years proposed by Desbureaux and Damania (2018) that suggested the expansion of cropland at the expenses of forest as a strategy to cope with droughts in Madagascar between 2000 and 2013. Over our montane biodiversity hotspot, shrink cropland was the strategy. Of particular concern to forest cover are the high deforestation rates and the transitions “forest-to-shrubland” after 2005. These transitions were recently identified as a proxy for forest degradation in biodiversity hotspots in a global assessment (Hu et al., 2021), and it may indicate that in addition to forest loss, degradation is also

a process shaping the remaining forests of Ankaratra Massif. From 1995 to 2005, there has been a rapid recovery of forest cover, resulting possibly from the local management of forest by a ‘federation of villagers’ associations, the Union Forestière d’Ambatolampy (UFA), which in 1998 signed a 20-year contract to manage Ankaratra. This agreement was suspended in 2007 (Amphibian Survival Alliance & Amphibian Specialist Group, 2010). "Shrubland-to-forest" transitions were seen between 1995 and 2005. Through the perspective of the literature on biodiversity hotspots (Hu et al., 2021), these changes would represent the development of young trees in 1995 into more largely and densely grown mature trees in 2016. This positive indicator was, however, severely interrupted in 2005 and forest loss has accelerated since there. This bidirectional pattern (forest expansion followed by forest decline) follows the previous findings for Madagascar (Vieilledent et al., 2018) that indicated the progressive increase of annual deforestation rates since 2005.

Our deforestation rates ($-4.1\% \text{ year}^{-1}$) were almost fourfold the reported for Madagascar at national level ($-1.1\% \text{ year}^{-1}$, Vieilledent et al., 2018), 1.7 times higher than that suggested to Bioko montane forests in the Gulf of Guinea ($-2.4\% \text{ ha year}^{-1}$, Cronin et al., 2014), and just slightly lower than that found in the scarp forests of Angola ($-4.6\% \text{ year}^{-1}$, Leite et al., 2018). This severe trend of deforestation may be in part related to the economic exploitation of pine-trees that have a turnover of about 20 years (Townsend et al., 2001) and to the turbulent political events that took place in the island during the last decade. The “coup d’état in” 2009 boosted a period of severe illegal exploitation of forested areas and bush fire intensification across the whole of Madagascar (Barrett et al., 2010). Overall, the magnitude of changes found in this biodiversity hotspot of Madagascar highlands suggests that region-specific assessments are highly necessary in the context of the African tropical change narrative (Ralimanana et al., 2022). These are extremely valuable in view of conservation policies tailored for local conditions (Yesuf et al., 2019). National assessments are masking rates of deforestation and land conversion that are unsustainable for the role of montane biodiversity hotspots (He et al., 2023). To reduce deforestation and land conversion rates is urgent.

4.2 Habitat change matters to biodiversity in the montane hotspots of Madagascar

Understanding the link between anthropogenic landscape change and biodiversity is necessary to identify ecological regulators, anticipate their effect on the composition of species communities and ultimately conserve biodiversity (Cabello et al., 2012). Safeguarding the biodiversity of the tropical montane forests of Madagascar highlands is a multipurpose need, which includes the basic human health of Malagasy communities as demonstrated by Golden et al. (2011). Our study used the amphibian diversity to progress in this regard. The sampling size is a limitation, but to some extent, it mirrors the difficulty of surveying and generate the knowledge in montane tropical systems. The repeated sampling strategy used helps however to deliver a more consistent overview of patterns with respect to the common single or short-time assessments (Muluvhahotho et al., 2021).

We found a significant association between habitat change and amphibian diversity, but only for species richness and on behalf the change in the NDVI_std. Surprisingly, we did not find a link between microendemism rates and any of the habitat change metrics selected. These results reject our hypothesis of a major role of deforestation rates in amphibian diversity and highlight the need of evaluate other habitat change metrics, particularly for the amphibian microendemism rates. This would not be possible in this study due the small sample size. Species richness was negatively linked to habitat change in the immediate surrounding of survey plots (100 m

