Title page

Title: Differential responses of amphibians and reptiles to land-use change in the biodiversity hotspot of north-eastern Madagascar

Running Title: Herpetofauna response to land-use change in Madagascar

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Abstract

Large expanses of tropical rainforest have been converted into agricultural landscapes cultivated by smallholder farmers. This is also the case in north-eastern Madagascar; a region that retains a significant proportions of forest cover despite shifting hill rice cultivation and vanilla agroforestry. The region is also a global hotspot for herpetofauna diversity, but how this diversity is affected by land-use change remains largely unknown. Using a space-for-time study design to uncover land-use effects, we compared species diversity and community composition in seven prevalent land uses: unburned (old-growth forest, forest fragment, and forest-derived vanilla agroforest) and burned (fallow-derived vanilla agroforest, woody fallow, herbaceous fallow) land-use types, and rice paddy. We conducted six comprehensives, time-standardized searches across at least ten replicates of each land-use type and applied genetic barcoding to confirm species identification. We documented an outstanding diversity of endemic herpetofauna (119 species): amphibian species richness at the plot level was highest in old-growth forest and significantly lower in all other land-use types. Plot-level reptile species richness was significantly higher in the unburned land-use types than burned land-use types. For both amphibians and reptiles, the less-disturbed land-use types showed more uneven communities and particularly in old-growth forest, the species composition differed significantly from all other land-use types. Amphibians showed a higher level of forest dependency compared to reptiles (38% versus 28% of species exclusively occurred in old-growth forest). Our analyses thus revealed that the two groups respond differently to land-use change: we found less pronounced losses of reptile species richness especially in unburned agricultural habitats, suggesting that reptiles are less susceptible to land-use change than amphibians. Overall, old-growth forest harboured a unique diversity, but some species also thrived in agroforestry systems, especially if these were forest-derived. This highlights the importance of conserving old-growth forests and non-burned land-use types within the agricultural landscape.

Key words: community and landscape ecology, herpetofauna, vanilla-agroforestry, human-dominated landscape, agriculture, land-use change, land-use history, Madagascar

1.Introduction

Demand for agricultural goods is on the rise due to a growing world population, rising per-capita consumption and changing diets (Tilman et al. 2011). This situation is leading to both an expansion of croplands into natural areas and an intensification within existing production systems (Tscharntke et al. 2012). Most agricultural expansion in the tropics happens at the expense of forest and leads to an increase of forest fragmentation (Gibbs et al. 2010; Hansen et al. 2020). Land-use change is thus the main driver of biodiversity decline globally (Powers and Jetz 2019), and this is particularly pronounced in the tropics (Newbold et al. 2020) where high land-use pressure and biodiversity coincide.

Tropical agricultural landscapes contribute to food security but also provide opportunities for nature conservation (Perfecto and Vandermeer 2010). The quality of the agro-ecosystem for biodiversity conservation depends on the farming systems. For example, agricultural landscapes dominated by large-scale industrial monocultures have lower conservation value than diverse mosaics of forest fragments, agroforestry systems and more intensively farmed annual crop fields (Mendenhall et al. 2016; Murray and Nowakowski 2021). Besides the value for biodiversity, small-scale land-use mosaics can also provide essential ecosystem services and livelihoods for rural people, making landscapes work for humans and nature (Kremen and Merenlender 2018). Most research investigating the value of tropical agricultural landscapes for biodiversity and humans was conducted in the Neotropics (Gardner et al. 2007; Philpott et al. 2008; Mendenhall et al. 2016) while the conservation value of Afrotropical agricultural landscapes is less understood (Powers et al. 2011).

Madagascar is a country with particular importance for global conservation. The country has lost around 44% of forest cover since the 1950s, mainly due to the transformation of natural ecosystems to agricultural lands (Vieilledent et al. 2018) along with unsustainable extraction rates (Whitehurst et al. 2009). In consequence, more than half of the Malagasy species evaluated are at risk of extinction (IUCN 2018). Outstanding levels of endemism (Brown et al. 2016) and ongoing threats qualify Madagascar as a global biodiversity hotspot (Myers et al. 2000). While the forests and protected areas of the island are increasingly well surveyed for biodiversity, the biodiversity in the agricultural landscapes is largely less known (Irwin et al. 2010).

Madagascar has a diverse and highly endemic herpetofauna: amphibian species diversity is currently estimated at around 370 with (AmphibiaWeb 2020) and almost all species are native (Goodman and Benstead 2005). Reptile diversity stand at around 440 species (Uetz 2020) with 91% endemism (Goodman and Benstead 2005). Due to cryptic taxonomic complexes, many species still await discovery and/or description, suggesting that total species richness will increase with more research including genetic barcoding (Vieites et al. 2009). Globally,

herpetofauna is sensitive to various anthropogenic threats (Vallan 2000; Trimble and van Aarde 2014; Nowakowski et al. 2017) including chytrid fungi, environmental pollution, collection for pet trade, climate change and conversion of forest habitat into agricultural lands (Hof et al. 2011). All of these factors are also threatening Malagasy herpetofauna, with deforestation being among the top pressures (Cordier et al. 2021).

The north-eastern Madagascar retains most forest cover (Vieilledent et al. 2018) and is a global priority area for amphibian research (Nori et al. 2018). Besides being known for its remarkable biodiversity, north-eastern Madagascar is also a global centre for vanilla cultivation (Hänke et al. 2018). The price boom of the spice between 2012 and 2019 has triggered an expansion (Llopis et al. 2019) of vanilla agroforests, and roughly 80% of rural households in the study region farm vanilla (Hänke et al. 2018). Besides farming vanilla, the rural population also practices shifting cultivation for hill rice production. Valleys and plains in the study region are commonly occupied by irrigated rice paddies, forming the backbone of staple crop supply. Nowadays the agricultural land uses occupy more land than the remaining old-growth forest (Vieilledent et al. 2018), yet research has focused mainly on protected areas, with little attention to agricultural land uses (D'Cruze et al. 2009).

In this study, we assessed the diversity and community composition of amphibians and reptiles across the small-scale agricultural landscape and compared this to continuous forest (old-growth forest inside Marojejy National Park) and forest fragments. Within the small-scale agricultural landscape mosaic, we sampled vanilla agroforest of contrasting land-use history (forest- and fallow-derived vanilla agroforests), as well as herbaceous fallow, woody fallow and rice paddy.