buffer), namely with changes that increase spatiotemporal variability in the NDVI (NDVI_std). Survey plots with less spatiotemporal variability in the NDVI presented large species richness values. This result emphasizes the role of stability in vegetation dynamics for amphibian diversity (Bonthoux et al., 2018; Nieto et al., 2015). This finding follows previous studies that also identified a strong relationship between energy/productivity of ecosystems proxy by the NDVI and species richness of different taxa (Coops et al., 2018; Fricker et al., 2015; Nieto et al., 2015; Suttidate et al., 2019). It also aligns with Buckley and colleagues (2007) that defined energy supply in ecosystems as the major driver for amphibian species richness if a single factor have to be mentioned. The negative link follows Toszogyova and Storch (2019) that in a global assessment with different taxa (including amphibians) found that high variation in productivity/energy (represented by the NDVI) has a negative effect on species richness in regions with moderate to high productivity levels. Such conditions prevail in our montane biodiversity hotspot. While we did not find an association between deforestation rates and richness, literature shows that amphibian species richness was significantly higher in old-growth forest than in all other land-use types in Madagascar (Fulgence et al., 2022). However, species composition more than species richness tends to vary with deforestation. Literature suggests that the presence of streams is more important for high species richness than the forest fragmentation status (Riemann et al., 2015). This also happened in the tropical forests of the Philippines, where amphibian abundance was noticeably higher in both forest and stream habitat, but species richness was similar regardless of the type of habitat change (Decena et al., 2020).

The lack of a link between microendemism rates and any of the habitat change metrics selected was surprising, because literature evidenced that habitat change via forest loss and deforestation is threatening endemism. Hedge et al. (2018) based on surveys of vertebrates in mountain tops suggested that endemic species have been lost with forest loss. The apparent extinction in insects in Madagascar was also related to forest loss within the historical range of the focal species (Hanski et al., 2007). Wollenberg et al. (2008) emphasized the need to establish larger protected areas covered by significant amounts of primary vegetation to safeguard the endemism patterns of Madagascar. Regarding the relationship between endemism and NDVI, the literature and unclear. Some studies described a relative low contribution of NDVI in explaining endemic plant or animal species over temperate (Mendoza-Fernández et al., 2022) or tropical mountains (Ran, 2018), respectively. Other reported that threatened plants tended to be placed in area with less change in NDVI irrespective of the habitat (Matas-Granados et al., 2022), emphasizing the role of habitat stability. Further research is needed to understand how endemic species respond to habitat change, namely by evaluating other predictors at different spatial scales (i.e., habitat quality metrics) and by expanding the sampling size. Overall, habitat change effects on amphibians were mostly detected in species richness and mainly through the alteration of the habitat functional attributes. The satellite NDVI_std can be a relevant indirect metric for monitoring such effect in montane biodiversity hotspots. Habitat reduction via deforestation rates has no support to explain amphibian diversity at local scale (100 m buffers).

4.3 Insights for conservation in the Ankaratra Massif biodiversity hotspot

Having monitored landscape dynamics and their link with amphibian diversity in the Ankaratra montane biodiversity hotspot, we point out the necessity of reduce the rates of land cover conversion. Nearly one-fifth of landscape changed in only two decades. Of high priority are the conversions affecting forest and the last remnants of Tropical Montane Cloud Forests (~900 ha). These alterations have multiple impacts, including in

the quality of upland water resources (Bruijnzeel & Proctor, 1995) and quantity of stream flow (Vågen et al., 2006), that will impact not only the amphibians but also the availability of water for drinking and farming in the Ankaratra community (Rakotozafy, 2017). Forest conversion was lower in the period where local community was involved. It is therefore crucial to achieve a community-involved strategic development plan that engages citizens to reduce deforestation and land conversion rates. In line with the Malagasy Government's commitment to meet the AFR100 goals (the African Forest Landscape Restoration Initiative, <http://afr100.org/content/madagascar>), a plans that consider also local livelihoods and well-being, including cultural dimensions, would be more successful (Llopis et al., 2021). In this framework it is valuable to consider the importance of secondary tropical forests to restore the functional attributes of old-growth forests (DeWalt et al., 2003) and also address the “forest-to-shrubland” transitions, which are a sign of forest degradation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10668-023-04187-9>.

Acknowledgements This work was supported by the Portuguese FCT – Fundação para a Ciência e Tecnologia in the framework of: ATM Junior researcher contract DL57/2016/CP1442/CP0005 and funding attributed to CEG-IGOT Research Unit (UIDB/00295/2020 and UIDP/00295/2020); Exploratory Research Project (IF/00209/2014/CP1256/CT0011), FCT Investigator grant (IF/00209/2014) of AC and 2020.00823. CEECIND/CP1601/CT0003 research contract of AC. We are grateful to the Malagasy authorities, in particular the Ministère de l'Environnement et des Forêts (now Ministère de l'Environnement et du Développement Durable) through Direction Général des Forêts et de l'Environnement, for issuing research permits, and the local NGO VIF that manage the site. We extend our thanks to Emilio Civantos, Walter Cocca, Bárbara Santos, Francesco Belluardo, Fulvio Licata for their fruitful comments on the interpretation of the results. Fieldwork was financially supported by Conservation International Foundation (Conservation Grants Number: 66355); this work was supported by Amphibian Survival Alliance and by the Critical Ecosystem Partnership Fund (grant number MAD-65823).

Funding Open access funding provided by FCTIFCCN (b-on).