2.Methods

2.1. Study region and study design

We conducted our study in the SAVA region in north-eastern Madagascar (Fig. 1A and B) where forests outside protected areas are now highly fragmented (Vieilledent et al. 2018) and the landscape is dominated by smallholder agriculture.

We collected data (Fulgence et al. 2021) on circular plots with a 25 m radius at low to mid-altitude (7-819 m above sea level; mean = 192 m±207 m) surrounding ten villages and in Marojejy National Park, a UNESCO World Heritage Site. In each village, we selected seven plots: three vanilla agroforests (forest-derived and/or fallow-derived vanilla agroforest), one forest fragment, one herbaceous fallow, one woody fallow, and one rice paddy. In the ten villages, we first selected 30 vanilla agroforests along a canopy cover gradient. After consultation with the agroforest owner and a visual confirmation on the plot, we found that twenty vanilla agroforests were fallow-derived while ten agroforests were forest-derived. This approach allowed us to understand the response of amphibians and reptiles to the land-use

history of vanilla agroforests. Additionally, we chose ten plots at two sites (five plots each) inside Marojejy National Park. All land-use types, except fallow-derived vanilla agroforests, were replicated ten times. The average minimum distance between one plot and the next closest plot was 719 m± 438 m, while the smallest minimum distance between two plots was 260 m. In total, we surveyed 80 plots (Fig. 1C and D).

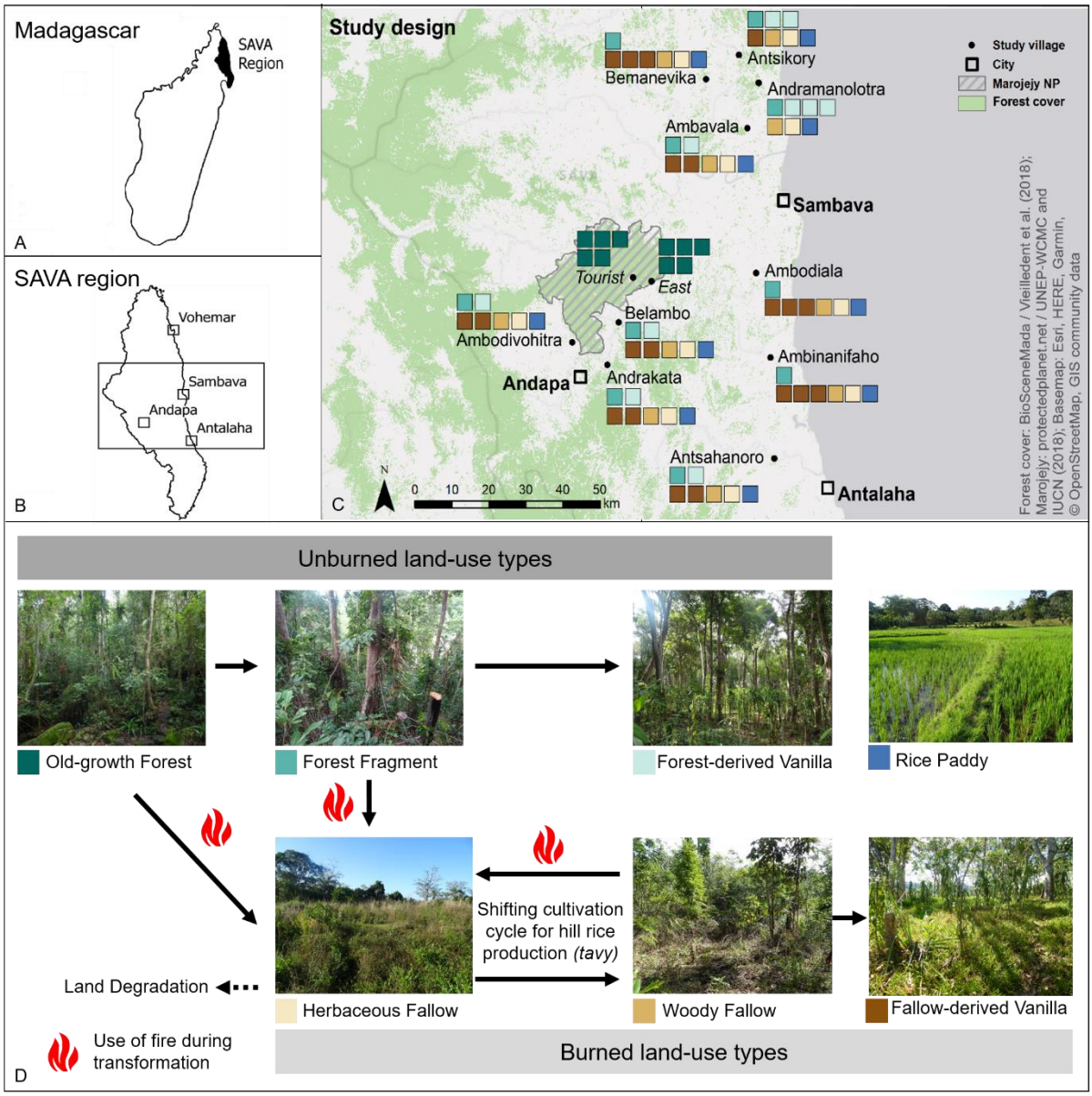

Figure. 1 Overview of the study region and the study design. **A** SAVA region in north-eastern Madagascar; **B** study area within SAVA region; **C** study design showing the distribution of 80 plots in ten villages and at two sites inside Marojejy National Park; and **D** overview of the studied land-use types and the typical land-use transformation trajectory from old-growth forest to forest fragments and agricultural land-uses. Panel D modified after (Martin et al. 2021) and Panel C modified after Dröge et al. 2021. Rice paddy is not part of the main land-use trajectory

2.2. Sampled land-use types

We selected 10 old-growth forest plots at two sites with five plots each. One of the sites has experienced some selective logging in the past but is now well protected (touristic zone in Manantenina valley; site *Tourist* on Fig. 1), the other site suffers from ongoing occasional selective logging and trapping (Bangoabe; site *East* on Fig. 1), but we chose plots that did not show signs of recent disturbance. The old-growth forest plots are a minimum of 300 m from the National Park boundary.