Data availability The manuscript has data included as electronic supplementary material. Additional datasets created during and/or analyzed during the current study are available from the corresponding author on request.

Declarations

Conflict of interest Authors declare no competing interests affecting directly or indirectly the work submitted for publication.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Andreone, F., Cadle, J. E., Cox, N., Glaw, F., Nussbaum, R. A., Raxworthy, C. J., & Vences, M. (2005). Species review of amphibian extinction risks in Madagascar: Conclusions from the global amphibian assessment. *Conservation Biology*, 19(6), 1790–1802. <https://doi.org/10.1111/j.1523-1739.2005.00249.x>

- Andreone, F., Crottini, A., Rabemananjara, F. C. E., Randrianirina, J. E., Razafindrabe, T., & Tessa, G. (2014). Age structure, population estimate and Bd-status of two Critically Endangered frogs from the Ankaratra Massif (Madagascar), *Boophis williamsi* and *Mantidactylus pauliani* (Amphibia: Mantellidae). *Scripta Herpetologica*, 17–29.
- Andrianarivelo, M. H., Rakotondrafara, A., Rakotosaona, R., Rakotoarimanana, V., Rakotonirina, C., Ratsiarivelo, J., & Richard, R. S. (2021). Medicinal Plants from the Ankaratra Mountain In Madagascar: Diversity and Uses.
- Appiah, M., Blay, D., Damnyag, L., Dwomoh, F. K., Pappinen, A., & Luukkanen, O. (2009). Dependence on forest resources and tropical deforestation in Ghana. *Environment, Development and Sustainability*, 11(3), 471–487. <https://doi.org/10.1007/s10668-007-9125-0>
- Barbier, N. (2021). African tropical montane forests store more carbon than was thought. *Nature*, 596(7873), 488–490. <https://doi.org/10.1038/d41586-021-02266-3>
- Barrett, M. A., Brown, J. L., Morikawa, M. K., Labat, J.-N., & Yoder, A. D. (2010). CITES designation for endangered rosewood in Madagascar. *Science*, 328(May), 1109–1111. <https://doi.org/10.1126/science.1187740>
- Becker, C. G., Fonseca, C. R., Haddad, C. F., Batista, R. F., & Prado, P. I. (2007). Habitat split and the global decline of amphibians. *Science*, 318(5857), 1775–1777. <https://doi.org/10.1126/science.1149374>
- Becker, C. G., & Zamudio, K. R. (2011). Tropical amphibian populations experience higher disease risk in natural habitats. *Proceedings of the National Academy of Sciences*, 108(24), 9893–9898. <https://doi.org/10.1073/pnas.1014497108>
- Blicharska, M., Smithers, R. J., Mikusiński, G., Rönnbäck, P., Harrison, P. A., Nilsson, M., & Sutherland, W. J. (2019). Biodiversity's contributions to sustainable development. *Nature Sustainability*, 2(12), 1083–1093. <https://doi.org/10.1038/s41893-019-0417-9>
- Bonthoux, S., Lefèvre, S., Herrault, P.-A., & Sheeren, D. (2018). Spatial and temporal dependency of NDVI satellite imagery in predicting bird diversity over france. *Remote Sensing*, 10(7), 1136.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45(1), 5–32. <https://doi.org/10.1023/A:1010933404324>
- Brujinzeel, L. A., & Proctor, J. (1995). Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In L. S. Hamilton, J. O. Juvik, & F. N. Skatena (Eds.), (Vol. 110, pp. 38–78). Springer. <https://doi.org/10.1007/978-1-4612-2500-3>
- Buckley, L. B., & Jetz, W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society. Biological Sciences*, 274(1614), 1167–1173. <https://doi.org/10.1098/rspb.2006.0436>
- Burney, D. A. (1996). Climate change and fire ecology as factors in the quaternary biogeography of Madagascar. *Biogéographie de Madagascar*, 49–58.
- Cabello, J., Fernández, N., Alcaraz-Segura, D., Oyonarte, C., Piñeiro, G., Altesor, A., & Paruelo, J. M. (2012). The ecosystem functioning dimension in conservation: Insights from remote sensing. *Biodiversity and Conservation*, 21(13), 3287–3305. <https://doi.org/10.1007/s10531-012-0370-7>
- Cáceres, A., Melo, M., Barlow, J., Cardoso, P., Maiato, F., & Mills, M. S. L. (2014). Threatened birds of the Angolan Central Escarpment: Distribution and response to habitat change at Kumbira Forest. *Oryx*, 49(4), 727–734. <https://doi.org/10.1017/S0030605313001415>
- CEPF. (2014). *Ecosystem profile Madagascar and Indian Ocean Islands. Final report to the Donor Council*.
- Christmann, T., & Menor, I. O. (2021). A synthesis and future research directions for tropical mountain ecosystem restoration. *Scientific Reports*, 11(1), 23948. <https://doi.org/10.1038/s41598-021-03205-y>
- Cochran, W. G. (1963). *Sampling techniques*. John Wiley and Sons Inc.
- contributors, G. O. (2020). GDAL/OGR Geospatial data abstraction software library. In *Open Source Geospatial Foundation*. <https://gdal.org>
- Coops, N. C., Rickbeil, G. J. M., Bolton, D. K., Andrew, M. E., & Brouwers, N. C. (2018). Disentangling vegetation and climate as drivers of Australian vertebrate richness. *Ecography*, 41, 1147–1160. <https://doi.org/10.1111/ecog.02813>
- Crausbay, S. D., Martin, P. H., & Kelly, E. F. (2015). Tropical montane vegetation dynamics near the upper cloud belt strongly associated with a shifting ITCZ and fire. *Journal of Ecology*, 103(4), 891–903. <https://doi.org/10.1111/1365-2745.12423>
- Cronin, D. T., Libalah, M. B., Bergl, R. A., & Hearn, G. W. (2014). Biodiversity and conservation of tropical montane ecosystems in the Gulf of Guinea, West Africa. *Arctic, Antarctic, and Alpine Research*, 46(4), 891–904. <https://doi.org/10.1657/1938-4246-46.4.891>
- Crowley, H. (2000a). Montane grasslands and shrublands: Madagascar. In