In the study region, isolated forest fragments occur around villages and represent remnants of the continuous forest cover that existed in the region prior to the large-scale deforestation that began in the early 20th century (Gade 1996). The ten fragments have not been burned in historic times with few larger trees remaining. The forest fragments are all used for extraction of timber and non-timber forest products.

Herbaceous fallows occur after shifting hill rice cultivation (locally referred to as *tavy*; Styger et al. 2007) and are sometimes used for grazing. The herbaceous fallow plots in this study had last burned at the end of 2016, one year before the onset of data collection in 2017.

Woody fallows represent successional stages of herbaceous fallows, containing shrubs and small trees. Woody fallows are also occasionally grazed by cows. The woody fallows in our study had last burnt 4-16 years before the onset of data collection in 2017, according to the reports of land owners.

The climbing orchid vanilla (*Vanilla planifolia)* is farmed in agroforestry systems with two distinct land-use histories (following Martin et al. 2020) in north-eastern Madagascar: forest-derived vanilla agroforests, where vanilla is directly planted inside the forest after removing understory trees and shrubs and managing tall trees for shade. In fallow-derived vanilla agroforests, vanilla is planted on fallow land which resulted from shifting cultivation in the past. In these fallow-derived vanilla agroforests, farmers allow natural regeneration of trees or plant trees to provide shade or as support structures for the vanilla vines.

Lastly, we studied irrigated rice paddies that occur in valley bottoms and flood plains throughout the whole study region. Rice is planted and harvested between one to three times per year. The rice paddies chosen for our study had wider-than-average banks to facilitate movement and sampling within the plots.

2.3. Sampling and data collection

To collect data in the villages, we organized two sampling campaigns during the driest period of the year (October to December 2017 and late August to December 2018) and one campaign during the wettest period (Mid-January to early April 2018). In Marojejy National Park, we organized the same round of sampling campaigns as in the villages: two during the driest period (late August – early September 2018 and December 2018) and one during the wettest

period (February 2019). During each campaign, we visited each plot once during the day (08:00 - 17:00) and once at night (18:30-23:00). Overall, we did six visits per plot i.e. three times during the day and three times at night.

We collected data on amphibian and reptile communities during time-standardized searches (Kadlec et al. 2012). During the survey, we systematically searched each plot in a zig-zag pattern (Kadlec et al. 2012). Each search was standardized to 45 minutes of searching time by two observers. With all visit, we thus conducted 270 minutes of searching time on each plot, summing up to 408 hours of searching time across all plots. To detect individuals hiding under rocks, in leaf axils, tree barks, tree holes, leaf-litter or deadwood, we actively inspected those microhabitats by lifting removable objects to check underneath.

To identify all individuals to species level we used morphological characteristics following 'A Field Guide to Amphibians and Reptiles of Madagascar' (Glaw and Vences 2007) and additional literature (Rakotoarison et al. 2017; Ratsoavina et al. 2019). For those individuals which we could not identify with confidence in the field, we extracted tissue samples for later DNA analysis and/or collected the specimen. We then resumed the searching time; thus abundance and diversity of amphibians and reptiles was independent of the time spent on the plot. Throughout this manuscript, we refer to each encountered individual as an 'encounter' rather than an individual as we cannot exclude the possibility of having encountered the same individual at more than one sampling event.

2.4. Species identification with DNA barcodes

We collected muscle or toe clips as tissue samples of individuals in those cases where a reliable identification based on morphological characteristics was not possible. We collected a total of 498 tissue samples for DNA barcoding, conserved in 90% ethanol, stored and analysed at the Evolutionary Biology laboratory of Prof. Miguel Vences at the University of Braunschweig, Germany. We extracted DNA following the standard single-tube salt extraction protocol (Bruford et al. 1992). Then, we ran DNA amplification (PCR) based on fragments of two mitochondrial genes, 16S (Vences et al. 2005) and COI with the primers 16SAL/16SBH (Palumbi et al. 1991). We first cleaned the obtained sequences with the software CodonCode Aligner version 8.0.2 (Codon Code Corporation, Centerville, MA, US). Then, we processed newly generated sequences for additional quality control with a Blast search (Altschul et al. 1990) which queries similar DNA sequences through GenBank database to provide information on closest taxa or potential contamination. Finally, we built a phylogenetic tree using MEGA-X (Kumar et al. 2018) to reveal clusters of each newly generated sequences, allowing us to reliably identify individuals to species level.

2.5. Data analysis and visualisation: species diversities and encounters

To compare species richness on plot-level among land-use types, we computed a generalized linear model with species richness as response, land-use type as explanatory variable, and village (respectively old-growth forest site) as a random factor and with Poisson family for count data as distribution. We then ran the glht function of the R-package 'multcomp' (Hothorn et al. 2008) applying a Tukey all-pair-comparison with Bonferroni correction.

We used the encounter data to compute sample-size-based rarefaction and extrapolation curves (Hsieh et al. 2016) with the iNEXT package to assess the diversity (species richness, Shannon and Simpson diversity) across land-use types using the Hill number framework (Chao et al. 2014). We calculated species richness, Shannon diversity and Simpson diversity (Hsieh et al. 2016). Chao and Jost (2012) define q=0 (0D) as species richness, i.e. the effective number of species in the community, giving equal weight to frequent and infrequent species; q=1 (1D) as Shannon diversity, giving more weight to more frequently observed species and q=2 (2D), as Simpson diversity interpreted as the effective number of abundant species.

To display the total species diversity in each land-use type, we sub-sampled 10 plots of the 20 fallow-derived vanilla agroforests. To do so, we randomly selected one fallow-derived vanilla agroforest from each village. As one of the villages lacks fallow-derived vanilla agroforests (village Andramanolotra, see Fig.1), this resulted in 9 agroforests. We proceeded to select one additional plot from all remaining fallow-derived vanilla agroforests, enabling a fair comparison of total species diversity across 10 plots of each land-use type.

2.6. Data analysis and visualization: species composition

To evaluate the differences in species community composition among land-use types, we used the *metaMDS* function of the R-package 'vegan' (with 1000 permutations; Oksanen 2018). We used non-metric dimensional scaling (NMDS) of Bray-Curtis dissimilarities to visualize the dissimilarity of species composition in two dimensions (Oksanen 2018). Furthermore, to test the differences between land-use types, we used the *adonis* function of the 'vegan' package (Oksanen et al. 2020) and computed pairwise differences using the *pairwise.adonis* function with Bonferroni correction of the '*pairwise.adonis*' package (Martinez 2020).

To analyse the degree of forest dependency, we plotted the proportion of encounters for each species across land-use types (Rembold et al. 2017).

We conducted all statistical analyses using R version 3.5.1 (R Core Team, 2019).

3.Results

3.1. Encounters and species richness

In total, we made 6215 encounters and found 119 species of amphibians and reptiles. The 3694 amphibian encounters belong to 58 species, 15 genera, and four families (see SI 1). The most species-rich genera of amphibians are *Boophis* (11 species), *Stumpffia* (10 species) and

Gephyromantis (eight species). We found all but one species to be endemic according to AmphibiaWeb (2020). Among the observed amphibian species, 22 (37%) could not be identified to species level and are counted as morphospecies. Eight of the observed amphibian species were recognized as candidates for new species based on genetic barcoding. Among the encountered amphibian species, seven are listed in the 'threatened' category (IUCN 2019). Among the threatened species, we recorded six vulnerable and one endangered species.

The 2521 reptile encounters represent 61 species, 28 genera, and five families (see SI 1). The most species-rich reptile genera were *Phelsuma* (11 species) and *Uroplatus* (six species). We found 83% of reptile species to be endemic (Uetz 2020). Amongst observed reptile species, 15 could not be identified reliably and were counted as morphospecies. Based on the IUCN red list (IUCN 2019), seven reptile species are listed as 'threatened'. Among the threatened species, we recorded four endangered and one critically endangered species.

Plot-level amphibian species richness differed significantly among land-use types ($F(6, 73) = 19.59$, p-value < 0.001). A Tukey post-hoc test revealed significant pairwise differences between land-use types (Fig. 2A and SI 2): Old-growth forests plots had significantly higher average amphibian species richness while rice paddies plots had significantly lower compared to other land-use types (Fig. 2A). The other land-use had similar amphibian species richness with no significant differences (see SI 2).

Plot-level reptile species richness also varied significantly among land-use types ($F(6, 73) = 18.55$, p-value < 0.001). Tukey post-hoc tests revealed non-significant pairwise differences between old-growth forest and forest fragment (p-value = 0.88) and between old-growth forest and forest-derived vanilla agroforest (p-value = 0.77). These three land-use types are recorded with the highest mean species richness, with 10 reptile species on average per plot. Rice paddy had the lowest reptile species richness yet compared to herbaceous fallow, there was no significant differences (p-value = 0.19)**.** Reptile species richness within forest-derived and fallow-derived vanilla varied significantly (p-value = 0.01; Fig. 2B and SI 3).

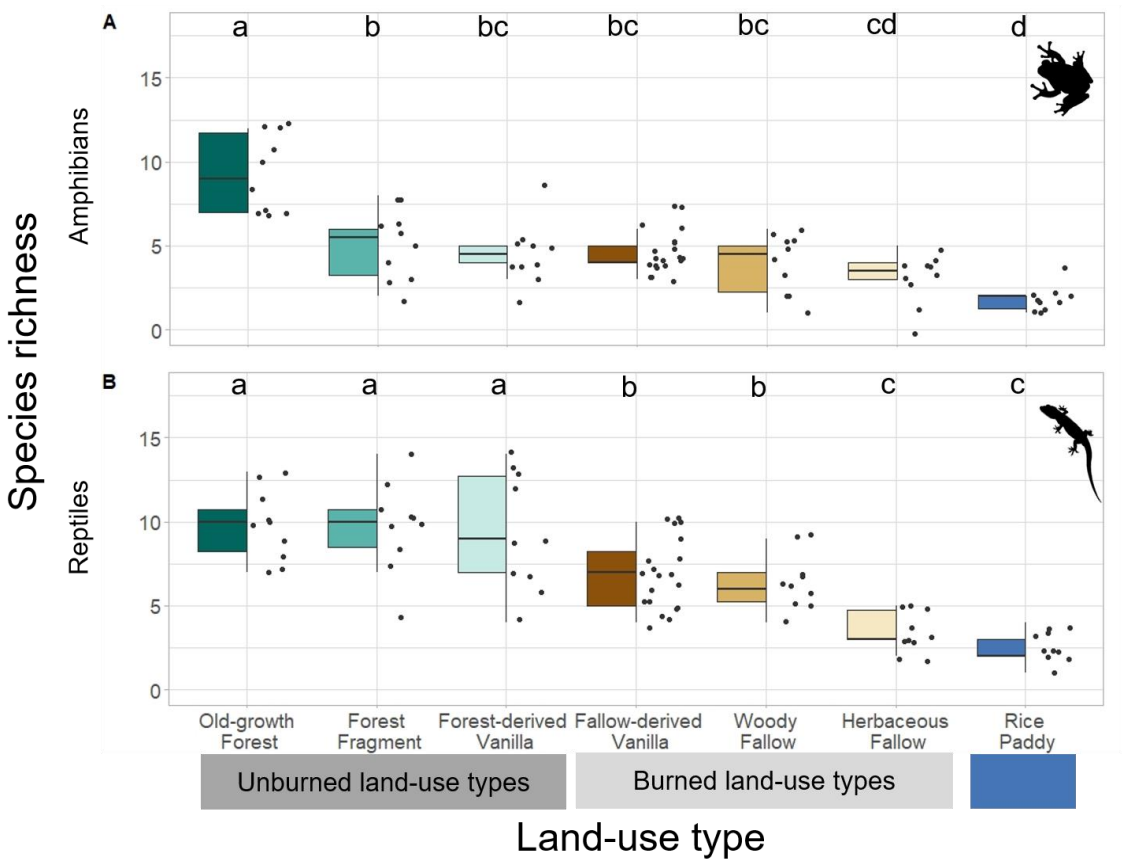

Figure. 2 Plot-level amphibian (A) and reptile (B) species richness across seven land-use types (replicated 10 times each except fallow-derived vanilla, which is replicated 20 times). The dots represent the species richness per plot in each land-use type. The black horizontal line in the box shows the median. Land-use types with letters in common did not differ significantly based on pairwise comparisons that controlled for inflated false positive errors using the Tukey HSD approach (Numeric results in SI: amphibians SI 2 & reptiles SI 3).