- Crowley, H. (2000b). Tropical and subtropical moist broadleaf forests. Southern Africa: Central Madagascar. In.
- Decena, S. C. P., Avorque, C. A., Decena, I. C. P., Asis, P. D., & Paclé, B. (2020). Impact of habitat alteration on amphibian diversity and species composition in a lowland tropical rainforest in Northeastern Leyte, Philippines. *Scientific Reports*, *10*(1), 10547. <https://doi.org/10.1038/s41598-020-67512-6>
- Desbureaux, S., & Damania, R. (2018). Rain, forests and farmers: Evidence of drought induced deforestation in Madagascar and its consequences for biodiversity conservation. *Biological Conservation*, *221*, 357–364. <https://doi.org/10.1016/j.biocon.2018.03.005>
- DeWalt, S. J., Maliakal, S. K., & Denslow, J. S. (2003). Changes in vegetation structure and composition along a tropical forest chronosequence: Implications for wildlife. *Forest Ecology and Management*, *182*(1–3), 139–151. [https://doi.org/10.1016/S0378-1127\(03\)00029-X](https://doi.org/10.1016/S0378-1127(03)00029-X)
- Fricker, G. A., Wolf, J. A., Saatchi, S. S., & Gillespie, T. W. (2015). Predicting spatial variations of tree species richness in tropical forests from high-resolution remote sensing. *Ecological Applications*, *25*(7), 1776–1789. <https://doi.org/10.1890/14-1593.1>
- Fulgence, T. R., Martin, D. A., Randriamanantena, R., Botra, R., Befidimanana, E., Osen, K., & Ratsoavina, F. M. (2022). Differential responses of amphibians and reptiles to land-use change in the biodiversity hotspot of north-eastern Madagascar. *Animal Conservation*, *25*(4), 492–507. <https://doi.org/10.1111/acv.12760>
- Glaw, F., & Vences, M. (2007). *A Fieldguide to the Amphibians and Reptiles of Madagascar* (3rd ed.).
- Golden, C. D., Fernald, L. C. H., Brashares, J. S., Rasolofoniaina, B. J. R., & Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proceedings of the National Academy of Sciences*, *108*(49), 19653–19656. <https://doi.org/10.1073/pnas.1112586108>
- Graham, C. H., Moritz, C. A., & Williams, S. E. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences*, *103*(3), 632–636. <https://doi.org/10.1073/pnas.0505754103>
- Group, I. S. A. S. (2019a). *Boophis williamsi*. The IUCN Red List of Threatened Species 2019: e.T57435A84165560. In.
- Group, I. S. A. S. (2019b). *Mantidactylus pauliani*. The IUCN Red List of Threatened Species 2019: e.T57509A84175039. In.
- Habel, J. C., Rasche, L., Schneider, U. A., Engler, J. O., Schmid, E., Rödder, D., & Stork, N. E. (2019). Final countdown for biodiversity hotspots. *Conservation Letters*, *12*(6), e12668. <https://doi.org/10.1111/conl.12668>
- Hamunyela, E., Brandt, P., Shirima, D., Do, H. T. T., Herold, M., & Roman-Cuesta, R. M. (2020). Space-time detection of deforestation, forest degradation and regeneration in montane forests of Eastern Tanzania. *International Journal of Applied Earth Observation and Geoinformation*, *88*, 102063. <https://doi.org/10.1016/j.jag.2020.102063>
- Hanski, I., Koivulehto, H., Cameron, A., & Rahagalala, P. (2007). Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters*, *3*(3), 344–347. <https://doi.org/10.1098/rsbl.2007.0043>
- He, X., Ziegler, A. D., Elsen, P. R., Feng, Y., Baker, J. C. A., Liang, S., & Zeng, Z. (2023). Accelerating global mountain forest loss threatens biodiversity hotspots. *One Earth*, *6*(3), 303–315. <https://doi.org/10.1016/j.oneear.2023.02.005>
- Hedges, S. B., Cohen, W. B., Timyan, J., & Yang, Z. (2018). Haiti's biodiversity threatened by nearly complete loss of primary forest. *Proceedings of the National Academy of Sciences*, *115*(46), 11850–11855. <https://doi.org/10.1073/pnas.1809753115>
- Hirschfeld, M., Blackburn, D. C., Doherty-Bone, T. M., Gonwouo, L. N., Ghose, S., & Rödel, M.-O. (2016). Dramatic declines of montane frogs in a Central African biodiversity hotspot. *PLoS ONE*, *11*(5), e0155129–e0155129. <https://doi.org/10.1371/journal.pone.0155129>
- Hu, X., Huang, B., Veronesi, F., Cavalett, O., & Cherubini, F. (2021). Overview of recent land-cover changes in biodiversity hotspots. *Frontiers in Ecology and the Environment*, *19*(2), 91–97. <https://doi.org/10.1002/fee.2276>
- Huang, S., Tang, L., Hupy, J. P., Wang, Y., & Shao, G. (2021). A commentary review on the use of normalized difference vegetation index (NDVI) in the era of popular remote sensing. *Journal of Forestry Research*, *32*(1), 1–6. <https://doi.org/10.1007/s11676-020-01155-1>
- Huete, A. R. (1988). A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment*, *25*, 295–309. [https://doi.org/10.1016/0034-4257\(88\)90106-X](https://doi.org/10.1016/0034-4257(88)90106-X)
- IUCN. (2019). The IUCN Red List of Threatened Species. Version 2019–2. In.
- Jenkins, M. D. (1987). *Madagascar, an environmental profile*. International Union for Conservation of Nature and Natural Resources.

- Kidane, Y., Stahlmann, R., & Beierkuhnlein, C. (2012). Vegetation dynamics, and land use and land cover change in the Bale Mountains, Ethiopia. *Environmental Monitoring and Assessment*, 184(12), 7473–7489. <https://doi.org/10.1007/s10661-011-2514-8>
- Koskikala, J., Kukkonen, M., & Käyhkö, N. (2020). Mapping natural forest remnants with multi-source and multi-temporal remote sensing data for more informed management of global biodiversity hotspots. *Remote Sensing*, 12(9), 1429.
- Kull, C. A. (2008). Saving land with a spade: Human landscape transformations in the Madagascar highlands. In J. C. Kaufmann (Ed.), (pp. 113–135). Africa Institute of South Africa.
- Kwok, R. (2018). Ecology's remote-sensing revolution. *Nature*, 556, 137–138.
- Leite, A., Cáceres, A., Melo, M., Mills, M. S. L., & Monteiro, A. T. (2018). Reducing emissions from Deforestation and forest Degradation in Angola: Insights from the scarp forest conservation 'hot-spot.' *Land Degradation & Development*, 29(12), 4291–4300. <https://doi.org/10.1002/ldr.3178>
- Llopis, J. C., Chastonay, J. F., Birrer, F. C., Bär, R., Andriatsitohaina, R. N. N., Messerli, P., & Zaehring, J. G. (2021). Year-to-year ecosystem services supply in conservation contexts in north-eastern Madagascar: Trade-offs between global demands and local needs. *Ecosystem Services*, 48, 101249. <https://doi.org/10.1016/j.ecoser.2021.101249>
- Los, S. O., Street-Perrott, F. A., Loader, N. J., & Froyd, C. A. (2021). Detection of signals linked to climate change, land-cover change and climate oscillators in Tropical Montane Cloud Forests. *Remote Sensing of Environment*, 260, 112431. <https://doi.org/10.1016/j.rse.2021.112431>
- Lucas, R. M., German, S., Metternicht, G., Schmidt, R. K., Owers, C. J., Prober, S. M., & Horton, C. (2022). A globally relevant change taxonomy and evidence-based change framework for land monitoring. *Global Change Biology*, 28(21), 6293–6317. <https://doi.org/10.1111/gcb.16346>
- Matas-Granados, L., Pizarro, M., Cayuela, L., Domingo, D., Gómez, D., & García, M. B. (2022). Long-term monitoring of NDVI changes by remote sensing to assess the vulnerability of threatened plants. *Biological Conservation*, 265, 109428. <https://doi.org/10.1016/j.biocon.2021.109428>
- Mendoza-Fernández, A. J., Fernández-Ceular, Á., Alcaraz-Segura, D., Ballesteros, M., & Peñas, J. (2022). The fate of endemic species specialized in island habitat under climate change in a mediterranean high mountain. *Plants*, 11(23), 3193.
- Muluvhahotho, M. M., Joseph, G. S., Seymour, C. L., Munyai, T. C., & Foord, S. H. (2021). Repeated surveying over 6 years reveals that fine-scale habitat variables are key to tropical mountain ant assemblage composition and functional diversity. *Science and Reports*, 11(1), 56. <https://doi.org/10.1038/s41598-020-80077-8>
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Nieto, S., Flombaum, P., & Garbulsky, M. F. (2015). Can temporal and spatial NDVI predict regional bird-species richness? *Global Ecology and Conservation*, 3, 729–735. <https://doi.org/10.1016/j.gecco.2015.03.005>
- Norman, M. (2003). Biodiversity hotspots revisited. *BioScience*, 53(10), 916–917. [https://doi.org/10.1641/0006-3568\(2003\)053\[0916:bhrj2.0.co;2](https://doi.org/10.1641/0006-3568(2003)053[0916:bhrj2.0.co;2)
- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P., & Schneeweiss, G. M. (2018). Hotspots within a global biodiversity hotspot—Areas of endemism are associated with high mountain ranges. *Scientific Reports*, 8(1), 10345. <https://doi.org/10.1038/s41598-018-28504-9>
- Olofsson, P., Foody, G. M., Herold, M., Stehman, S. V., Woodcock, C. E., & Wulder, M. A. (2014). Good practices for estimating area and assessing accuracy of land change. *Remote Sensing of Environment*, 148, 42–57. <https://doi.org/10.1016/j.rse.2014.02.015>
- Panuju, D. R., Paull, D. J., & Griffin, A. L. (2020). Change detection techniques based on multispectral images for investigating land cover dynamics. *Remote Sensing*, 12(11), 1781.
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau, D., Brucher, M., Perrot, M., & Duchesnay, E. (2011). Scikit-learn: Machine learning in Python. *Jmlrjournal of Machine Learning Research*, 12, 2825–2830.
- Pettorelli, N., Schulte to Bühne, H., Tulloch, A., Dubois, G., Macinnis-Ng, C., Queirós, A. M., & Nicholson, E. (2018). Satellite remote sensing of ecosystem functions: Opportunities, challenges and way forward. *Remote Sensing in Ecology and Conservation*, 4(2), 71–93. <https://doi.org/10.1002/rse2.59>
- Puyravaud, J. P. (2003). Standardizing the calculation of the annual rate of deforestation. *Forest Ecology and Management*, 177(1–3), 593–596. [https://doi.org/10.1016/S0378-1127\(02\)00335-3](https://doi.org/10.1016/S0378-1127(02)00335-3)
- Rabemananjara, F. C. E., Randriamahazo, H., Rahantamalala, J., Rahantalisoa, H., Rakotoarisoa, J. M., Rabibisoa, N. H. C., & Andreone, F. (2012). The conservation effort for two Critically Endangered