3.2. Species accumulation curves, diversity, and estimated species richness

Encounter-based accumulation curves revealed the highest species richness and Shannon diversity in old-growth forest (for amphibians and reptiles) and the lowest in rice paddy for amphibians but in herbaceous fallow for reptiles (Fig. 3 and Table 1). In most land-use types, amphibian and reptile species richness curves flattened off, except for old-growth forest and forest fragment. We also found the same pattern in reptile species richness, except in woody fallow and fallow-derived vanilla agroforest. The overlap of the 95% confidence interval of extrapolated amphibian richness for old-growth forest and forest fragment (Fig. 3A) indicates no differences in species richness. Regarding the accumulated amphibian species diversity for Shannon and Simpson diversity, old-growth forest varied significantly compared to all other land-use types. Shannon and Simpson diversity also did not differ significantly between forest fragment and forest-derived vanilla agroforest, respectively, compared to burned land uses,

except to rice paddy. We found no difference in extrapolated reptile richness among unburned and burned land-use types, respectively (Fig. 3C and D), but found a difference for Shannon diversity and Simpson diversity. The species diversity dropped stronger in amphibians than in reptiles after old-growth forest transformation across all diversity indices (Fig. 3, SI 4 and SI 5), highlighting that amphibian communities were more uneven than reptile communities.

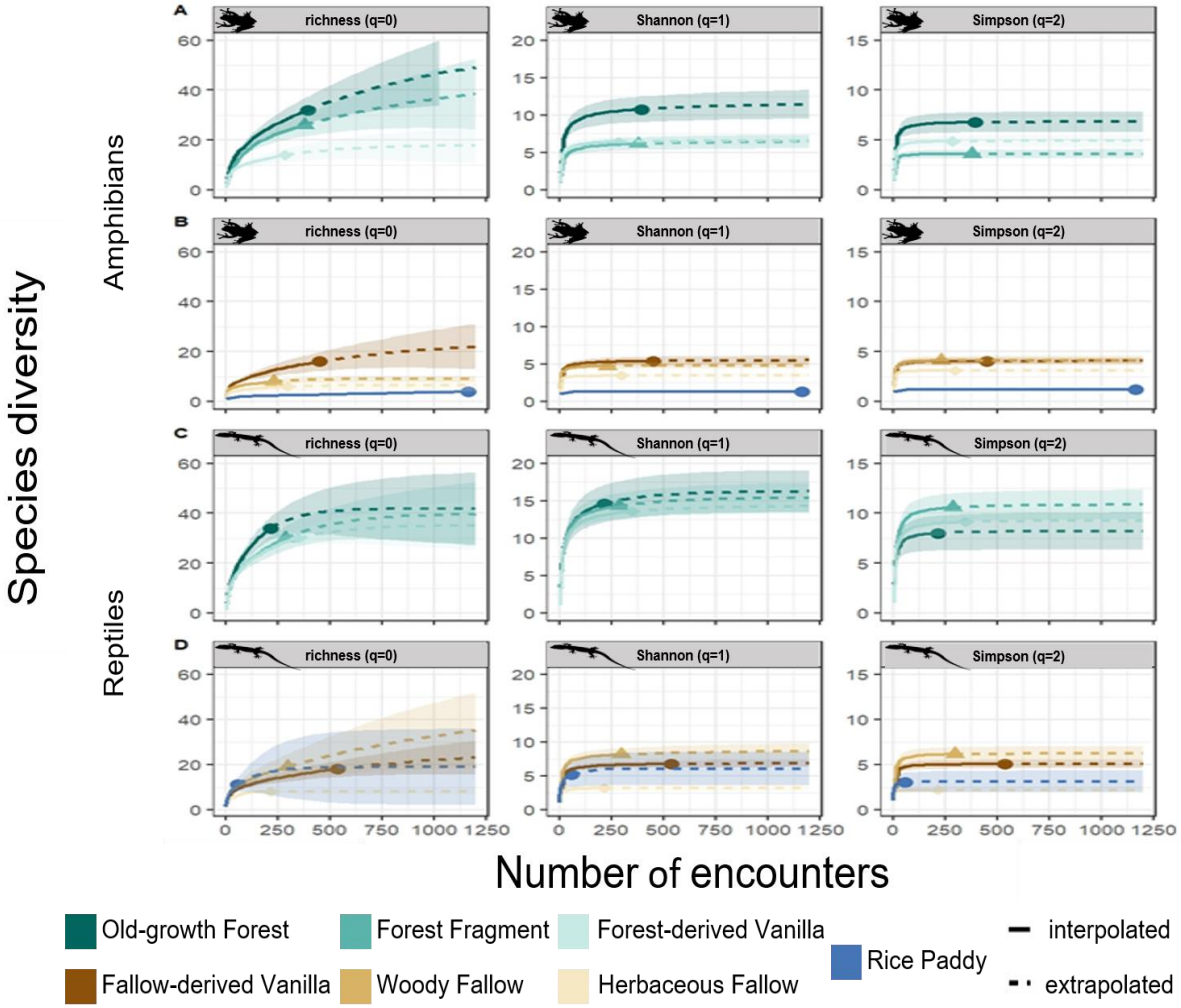

Figure. 3: Encounter-based accumulation curves showing interpolated (solid line) and extrapolated (dotted line) diversities for amphibians (A, B) and reptiles (C, D). Unburned (A, C) and burned (B, D) land-use types are separated. The species richness represented by q = 0 (left panel), Shannon diversity, q=1 (middle panel) and Simpson diversity q=2 (right panel) with 95% confidence intervals (shaded areas) for the amphibian and the reptile data of seven land-use types. The solid dots, triangles and diamonds represent the reference samples, i.e. the observed number of encounters and species richness.