- amphibian species of the Ankaratra Massif, *Boophis williamsi* and *Mantidactylus pauliani*. *FrogLog*, 29–31.
- Rabemananjara, F. C. E., Randrianirina, J. E., Randriambahinirime, M. O., Randrianasolo, T., Razafindrabe, J., Andreone, F., & Rabibisoa, N. H. C. (2011). Brief note on the most threatened Amphibian species from Madagascar: *Boophis williamsi* (CR) and *Mantidactylus pauliani* (CR) in Ankaratra massif, Madagascar. *FrogLog*, 38–38.
- Rahantalihoa, H., Rakotomalala, M., Rabemananjara, F. C. E., Rahantamalala, J., & Rabibisoa, N. H. C. (2011). Ankaratra massif: Highland focal amphibian site for conservation. *FrogLog*, 36–37.
- Rakotozafy, S. (2017). Conducting Research in The Misty Mountain Cold Forest of Madagascar! In.
- Ralimanana, H., Perrigo, A. L., Smith, R. J., Borrell, J. S., Faurby, S., Rajaonah, M. T., & Antonelli, A. (2022). Madagascar's extraordinary biodiversity: Threats and opportunities. *Science*, 378(6623), eadf1466. <https://doi.org/10.1126/science.adf1466>
- Ran. (2018). Predicting suitable distribution for an endemic, rare and treated species (Grey-shanked douc landrug, *Pygathrix cinerea* Nadler, 1997) using Maxent Model. *Applied Ecology and Environmental Research* 2018 (Vol. 16, No. 2, pp.1275–1291 ref.49).
- Ranarilalantiana, T., Razafindralava, H. A., Granath, G., Bukontaite Malm, R., Rakotonirina, J. C., Razafindranaivo, V., & Bergsten, J. (2022). Remaining forests on the Central Highlands of Madagascar—Endemic and endangered aquatic beetle fauna uncovered. *Ecology and Evolution*, 12(12), e9580. <https://doi.org/10.1002/ece3.9580>
- Raxworthy, C. J., & Nussbaum, R. A. (1996). Montane amphibian and reptile communities in Madagascar. *Conservation Biology*, 10(3), 750–756. <https://doi.org/10.1046/j.1523-1739.1996.10030750.x>
- Razgour, O., Kasso, M., Santos, H., & Juste, J. (2021). Up in the air: Threats to Afromontane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evolutionary Applications*, 14(3), 794–806. <https://doi.org/10.1111/eva.13161>
- Riemann, J. C., Ndriantsoa, S. H., Raminosoa, N. R., Rödel, M.-O., & Glos, J. (2015). The value of forest fragments for maintaining amphibian diversity in Madagascar. *Biological Conservation*, 191, 707–715. <https://doi.org/10.1016/j.biocon.2015.08.020>
- Riemann, J. C., Ndriantsoa, S. H., Rödel, M.-O., & Glos, J. (2017). Functional diversity in a fragmented landscape—Habitat alterations affect functional trait composition of frog assemblages in Madagascar. *Global Ecology and Conservation*, 10(10), 173–183. <https://doi.org/10.1016/j.gecco.2017.03.005>
- Roberts, P., Hamilton, R., & Piperno, D. R. (2021). Tropical forests as key sites of the “Anthropocene”: Past and present perspectives. *Proceedings of the National Academy of Sciences*, 118(40), e2109243118. <https://doi.org/10.1073/pnas.2109243118>
- Rocchini, D., Leutner, B., & Wegmann, M. (2016). From spectral to ecological information. In M. Wegmann, B. Leutner, & S. Dech (Eds.), (pp. 150–165). Pelagic Publishing.
- Salinas, N., Cosio, E. G., Silman, M., Meir, P., Nottingham, A. T., Roman-Cuesta, R. M., & Malhi, Y. (2021). Editorial: Tropical montane forests in a changing environment [editorial]. *Frontiers in Plant Science*. <https://doi.org/10.3389/fpls.2021.712748>
- Schneider-Maunoury, L., Lefebvre, V., Ewers, R. M., Medina-Rangel, G. F., Peres, C. A., Somarriba, E., & Pfeifer, M. (2016). Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. *Biological Conservation*, 200, 207–215. <https://doi.org/10.1016/j.biocon.2016.06.011>
- Schott, J. R., Salvaggio, C., & Volchok, W. J. (1988). Radiometric scene normalization using pseudo-invariant features. *Remote Sensing of Environment*, 26(1), 1–16. [https://doi.org/10.1016/0034-4257\(88\)90116-2](https://doi.org/10.1016/0034-4257(88)90116-2)
- Soh, M. C. K., Mitchell, N. J., Ridley, A. R., Butler, C. W., Puan, C. L., & Peh, K.S.-H. (2019). Impacts of habitat degradation on tropical montane biodiversity and ecosystem services: A systematic map for identifying future research priorities [systematic review]. *Frontiers in Forests and Global Change*. <https://doi.org/10.3389/ffgc.2019.00083>
- Suttidate, N., Hobi, M. L., Pidgeon, A. M., Round, P. D., Coops, N. C., Helmers, D. P., & Radeloff, V. C. (2019). Tropical bird species richness is strongly associated with patterns of primary productivity captured by the dynamic habitat indices. *Remote Sensing of Environment*, 232, 111306. <https://doi.org/10.1016/j.rse.2019.111306>
- Topp-Jørgensen, E., Poulsen, M. K., Lund, J. F., & Massao, J. F. (2005). Community-based monitoring of natural resource use and forest quality in montane forests and miombo woodlands of Tanzania. *Biodiversity & Conservation*, 14(11), 2653–2677. <https://doi.org/10.1007/s10531-005-8399-5>
- Toszygova, A., & Storch, D. (2019). Global diversity patterns are modulated by temporal fluctuations in primary productivity. *Global Ecology and Biogeography*, 28(12), 1827–1838. <https://doi.org/10.1111/geb.12997>