Table 1 Amphibian and reptile species richness (q = 0) for all land-use types and separated per land-use type showing the observed and extrapolated total species richness. Each land-use type is represented by 10 plots; for fallow-derived vanilla, the 10 plots are down-sampled from 20 plots. Extrapolated species richness is based on 5000 encounters and includes the

lower and upper 95% confidence interval in italics below. See SI for results of q = 1 and q =2 (amphibians: table SI 4; reptiles: table SI 5).

Land- use type / **Species Group** (measure)	**All 80 plots**	**Old-growth forest**	**Forest fragment**	**Forest-derived vanilla**	**Fallow-derived vanilla**	**Woody fallow**	**Herbaceous fallow**	**Rice paddy**
Amphibian (observed)	58	32	26	14	16	8	6	4
Amphibian (extrapolated)	NA	60.0 *20.4 - 99.6*	46.1 *12.4 - 79.8*	18.0 *9.1 - 26.9*	25.0 *7.0 - 42.9*	9.0 *7.4 - 10.6*	6.5 *3.9 - 9.1*	5.0 *4.3 - 5.6*
Reptile (observed)	61	34	30	30	18	19	8	11
Reptile (extrapolated)	NA	42.0 *20.4 - 63.5*	40.1 *10.2 - 69.9*	35.1 *18.2 - 52.4*	26.9 *8.2 - 45.7*	46.6 *11.5 - 81.7*	8.0 *6.8 - 9.2*	18.9 *4.3 - 33.4*
Total (observed)	119	66	56	44	34	27	14	15

3.3. Species composition and forest dependency

The composition of amphibian communities differed significantly across land-use types (R^2=0.50, p-value<.001, Df=6). Pairwise comparisons showed that amphibian communities in old-growth forest and rice paddy were significantly different from that of other land-use types. Forest fragments differed significantly from fallow-derived vanilla, woody fallow and herbaceous fallow, but no significant differences were observed between forest fragment and forest-derived vanilla. No significant differences were found between forest-derived vanilla, fallow-derived vanilla, woody fallow, and herbaceous fallow for amphibian communities (Fig. 4A, see SI 6).

Reptile species composition showed significant differences among land-use types (R^2=0.40, p-value<.001, Df=6). Pairwise comparisons showed that the reptile communities in old-growth forest and forest fragment were significantly different from all other land-use types. The communities in other land-use types showed no significant differences (Fig. 4C, SI 7). Old-growth forest shows unique communities of reptiles and amphibians.

Finally, the analyses for forest dependency revealed that 22 species (38%) were found exclusively in old-growth forest, 11 species (19%) exclusively in forest fragment, three species (5%) exclusively in forest-derived vanilla agroforest and four species (7%) exclusively in fallow-derived vanilla agroforest of amphibians (Fig. 4B). We observed 17 species (28%) of reptiles

exclusively occurred in old-growth forest, three species (5%) exclusively in forest fragment, four species (7%) exclusively in forest-derived vanilla agroforest and one species (2%) exclusively in fallow-derived vanilla agroforest (Fig. 4D). No species was exclusively found in woody fallow, herbaceous fallow and rice paddy for both groups.

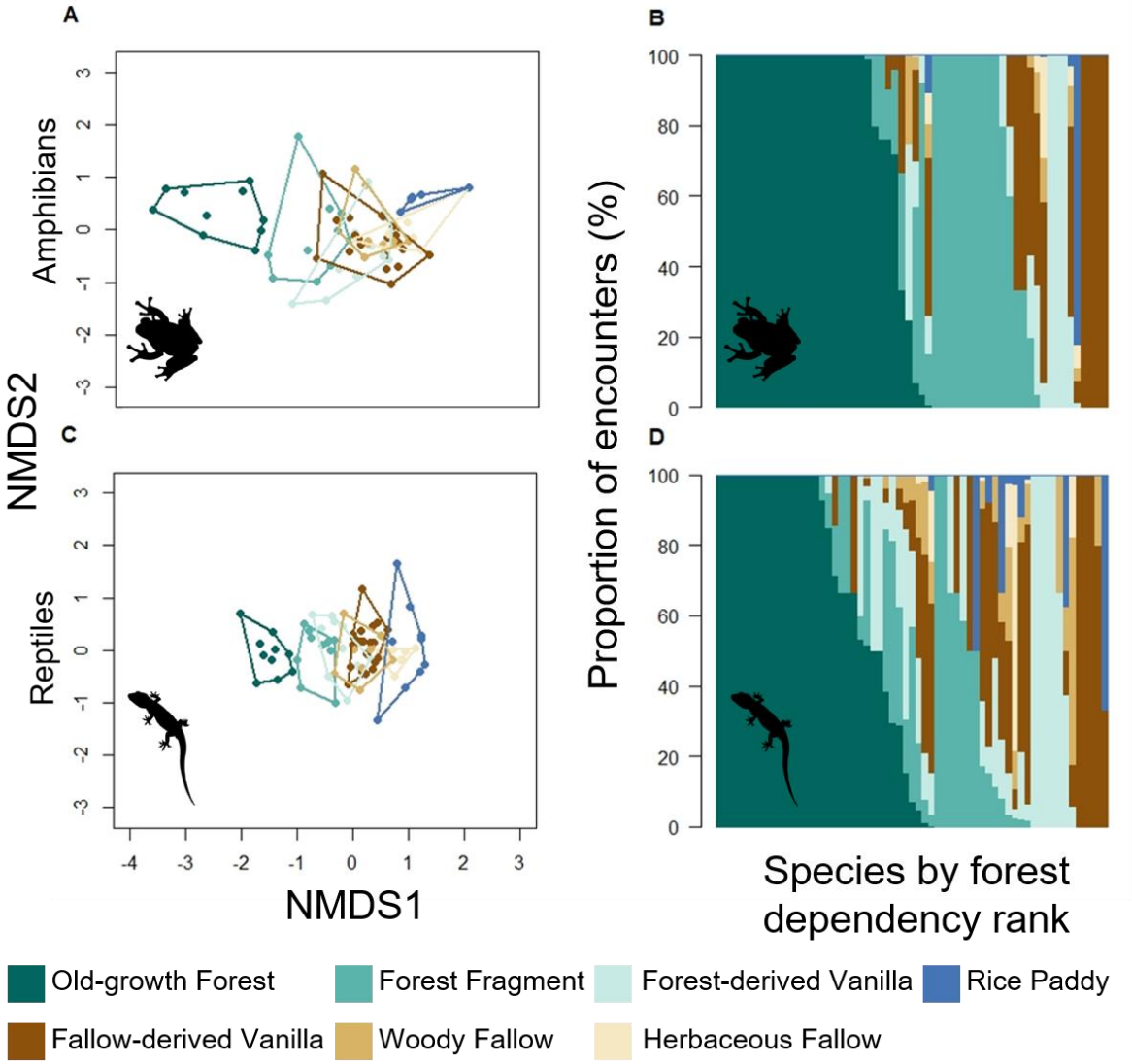

Figure. 4: Species composition across seven land-use types. Non-metric dimensional scaling (NMDS) showing community dissimilarity of amphibian (A) and reptile communities (C). All 58 amphibian species with 3694 encounters (B) and all 61 reptile species (D) with 2521 encounters are displayed by forest dependency rank. 38% of amphibian species and 28% of reptile species exclusively occurred in old-growth forest, despite the latter is only accounting for 12.5% of the total plots.

4.Discussion

Based on a rigorous study design, extensive field sampling, and DNA barcode-aided species identification, we provide a comprehensive assessment of the response of amphibian and reptile species diversity to land-use change in the biodiversity hotspot of north-eastern

Madagascar. Our findings fill an important gap in the literature by documenting a highly diverse herpetofauna with 58 amphibian and 61 reptile species and high proportion of endemic species, 98% for amphibians and 83% for reptiles.

At a plot-level, species richness for both amphibians and reptiles was very high, with up to 12 and 14 species, respectively. For both groups, old-growth forest was significantly different from all other land-use types in terms of total species richness and community composition. Rice paddy for amphibian and herbaceous fallow for reptile harboured the lowest species richness. Reptile species diversity varied significantly between forest-derived and fallow-derived vanilla agroforests whereas amphibian species showed no difference. For woody fallow, herbaceous fallow and rice paddy, there were no unique species occurring in one of those land-use types. Importantly, we found that amphibians and reptiles responded differently to land-use history. After any kind of old-growth forest conversion, whether through burning or not, amphibian species communities were decimated and showed high shift in community structure compared to old-growth forest. In reptile communities, the forest alteration through shifting cultivation showed a strong species loss as well, but changes were less pronounced if old-growth forest was transformed to forest fragment or forest-derived vanilla agroforest, since these transformations refrain from using fire.

4.1. Outstanding diversity of amphibians and reptiles in the north-eastern Madagascar

The diversity of amphibians and reptiles documented here was outstanding, both within Madagascar and compared to other tropical biodiversity hotspots. The few available studies on the response of amphibian communities to land-use change in Madagascar reported lower overall values, with 32 and 28 species, respectively (Vallan 2000; Ndriantsoa et al. 2017). Andreone et al. (2000) found 42 amphibian and 23 reptile species between the Anjanaharibe-Sud and Marojejy massifs in a north-eastern Malagasy rainforest. Despite differences in methodology and study sites, our study provided additional evidence that the north-eastern of Madagascar is one of the most species-rich regions for herpetofauna, as previously suggested (Brown et al. 2016). The documented diversity also exceeds values found in other tropical biodiversity hotspots (Cordier et al. 2021; Murray and Nowakowski 2021) – for example Urbina-Cardona et al. (2006) found 21 amphibian and 33 reptile species, and Kurz et al. (2014) found 25 amphibian and 20 reptile species (vs with 58 and 61 species in this study). The high species diversity may partly be driven by our extensive sampling effort, in terms of number of plots (total n=80), diversity of different land-use types (seven), and search effort (total of 270 min searching time by two observers per plot), and is likely also influenced by the use of genetic samples for species identification.

4.2. Response of amphibian diversity to land-use change

We found a strong negative response of amphibian species richness to any anthropogenic land uses. Old-growth forest had a significantly higher amphibian species richness with 38%

species exclusively occurring there. Besides, the amphibian species composition is unique compared to all other land-use types. Only forest fragments harboured comparably high values to old-growth forest for accumulated amphibian species richness. Subsequently, we found that amphibians are very sensitive to habitat change. This result is in line with findings from Ndriantsoa et al. (2017) in disturbed habitats of eastern Madagascar which documented strongly impoverished frog communities in secondary vegetation and rice fields compared to forests. Forest fragments are valuable for Malagasy amphibians to maintain diversity within the agricultural landscape, though forest fragments cannot substitute large and continuous old-growth forest (Riemann et al. 2015; Vallan 2000).

The other land-use types (fallows that form part of the shifting cultivation cycle, vanilla agroforests, and rice paddies) are of minor importance for amphibian conservation, given the low species diversity that consists mainly of common species. Nonetheless, amphibians could play an important functional role in these habitats: abundance of amphibians is high throughout, reflected by high number of encounters, particularly in rice paddies (see Fig. 3B). As such, they may be an important food source for other taxa or could provide pest control services (Hocking et al. 2014).

The strong negative response of amphibians to deforestation could be explained by the fact that numerous species rely on moist environments to avoid dehydration (Clarke 1997), especially species living in evergreen forest habitat (Hof et al. 2011). Given that selective logging, forest fragmentation and deforestation severely change microclimate conditions (Ewers and Banks-Leite 2013), many species may struggle to cope. Furthermore, amphibians have different habitat requirements throughout their life cycle stages (Hof et al. 2011; Hocking et al. 2014). Such diversification is often lost in concert with the simplification in forest structure (Wanger et al. 2009), making new habitats unsuitable for many species.

4.3. Response of reptile diversity to land-use change

We found a strong effect of land-use history on reptile diversity. Unburned land-use types had a significantly higher average species richness, more uneven communities, more unique species, and a distinct species composition compared to burned land-use types and rice paddy. This is, to our knowledge, the first study shedding light on the response of reptiles to land-use change in humid eastern Madagascar forest. Studies from the drier southern region (Scott et al. 2006; Gardner et al. 2016; Nopper et al. 2018) show that Malagasy reptile species react less strongly to habitat change than other taxa, especially if diurnal (Nopper et al. 2018).

Interestingly, the less pronounced effects of land-use change on reptiles compared to amphibians in tropical landscapes has also been demonstrated by others (Wanger 2010; Kurz et al. 2014) and was found in a review by Palacios et al. (2013). This may be due to the high thermotolerance in reptiles (Thompson and Donnelly 2018) thanks to a fairly impermeable skin

covered with scales. This structure prevents excessive evaporative water loss and adapts reptiles to various microclimates (Morin 2005). Furthermore, egg development is not heavily impacted by temperature rise, which only influences the size of hatchlings (smaller) and the duration of incubation (faster, Packard et al. 1982; Phillips et al. 1990). Reptile life style and traits may thus enable reptiles to adapt to more open, hotter, and drier environments (Morin 2005), as found after deforestation of tropical forests.

4.4. Land-use history of vanilla agroforests affects reptiles but not amphibians

In our study, we have separated forest-derived vanilla from fallow-derived vanilla agroforests, thereby explicitly accounting for land-use history (Martin et al. 2020). For amphibians, we found no differences between the two agroforestry systems across metrics. Reptile communities, on the other hand, were significantly more diverse in forest-derived vanilla agroforests on plot level, more species rich overall, more uneven, and compositionally different compared to fallow-derived vanilla. Reptile communities observed in forest-derived vanilla agroforests are thus more similar to old-growth forest and forest fragment. The reptile communities recorded in fallow-derived vanilla agroforests were comparable to fallow land. Both kinds of agroforest thus resembled the land-use types they were derived from. An increase in accumulated species richness is also demonstrated from fallow-derived vanilla agroforest over fallow land, which may emphasize the rehabilitation opportunity of fallow land through agroforestry (Osen et al. 2021). These findings are in line with the prediction from a recent study of Martin et al. (2020) stating that the land-use history of agroforestry systems matters for biodiversity.

We further hypothesize, that the strong importance of forest-derived vanilla agroforests for reptiles may be in part driven by leaf-litter depth, which is known to positively influence reptile diversity and abundance (Urbina-Cardona et al. 2006). According to the same study, this microenvironmental variables also showed positive effects on amphibians and thus cannot explain why there are no differences between the two kinds of agroforests for amphibians. Other factors such as loss of canopy cover showed negative impacts to amphibian and reptile species (Scott et al. 2006). The latter factor differed significantly between forest-derived vanilla agroforest (higher) and fallow-derived vanilla agroforest (lower) in the same study site (Osen et al. 2021). This is calling for further investigation combining habitat characteristics with species traits (Oliveira et al. 2017) to elucidate the drivers of change in both species groups.

4.5. Conservation implications

The strong negative response of amphibians to old-growth forest modification and the high old-growth forest dependency of reptiles calls for the effective protection of the last remaining old-growth forests. Additionally, conserving forest fragments within the agricultural landscape will be important to many reptile and amphibian species that are absent from other land-use types. This is particularly important given that numerous species are micro-endemics (Brown et al.

2014), meaning that they may only consist of few fragmented populations (Vieites et al. 2009). Management strategies are thus needed to safeguard the long-term existence of these fragments and to improve the connectivity between fragments. The protection of large continuous forests throughout the region is also important under a changing climate (Raxworthy et al. 2008; Hof et al. 2011) and in light of emerging threats, such as the chytrid fungi (Kolby and Skerratt 2015; O'Hanlon et al. 2018) and the recent spread of the invasive Asian common toad (*Duttaphrynus melanostictus*).

We further show that while agroforestry systems play a limited role for rare amphibians, they may be more important for reptile species which prefer forest-derived vanilla agroforests over shifting cultivation and fallow-derived agroforests. Supporting the maintenance of existing forest-derived vanilla agroforests while avoiding the establishment of new forest-derived vanilla agroforests, which represent a forests degradation (Martin et al. 2020; Osen et al. 2021), should thus be set as a priority.

These conservation needs are further underscored by the exceptional diversity of reptiles and amphibians in north-eastern Madagascar as well as by the high proportion of endemic species.

6. Acknowledgements

We are grateful to all *chef de fokontany*, landowners, and Madagascar National Parks for granting us access to sites and information. We thank Prof. Miguel Vences and his laboratory staff for invaluable support with the DNA barcoding and Saskia Dröge for preparing panel C of Fig. 1. We also thank 'CodonCode grants' for offering us a free two-year license under the CodonCode Aligner License Grant Program. We collected data under research permits N°100/17/MEEF/SG/DGF/DSAP/SCB.Re, N°163/17/MEEF/SG/DGF/DSAP/SCB.Re, N°18/18/MEEF/SG/DGF/DSAP/SCB.Re and N°254/18/MEEF/SG/DGF/DSAP/SCB.Re granted by the Ministry of Environment and Sustainable Development, Antananarivo. We transported DNA samples domestically under the transport permit N° 34/17-MEEF/SG/DREEF/SAVA/SRF granted by the Regional Office of the Ministry of Environment and Sustainable Development, Sambava. We exported the samples from Madagascar under CITES permits N°323C-EA05/MG18 and N°180C-EA03/MG19 granted by the Ministry of Environment and Sustainable Development, Antananarivo, and imported the samples to Germany under CITES permits DE-E-03377/18, DE-E-03378/18, DE-E-02422/19, DE-E-02423/19, DE-E-02424/19, and DE-E-02425/19 granted by the German Federal Agency for Nature Conservation, Bonn. This study was financially supported by the Niedersächsisches Vorab of Volkswagen Foundation as part of the research project 'Diversity Turn in Land Use Science' (Grant number 11-76251-99-35/13 (ZN3119)) and by the German Academic Ex-Change Service (DAAD) within the 'Partnerships for Supporting Biodiversity in Developing Countries' initiative (Project Nr. 57449386).

7. Conflict of interest

No conflict of interest to declare.

8. Author's contributions

TRF, DAM, KO, AW, HK, AA, and FMR designed the study. TRF, EB, RB, and RR collected amphibian and reptile data under the lead of TRF. TRF and DAM analysed the data. TRF and DAM wrote the first manuscript draft. All authors revised the manuscript.

9. Data availability

Data are available from Zenodo: http://doi.org/10.5281/zenodo.4548955

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