- Townsley, J., Gaulke, P., & Ingram, D. (2001). *USDA Forest Service Mission, Fianarantsoa, Madagascar In Support of the Landscape Development Interventions Project. Section 3: Economic Analysis Of Pine Plantation Management in Haute Matsiatra.*
- Vågen, T.-G., Shepherd, K. D., & Walsh, M. G. (2006). Sensing landscape level change in soil fertility following deforestation and conversion in the highlands of Madagascar using Vis-NIR spectroscopy. *Geoderma*, 133(3–4), 281–294. <https://doi.org/10.1016/j.geoderma.2005.07.014>
- Vedeld, P., Angelsen, A., Bojö, J., Sjaastad, E., & Kobugabe Berg, G. (2007). Forest environmental incomes and the rural poor. *Forest Policy and Economics*, 9(7), 869–879. <https://doi.org/10.1016/j.forpol.2006.05.008>
- Vences, M., Andreone, F., Glaw, F., Raminosoa, N., Randrianirina, J. E., & Vieites, D. R. (2002). Amphibians and reptiles of the Ankaratra Massif: Reproductive diversity, biogeography and conservation of a montane fauna in Madagascar. *Italian Journal of Zoology*, 69(3), 263–284. <https://doi.org/10.1080/11250000209356469>
- Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J. R., Allnut, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222(January), 189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>
- Vorontsova, M. S., Besnard, G., Malakasi, P., Moat, J., Clayton, W. D., Ficinski, P., & Linder, H. P. (2016). Madagascar's grasses and grasslands: Anthropogenic or natural? *Proceedings of the Royal Society B*, 283, 2015–2262. <https://doi.org/10.1098/rspb.2015.2262>
- Wollenberg, K. C., Vieites, D. R., Van Der Meijden, A., Glaw, F., Cannatella, D. C., & Vences, M. (2008). Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. *Evolution*, 62(8), 1890–1907. <https://doi.org/10.1111/j.1558-5646.2008.00420.x>
- Yesuf, G. U., Brown, K. A., & Walford, N. S. (2019). Assessing regional scale variability in deforestation and forest degradation rates in a tropical biodiversity hotspot. *Remote Sensing in Ecology and Conservation*.
- Zhang, M., Huang, H., Li, Z., Hackman, K. O., Liu, C., Andriamiarisoa, R. L., & Gong, P. (2020). Automatic high-resolution land cover production in madagascar using sentinel-2 time series, tile-based image classification and google earth engine. *Remote Sensing*, 12(21), 3663.
- Zimkus, B. M., Lawson, L. P., Barej, M. F., Barratt, C. D., Channing, A., Dash, K. M., & Lötters, S. (2017). Leapfrogging into new territory: How Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. *Molecular Phylogenetics and Evolution*, 106, 254–269. <https://doi.org/10.1016/j.ympev.2016.09.018>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Authors and Affiliations

Antonio T. Monteiro^{1,2}  · Sophia Rosa³  · Franco Andreone⁴  · Serge Ndriantsoa⁵ · Tsanta Rakotonanahary⁵ · Jeff Dawson⁶ · Falitiana C. E. Rabemananjara⁷ · Nirhy H. C. Rabibisoa⁸ · Richard Lucas⁹  · Angelica Crottini^{10,11,12} 

✉ Antonio T. Monteiro
monteiroantonio@edu.ulisboa.pt

¹ Centro de Estudos Geográficos (CEG) and Laboratório Associado TERRA, Instituto de Geografia e Ordenamento do Território (IGOT), Universidade de Lisboa, Rua Edmée Marques, 1600-276 Lisbon, Portugal

² Istituto di Geoscienze e Georisorse, Consiglio Nazionale delle Ricerche (CNR), Via Moruzzi 2, 56124 Pisa, Italy

³ World Food Program, Food and Agriculture Organization of the United Nations, Via Cesare Viola, 00148 Rome, Italy

- ⁴ Museo Regionale di Scienze Naturali, Via G. Giolitti, 36, 10123 Turin, Italy
- ⁵ Amphibian Survival Alliance c/o Durrell Wildlife Conservation Trust, Madagascar Programme, Lot II Y J Ampasimalo, BP 8511 101, Antananarivo, Madagascar
- ⁶ Durrell Wildlife Conservation Trust, Les Augrès Manor, La Profonde Rue, Trinity, Jersey, Channel Islands JE3 5BP, United Kingdom
- ⁷ Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, BP 906, 101 Antananarivo, Madagascar
- ⁸ Département de Biologie Animale et Ecologie, Faculté des Sciences, University of Mahajanga, B.P. 652, 401 Ambondrona, Mahajanga, Madagascar
- ⁹ Department of Geography and Earth Sciences, University of Aberystwyth, Penglais, Aberystwyth SY23, United Kingdom
- ¹⁰ CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, InBIO Associate Laboratory, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas 7, 4485-661 Vairão, Portugal
- ¹¹ Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, rua do Campo Alegre s/n, 4169-007 Porto, Portugal
- ¹² BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal