Herpetofaunal diversity in northern Madagascar: The Andrafiamena-Andavakoera protected area

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Abstract

We present the results of a herpetofaunal survey in the Andrafiamena-Andavakoera protected area with the aim of establishing a baseline dataset for local reptile and amphibian species diversity and future monitoring efforts. This area has not been previously surveyed in any detail for reptiles and amphibians. Survey data were collected between 16 November and 6 December 2023 during the rainy season. In the context of this study, data on the local amphibians and reptiles were collected via visual encounter surveys, opportunistic encounters, pitfall trapping, and bioacoustic monitoring. We encountered 52 species in total (13 amphibians and 39 reptiles) across three study sites characterized by different types of dry forest habitat. These relict habitats display unique diversity, including karst formations (locally called *tsingy*) and different forms of transitional humid to dry semi-deciduous forests. The karst formations can operate as "islands" for biological speciation, and harbor many regionally endemic species. We found within the herpetological communities, a predominance of reptile species that showed considerable biogeographic affinities with nearby sites. Thus, the Andrafiamena-Andavakoera's herpetofaunal assemblage is representative of other reptile communities in northern Madagascar. This study provides natural history data that can be used to further understand community structure and composition and be leveraged for advancing conservation programs. Because amphibians and reptiles can operate as "indicator species" for habitat quality and environmental change, these data can be used to prioritizing management of these remaining forest areas, in particular zones of forest on karst.

Keywords: herpetofaunal survey, reptile, amphibian, biodiversity, northern Madagascar, species checklist, conservation

Résumé détaillé

L'inventaire des communautés d'amphibiens et reptiles dans le Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera a été effectué pendant la saison chaude et humide du 16 novembre jusqu'au 6 décembre 2023. Trois sites ont été priorisés dans l'aire protégée en fonction de l'hétérogénéité, incluant des forêts semi-décidue (Site 1), les forêts sur « *tsingy* » ou formations karstiques (Site 2) et la forêt de transition entre la forêt humide et la forêt sèche (Site 3). L'objectif est de recenser les communautés d'amphibiens et de reptiles dans la zone protégée afin de donner un protocole de suivi des habitats. Des techniques standards ont été utilisées, tels la fouille systématique, l'observation directe accompagnée des recherches bioacoustiques et le système de trou-piège. La présente étude révèle la présence de 13 espèces d'amphibiens et 39 espèces de reptiles dans l'aire protégée et met en exergue l'importance des forêts de transition et sèche de Madagascar jouant un rôle de refuge pour les espèces herpétofauniques. Les résultats ont montré que les portions de forêts sur « *tsingy* » hébergent des espèces endémiques régionales et ont une affinité biogéographique avec quelques aires protégées environnant malgré les menaces qui pèsent sur ces écosystèmes particuliers. La présence des espèces d'amphibiens et de reptiles bio-indicateurs et sensibles aux changements de l'habitat souligne que ce serait mieux de prioriser la conservation de la forêt restante actuelle de l'aire protégée d'Andrafiamena-Andavakoera et surtout

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celles associées au « *tsingy* » afin de préserver les assemblages biologiques uniques à cette formation.

Mots-clés : herpétofaune, diversité, habitat, bio-indicateurs, conservation, Madagascar, reptiles, amphibiens

Introduction

Among the Malagasy vertebrate fauna, amphibians and reptiles have remarkable diversity, with 424 and 436 native and currently described species, respectively (Glaw *et al*., 2022; AmphibiaWeb, 2025). Each year, new species of amphibians and reptiles are identified and described, and projections estimate many have yet to be discovered (Carné & Vieites, 2024). Herpetofaunal communities can be found throughout all major ecosystems on the island, with patterns of endemism and diversity often corresponding with phytogeographic forest ecosystem subdivisions. Despite this pattern, species richness, microendemism, and community composition varies greatly across the island (Antonelli *et al*., 2022; Scherz *et al*., 2023), and some taxonomic groups are restricted to specialized habitats (Raselimanana, 2008; Pabijan *et al*., 2015).

Northern Madagascar has the highest herpetological species richness including local and regional endemism (Andreone *et al*., 2000; D'Cruze *et al*., 2008; Megson *et al*., 2009a; Brown *et al*., 2016; Goodman, 2022). This region is regarded as the cradle of Malagasy reptilian diversity, particularly for chameleons (Raxworthy & Nussbaum, 1995). Many species found in this region are microendemics with restricted geographical distributions (Brown *et al*., 2016) and/or habitat specialization (Raxworthy & Nussbaum, 1994; 1995). In many cases, some of these specialist species are known from only one or two localities (Glaw *et al*., 2001; 2005a; 2005b., 2010, 2014; Köhler *et al*., 2010; Jono *et al*., 2015; Ruane *et al*., 2016; Rakotoarison *et al*., 2017; Scherz *et al*., 2017a) or from fragmented, isolated habitats (Ramanamanjato *et al*., 1999; Megson *et al*., 2009a). Several species in these herpetofaunal communities are already considered threatened, including recently discovered and described taxa (Glaw *et al*., 2006; 2010; Rakotoarison *et al*., 2017), a situation which continues to escalate due to ongoing anthropogenic habitat modification, such as slash-and-burn agriculture, mining, and illegal hardwood logging. Loss of original vegetation cover was previously estimated at 90% (Harper *et al*., 2007), and numerous species on Madagascar are confined to forest ecosystems (Goodman, 2022). Such disturbance has extensive repercussions for the endemic fauna, including amphibians and reptiles, as many species are highly sensitive to habitat change, forest fragmentation, and clearing (Vallan, 2000; Vallan *et al*., 2004; Scott *et al*., 2006; Riemann *et al*., 2015). Because of this sensitivity, amphibians and reptiles are often considered good biological indicators of forest health and integrity (Raxworthy & Nussbaum, 1994; Rabearivony & Raselimanana, 2022), but also among the most at-risk as forested areas suffer degradation.

Over the past two decades, significant efforts have been made to survey amphibians and reptiles at many protected area sites across northern Madagascar (Hawkins *et al*., 1990; Rakotondravony, 2006; D'Cruze *et al*., 2006, 2007; Megson *et al*., 2009b; Raherilalao *et al*., 2022; Radonirina *et al*., 2023; Randriamialisoa *et al*., 2023). However, the complexity of many landscapes has left a number of areas still awaiting rigorous exploration (Durkin *et al*., 2011). This is the case of the Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera. This mosaic habitat is located in northern Madagascar and managed by the non-profit organization Fanamby Association. Information on the biodiversity of this protected area, including the ecology, distribution, and evolutionary history of its various constituents is crucial for management and conservation planning (Andreone *et al*., 2005; Kremen *et al*., 2008; Vieites *et al*., 2008; D'Cruze *et al*., 2009; D'Cruze & Kumar, 2011; Jenkins *et al*., 2014). This is especially the case for protected areas, where biodiversity preservation is a priority (DeFries *et al*., 2007).

This study aims to advance knowledge of the reptile and amphibian diversity and their natural history in the Andrafiamena-Andavakoera protected area, while examining the impact of human activities on their habitats and assessing the effectiveness of protected zones in conserving herpetofaunal diversity. Our objectives were: (1) to investigate diversity patterns of amphibians and reptiles in Andrafiamena-Andavakoera, (2) to summarize local amphibian and reptile ecological structure and habitats, and (3) to use both (1) and (2) to provide data-driven guidelines for the conservation management of herpetofaunal communities in these forests. Our results may inform conservation management of amphibian and reptile communities in similar habitats throughout northern Madagascar.

Methodology

Study site and sampling survey

The Andrafiamena-Andavakoera protected area is characterized by semi-dry deciduous forests. In this study, three sites were surveyed: Site 1, Binara Forest (13.101°S, 49.240°E, 300 m); Site 2, Antsahabe Forest (12.894°S, 49.294°E, 360 m); and Site 3, Andrafiamena Forest (12.913°S, 49.328°E, 420 m). Each site is characterized by semi-dry deciduous forests growing on different types of substrate; Site 2 was largely a karstic formation with dry deciduous forest. Between 16 November and 6 December 2023, we conducted inventories of amphibians and reptiles at these three sites.

This survey utilized three standard techniques recommended for herpetofaunal surveys by Raxworthy and Nussbaum (1994), which have already been implemented in other surveys throughout Madagascar: (1) direct observations along biotope transects, (2) refuges examinations (under and/or in fallen trees and rotten tree stumps; under bark; under rocks; in leaf litter and soil), and (3) pitfall trap systems. In addition to these three survey approaches, we also incorporated a fourth method that utilized call data from vocalizing species (frogs) to better capture cryptic and rare amphibian diversity (Vences *et al*., 2006). During the day or night surveys, specifically near water sources and honing in on the calls of male frog species, we were able to identify certain species. Our sampling took place during the period of transition between the dry and rainy seasons, coinciding with increased activity of most reptile and amphibian species. Sampling was conducted opportunistically during the day and at night using headlamps and hand-held torchlights along transects and trails as well as in and around streams and temporary ponds. Throughout the survey, three pitfall lines were placed following topographical features within each study site: along ridge crests, (2) sloped, and (3) valleys within 200 m of a stream. Representative individuals of most encountered taxa were photographed to document coloration and pattern. Voucher specimens were euthanized using chlorobutanol, then fixed in 12.5% buffered formalin and transferred to 65% ethanol (amphibians) and 75% ethanol (reptiles) for permanent storage. Collected materials were deposited at the Université d'Antananarivo, Mention Zoologie et Biodiversité Animale (Madagascar, UADBA).

We classified species occurrence records following the distribution records of Glaw and Vences (2007) and updated scientific names following the taxonomy of recent publications (Goodman *et al*., 2018; Antonelli *et al*., 2022; Goodman, 2022; Uetz *et al*., 2024; AmphibiaWeb 2025). In this study, we also incorporated species lists from Goodman *et al*. (2018) and new information from subsequent fieldwork (Raherilalao *et al*., 2022; Radonirina *et al*., 2023). In cases when we were uncertain about species identification (e.g., juveniles) or the first record for a taxon known a considerable distance from the site, we used the specific epithet of the morphologically most similar species, using the prefix "cf." to designate this uncertainty. In certain cases for potentially new species awaiting formal description, we highlighted this aspect with "sp."

Data analysis

We categorized our observations into one of three categories: rare, abundant, and very abundant. Species represented by one or two observations were categorized as rare (+). Depending on the known behavior of the species in consideration, this class included both fossorial species and cryptically-colored species. Species represented by 5-10 observations were categorized as abundant (++) and species that we recorded between 11-20 observations for were categorized as very abundant (+++).

To assess the relative contributions of the Andrafiamena-Andavakoera protected area to the maintenance of northern Madagascar herpetofaunal diversity, a comparative analysis was carried out using the Jaccard similarity index (Magurran, 1988) based on the presence or absence of the species at other sites in the northern portion of the island that have already been inventoried using the same techniques. The sites considered have comparable ecological characteristics to the three principal study sites within Andrafiamena-Andavakoera. These sites include the Montagne des Français, Ankarana, and Analamerana. We used a hierarchical clustering analysis based on Jaccard's similarity coefficients for binary data to generate dendrograms based on amphibian and reptile species presence/absence. We identified clusters and subclusters for amphibians and reptiles by visually examining the resulting cluster tree and grouping states that shared common nodes, taking into account the Jaccard distances using the base R environment (R Core Team, 2024).

To evaluate the proportion of threatened and endangered species in the protected area, we used the conservation risk assignments for each species following the most up to date global IUCN Red List

(IUCN, 2024). We also evaluated the population trends for each species based on the IUCN Red List in comparison to our updated observations in this region.

Results

Species richness and composition

The amphibian and reptile diversity of the Andrafiamena-Andavakoera protected area recorded during this survey included a total of 52 species, 13 amphibians and 39 reptiles, at the three survey sites (Table 1), with some species representing new taxa for the site or undescribed species. Across all the three study sites, we detected a clear dominance of reptile diversity relative to amphibian diversity with respect to species richness (Figure 1). All three sites had equivalent reptile species richness, whereas amphibian species richness varied more widely. The highest number of amphibian and reptiles species was recorded at Site 2 (n = 36), and the lowest was at Site 1 (n = 31).

Our biological inventory revealed the presence of 13 different frog species, frequently observed along streams. Of the total reptile diversity, 24 species records were lizards, including the geckos *Phelsuma roesleri* (Figure 2A), *Geckolepis megalepis* (Figure 2B), *Uroplatus fetsy* (Figure 2C), *U. garamaso* (Figure 2D), and *U. fivehy* (Figure 2E), as well as numerous chameleons. Other reptile diversity included snakes, 15 species in total, such as the nocturnal *Madagascarophis colubrinus* (Figure

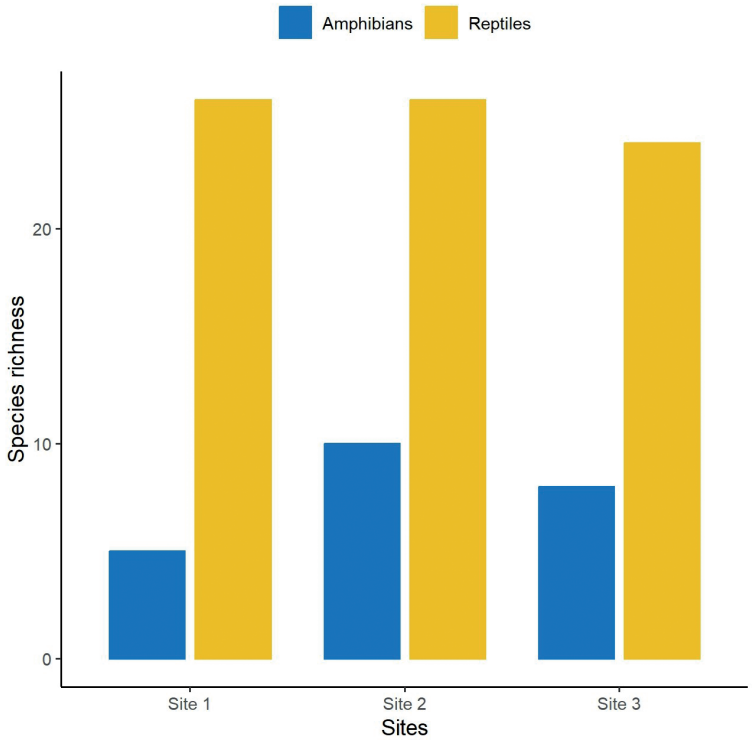

Figure 1. Species richness of the amphibians and reptiles among the three surveyed sites in the Andrafiamena-Andavakoera protected area.

Table 1. Checklist of amphibians and reptiles for all three surveyed sites in the Andrafiamena-Andavakoera protected area along with regional endemism, IUCN Red List status and habitat preference. Regionally designated endemism categories for Madagascar: N: north, NW: northwest, NE: northeast, E: east, W: west; No: Not endemic to Madagascar; IUCN Red List Categories: LC: Least Concern; VU, Vulnerable; EN: Endangered.

Taxa	Endemism	IUCN status	Habitat	Site 1	Site 2	Site 3
AMPHIBIANS						
Hyperoliidae						
Heterixalus luteostriatus	Madagascar	LC	Forest edge		+	
Mantellidae						
Aglyptodactylus securifer	W, NW	LC	Dry forest, terrestrial, sandy and litter	+++	++	+++
Blommersia wittei	N, NW	LC	Streamside habitats		++	
Boophis cf. *occidentalis*	N, NW		*Tsingy* forest		++	

Table 1. (continued)

Taxa	Endemism	IUCN status	Habitat	Site 1	Site 2	Site 3
Boophis tephraeomystax	Madagascar	N	Degraded forest , open area	++	++	++
Gephyromantis cf. *atsingy*	W	EN	*Tsingy* forest	++	+++	
Mantidactylus ambreensis	N, NW	LC	Forest, semi-aquatic, streamside habitat			++
Mantidactylus bellyi	N, NE	LC	Forest, semi-aquatic, streamside habitat	+++		+++
Mantidactylus cf. *biporus*	N		Forest, semi-aquatic, streamside habitat			++
Mantidactylus manerana	N, NW		Forest, semi-aquatic, streamside habitat		+++	++
Mantella viridis	N	EN	Streamside open forest	+++	+++	
Microhylidae						
Stumpffia larinki	N		Forest edge, terrestrial, litter		++	++
Ptychadenidae						
Ptychadena mascareniensis	N	LC	Open area humid, ubiquitous		+++	++
Total amphibians: 13				**5**	**10**	**8**
REPTILES						
Chamaeleonidae						
Brookesia stumpffi	N, NW	LC	Forest, litter	++	++	++
Furcifer oustaleti	Madagascar	LC	Open area, dry forest, arboreal			++
Furcifer pardalis	N, NW, NE	LC	Forest edge, arboreal	++	+++	++
Furcifer petteri	N, NW, NE	LC	Forest edge, arboreal	++	++	++
Scincidae						
Flexiseps cf. *tanysoma*	NW		Forest, thick litter associated with sandy soil	+++		
Flexiseps ornaticeps	Madagascar	LC	Forest, thick litter associated with sandy soil			+
Madascincus miafina	N		Forest, thick litter associated with sandy soil	+++	++	++
Trachylepis elegans	Madagascar	LC	Forest, forest edge, open area, terrestrial	+++	++	
Trachylepis gravenhorstii	Madagascar	LC	Forest, forest edge, open area, terrestrial	++		
Gerrhosauridae						
Zonosaurus haraldmeieri	N	LC	Forest, forest edge, terrestrial	+++	++	
Zonosaurus laticaudatus	Madagascar	LC	Forest, streamside forest, terrestrial, rupicolous	+++		
Zonosaurus rufipes	N, NW, NE	LC	Forest, terrestrial, litter	+++		
Gekkonidae						
Blaesodactylus boivini	N	VU	Dry forest, arboreal, hole in tree trunk		++	++
Geckolepis megalepis	N	LC	Dry forest, arboreal, hole in tree trunk	++	++	+++
Hemidactylus mercatorius complex	Not	LC	Open degraded forest, habitation		++	
Lygodactylus heterurus	N	LC	Forest, *tsingy,* arboreal, litter	++	++	++
Paroedura oviceps	N,NW	LC	Forest, dead tree, arboreal	+++		
Paroedura stumpffi	N, NW	LC	Forest, litter, terrestrial and rupicolous		++	++
Phelsuma abbotti	N, W, NE, NW	LC	Forest edge and open forest, arboreal	++	++	++
Phelsuma grandis	N	LC	Forest, forest edge, habitation, arboreal	+++	+++	++
Phelsuma roesleri	N	EN	Forest, *Pandanus* associated with *tsingy* forest		++	++
Uroplatus fetsy	N		Dry forest on *tsingy*, arboreal (branch)	+	++	
Uroplatus garamaso	N		Dry forest, arboreal (branch, tree trunk)	++	++	++
Uroplatus cf. *fivehy*	N		Dry forest, arboreal (branch, leaf, lianas)	+		
Sanziniidae						
Sanzinia cf. *volontany*	Madagascar		Forest, streamside habitat, wetland			+
Pseudoxyrhophiidae						
Dromicodryas quadrilineatus	N, NE	LC	Forest edge, open area, terrestrial	++	++	++
Ithycyphus miniatus	Madagascar	LC	Forest, forest edge, arboreal	++	++	++
Langaha cf. *madagascariensis*	Madagascar	LC	Forest, forest edge, arboreal			+
Leioheterodon madagascariensis	Madagascar	LC	Forest edge, open area, terrestrial	++		++
Leioheterodon modestus	Madagascar	LC	Forest edge, open area, terrestrial		++	++
Liophidium therezieni	N	VU	*Tsingy* forest, litter, terrestrial		+	
Liophidium torquatum	Madagascar	LC	Forest, litter, terrestrial	++		++
Lycodryas inopinae	N	EN	Dry *tsingy* forest, arboreal (*Pandanus*)		++	
Madagascarophis colubrinus	Madagascar	LC	Forest, streamside habitat, terrestrial, rupicolous	++	++	++
Madagascarophis cf. *fuchsi*	N		Forest, streamside habitat, terrestrial, rupicolous	++	++	
Phisalixella variabilis	Madagascar	EN	Forest, arboreal	+	+	
Thamnosophis lateralis	Madagascar	LC	Open area, terrestrial	++		++
Psammophiidae						
Mimophis occultus	N, NW		Open area, terrestrial		++	++
Typhlopidae						
Madatyphlops mucronatus	N		Forest, thick litter, sandy soil	+	+	+
Total reptiles: 39				**26**	**26**	**24**
Total amphibians and reptiles: 52				**31**	**36**	**32**

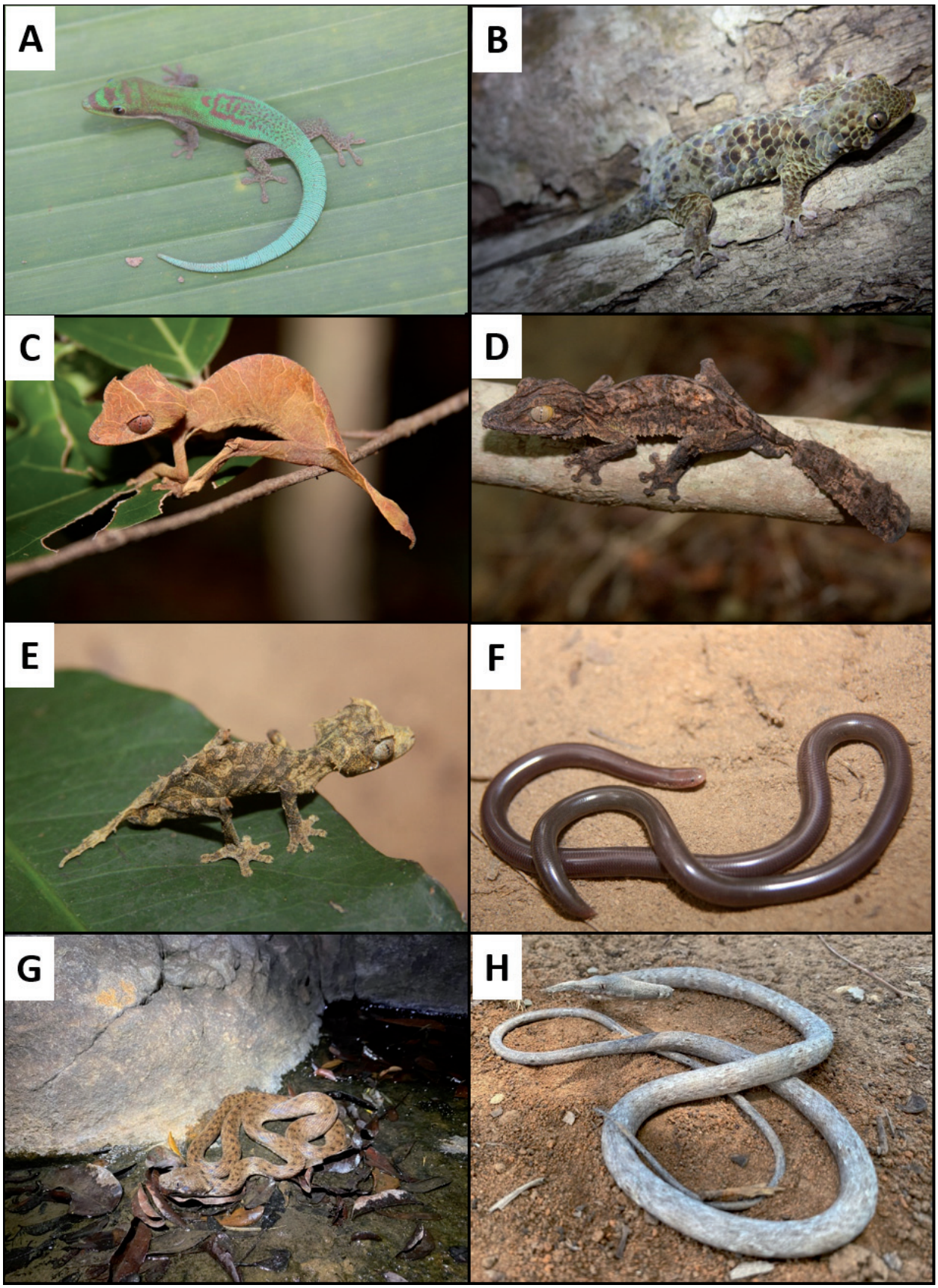

Figure 2. Photos of charismatic species present in Andrafiamena-Andavakoera **A**) *Phelsuma roesleri*, **B**) *Geckolepis megalepis*, **C**) *Uroplatus fetsy*, **D**) *U. garamaso*, **E**) *U. fivehy,* **F**) *Madatyphlops mucronatus*, **G**) *Madagascarophis colubrinus*, and **H**) *Langaha* cf. *madagascariensis*.

2G), and the fossorial worm snake *Madatyphlops mucronatus* (Figure 2F). During our fieldwork, we recorded a species of *Langaha* listed here as *Langaha* cf. *madagascariensis* (Figure 2H), based on morphological characters that we cannot attribute to other species of the genus (*L. alluaudi* or *L. pseudoalluaudi*), which are primarily identified based on the nasal appendage structures.

Most encounters took place within forest environments, with the exception of one frog (*Ptychadena mascareniensis),* four snakes (*Dromicodryas quadrilineatus*, *Leioheterodon modestus*, *Mimophis occultus,* and *Thamnosophis lateralis*) and one skink (*Trachylepis elegans*), which were all found near campsites or heavily modified open areas. A few species were recorded at the ecotone between forest and degraded secondary forest habitat. Based on our observations, spatial occupancy of both amphibians and reptiles varied from edge to the forest center. Some species were primarily found in open environments, but also observed occasionally at the forest edge and open unforested areas, such as the snakes *Dromicodryas quadrilineatus*, *Mimophis occultus*, and *Leioheterodon madagascariensis*. At Site 3, some species such as the snakes *Madagascarophis colubrinus* and *Sanzinia* cf. *volontany* and most frogs were primarily found in riparian habitats in largely intact forest areas. On the other hand, there are several species that were only observed in open forest, such as the lizards *Zonosaurus rufipes*, *Blaesodactylus boivini*, *Geckolepis megalepis*, *Paroedura oviceps*, *Phelsuma roesleri*, *Uroplatus fetsy*, and *U. garamaso*, as well as snakes such as *Liophidium therezieni*, *Lycodryas inopinae*, and *Phisalixella variabilis*.

Site 2 had the greatest habitat heterogeneity, with vegetation gradients influencing the spatial distribution of species in the local community. Across all three surveyed sites, chameleons were found in vertical vegetation strata, from the lower levels up to the high canopy, but structured by species and size. For example, we observed *Brookesia stumpffi* in the terrestrial leaf litter or perched on young shoots and small branches no more than 1 m high, while other larger species such as *Furcifer pardalis* and *F. petteri* were found perching in the upper or middle stratum. Arboreal snakes and geckos also exploit different vegetation heights from the lower stratum to the top, depending on the species. For the most part, the amphibians and reptiles recorded in the Andavakoera-Andrafiamena protected area represent widely distributed species in northern Madagascar. The ranges of many species recorded in our survey represent taxa with distributions throughout much of the dry deciduous or semi-deciduous forests of the north.

Conservation status

The three surveyed forest parcels of the Andrafiamena-Andavakoera protected area are home to seven species currently classified as threatened on the IUCN Red List. Of these, two are classified as Vulnerable, including one gecko (*Blaesodactylus boivini*) and one snake (*Liophidium therezieni,* Figure 3A). Five are listed as Endangered, including two frogs (*Gephyromantis* cf. *atsingy* [Figure 3B] and *Mantella viridis* [Figure 3C]), one gecko (*Phelsuma roesleri*) and two snakes (*Lycodryas inopinae* [Figure 3D] and *Phisalixella variabilis*). It should be noted that most of these species currently have disjunct distributions, probably associated with human-induced forest fragmentation; many known only from two or three localities and are rarely encountered during herpetological surveys. The exception is *Mantella viridis,* which occurs at multiple localities throughout extreme northern Madagascar. Our survey results help elucidate the habitat preferences of these threatened species, and clearly shows the important role of the Andrafiamena-Andavakoera protected area in the protection of remaining suitable forest habitat.

Conservation threats

The amphibians and reptiles of the Andrafiamena-Andavakoera protected area are not under immediate, direct threats. However, human activities, particularly along riparian and in swamp habitats, are resulting in habitat disturbance and degradation, and in turn, impact abundance and distribution of forest-dependent species. Plants of the genera *Pandanus*, *Raphia*, and *Ravenala*, especially those found in wetlands, constitute specific biotopes for numerous species of amphibians and certain reptiles, as well as acting as important habitat for hunting and reproduction. Dead wood with holes, cracks or detachable bark, whether standing or fallen, are hiding places for many species of lizard, especially as daytime retreats for nocturnal geckos such as *Blaesodactylus boivini* and *Geckolepis megalepis.* These woody resources are frequently exploited as firewood by local communities. In the long term, these ongoing activities could contribute to population

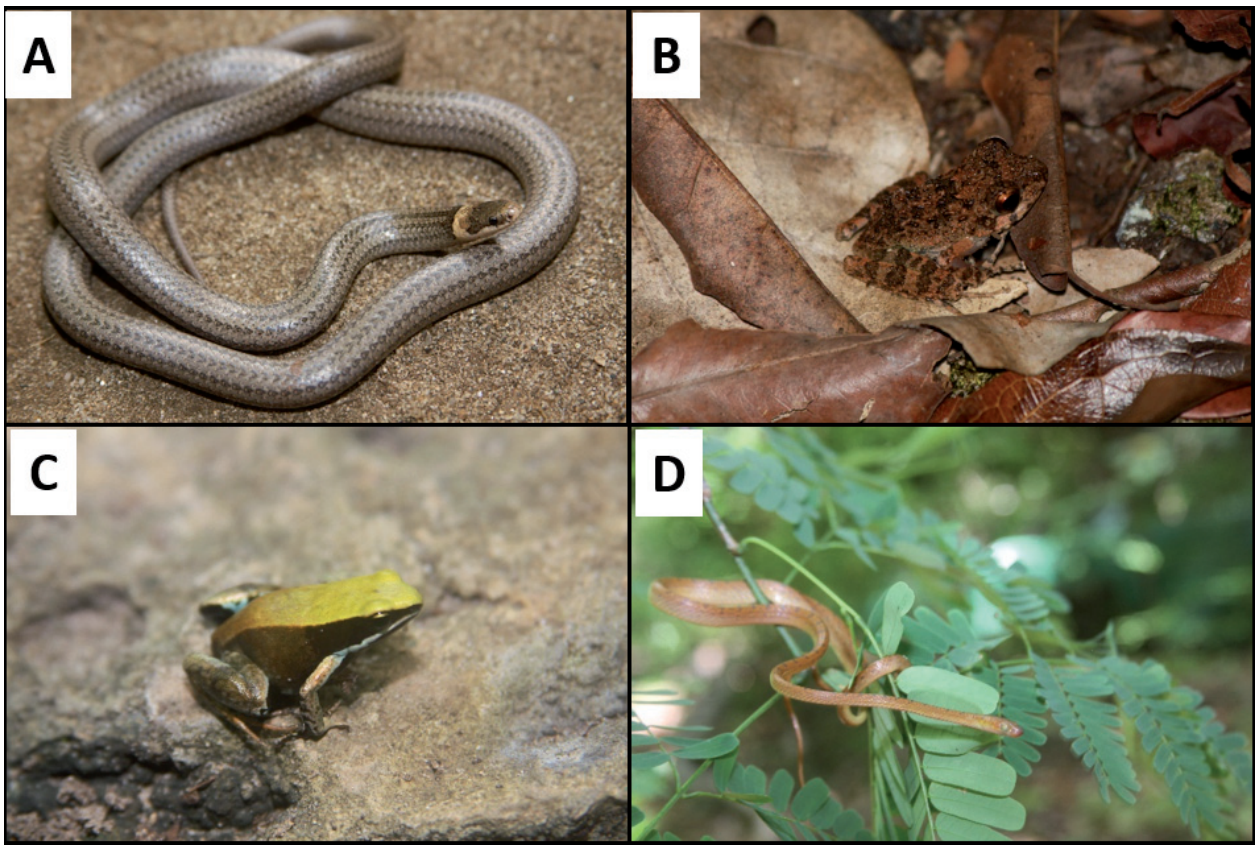

Figure 3. Photographs of representative snake and frog species recorded in Andrafiamena-Andavakoera protected area: **A**) *Liophidium therezieni*, **B**) *Gephyromatis* cf. *atsingy*, **C**) *Mantella viridis*, and **D**) *Lycodryas inopinae*.

declines, especially for tree-dwelling geckos that rely on dead wood habitat to lay their eggs.

Biogeographic affinities

The Andrafiamena-Andavakoera forests, composed of forest habitat mosaics, have shaped the structure of the local herpetofaunal community, in particular its diversity and spatial distribution. For example, the *tsingy* habitat with its geological and vegetational particularities, has a reptile and amphibian fauna with numerous morphological adaptations. To underscore the role of this protected area in conserving reptile and amphibian diversity in dry forest formations of northern Madagascar, we performed a comparative biogeographic analysis of the amphibian and reptile communities at the three sites and made comparisons to other nearby reasonably well-studied protected areas with similar vegetation formations: Analamerana, Montagne des Français, and Ankarana. Table 2 summarizes species richness and composition of each respective herpetofaunal community of the compared sites.

These four sites share 21 species of amphibians and reptiles, but each showing some differences with respect to the other sites. It should be noted that some taxa only identified to the genus level in Goodman *et al*. (2018) have representative specimens in the scientific collections at the University of Antananarivo and obtained before 2023. We worked on these collections based on the recent taxonomic literature to provide species determinations and compare material from the 2023 fieldwork. These include *Uroplatus* sp.1 and *Uroplatus* cf. *henkeli* in Goodman *et al*. (2018) and both are identified as the recently named species, *U*. *garamaso* (Glaw *et al*., 2023). Some names have also been corrected in line with recent taxonomic revisions, including *Ebenavia inunguis,* now recognized as *E*. *safari* (Hawlitschek *et al*., 2018), and *Mimophis mahfalensis* does not exist in the north of the island and is represented by *M*. *occultus* (Ruane *et al*., 2018).

To assess the biogeographic affinities of the herpetofaunal communities across these four sites, we present a dendrogram showing the relationships between them (Figure 4). Andrafiamena-Andavakoera, with its 52 documented species, shows a close affinity with Ankarana, with 47% similarity, as compared to the two other sites. The two sites are not only geographically proximate, but also very similar ecologically, with dry deciduous forest occurring on karst formations. Nevertheless,

Table 2. Comparisons of species richness across three ecologically similar protected areas in northern Madagascar – Analamerana (ANA), Ankarana (ANK), Montagne des Français (MDF) compared to Andrafiamena-Andavakoera (AND) (Goodman *et al*., 2018; Raherilalao *et al*., 2022; Radonirina *et al*., 2023, present study, and recent publications and systematic revisions (Hawlitschek *et al*., 2018; Ruane *et al*., 2018; Rakotoarison *et al*., 2022; Glaw *et al*., 2023). *= presence of the species

Taxa	ANA	ANK	MDF	AND
Amphibians				
Heterixalus luteostriatus	*	*		*
Heterixalus variabilis		*		
Boophis tephraeomystax	*		*	*
Boophis roseipalmatus	*			
Boophis cf. *occidentalis*			*	*
Aglyptodactylus securifer	*	*	*	*
Laliostoma labrosum	*	*	*	
Blommersia wittei	*	*		*
Gephyromantis atsingy				*
Gephyromantis pseudoasper		*		*
Mantella ebenaui	*			
Mantella viridis		*	*	*
Mantidactylus ambreensis				*
Mantidactylus bellyi	*	*	*	*
Mantidactylus manerana				*
Mantidactylus cf. *biporus*				*
Tsingymantis antitra		*		
Ptychadena mascareniensis	*	*	*	*
Cophyla phyllodactyla		*		
Rhombophryne sp.	*			
Stumpffia angeluci			*	
Stumpffia be		*		
Stumpffia larincki		*		*
Stumpffia madagascariensis			*	
Stumpffia mamitika		*		
Stumpffia staffordi			*	
Stumpffia sp.	*			
Hoplobatrachus tigerinus	*	*	*	
Total amphibians	**12**	**15**	**11**	**14**
Reptiles				
Crocodylus niloticus		*		
Pelusios castanoides	*		*	
Brookesia confidens		*		
Brookesia ebenaui		*	*	
Brookesia peyrierasi	*			
Brookesia stumpffi	*	*	*	*
Brookesia tristis			*	
Furcifer oustaleti	*	*	*	*
Furcifer pardalis	*	*	*	*
Furcifer petteri	*	*	*	*
Blaesodactylus boivini	*	*	*	*
Blaesodactylus microtuberculatus		*		
Ebenavia safari			*	
Geckolepis maculata	*	*	*	*
Geckolepis megalepis		*		*
Geckolepis sp.			*	
Hemidactylus frenatus			*	
Hemidactylus mercatorius			*	*
Lygodactylus expectatus		*		
Lygodactylus heterurus	*	*	*	*
Lygodactylus rarus		*		
Paroedura homalorhina		*		
Paroedura hordiesi			*	
Paroedura karstophila		*		
Paroedura lohatsara			*	
Paroedura oviceps				*
Paroedura stumpffi	*	*	*	*
Phelsuma abbotti	*	*	*	*
Phelsuma grandis	*	*	*	*
Phelsuma roesleri		*		*
Uroplatus ebenaui			*	*
Uroplatus sp. 1		*		*
Uroplatus fetsy		*		*
Uroplatus garamaso	*			*
Zonosaurus boettgeri		*	*	
Zonosaurus laticaudatus				*
Zonosaurus haraldmeieri	*	*		*
Zonosaurus rufipes		*		*
Zonosaurus tsingy		*	*	
Flexiseps alluaudi		*		
Flexiseps ardouini	*		*	
Flexiseps melanurus	*			*
Flexiseps ornaticeps		*		*
Flexiseps cf. *tanysoma*				*
Madascincus miafina		*	*	*
Madascincus stumpffi	*		*	*
Paracontias hildebrandti	*			
Trachylepis elegans	*	*	*	*
Trachylepis tavaratra	*	*	*	*
Trachylepis gravenhorstii				*
Acrantophis madagascariensis	*	*	*	
Sanzinia cf. *volontany*	*	*	*	*
Alluaudina bellyi		*	*	
Alluaudina mocquardi		*		
Dromicodryas bernieri			*	
Dromicodryas quadrilineatus	*	*	*	*
Heteroliodon fohy			*	
Heteroliodon lava		*		
Ithycyphus miniatus			*	*
Langaha madagascariensis		*	*	
Langaha pseudoalluaudi			*	
Leioheterodon madagascariensis	*	*	*	*
Leioheterodon modestus		*	*	*
Liophidium therezieni		*	*	*
Liophidium torquatum	*	*	*	*
Lycodryas gaimardi	*			
Lycodryas granuliceps		*	*	*
Lycodryas inopinae		*	*	*
Madagascarophis colubrinus	*	*	*	*
Madagascarophis cf. *fuchsi*	*		*	*
Madagascarophis lolo		*		
Pararhadinaea melanogaster	*	*		
Phisalixella variabilis		*		*
Pseudoxyrhopus microps				*
Pseudoxyrhopus quinquelineatus			*	
Thamnosophis lateralis	*		*	*
Thamnosophis martae			*	
Thamnosophis stumpffi			*	
Mimophis occultus	*	*	*	*
Indotyphlops braminus			*	
Madatyphlops mucronatus	*	*		*
Madatyphlops sp. 2			*	
Total reptiles	**32**	**50**	**51**	**46**
Total amphibians and reptiles	**44**	**65**	**62**	**52**

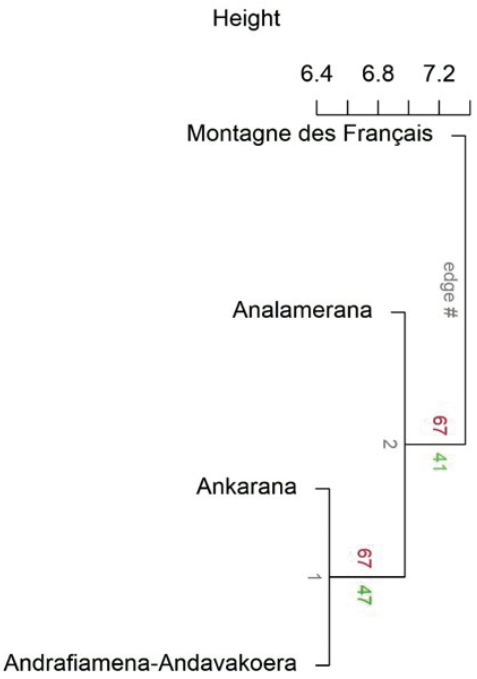

Figure 4. Dendrogram of clustering results displaying affinities of amphibian and reptile communities in four protected areas of northern Madagascar: Analamerana, Ankarana, Andrafiamena-Andavakoera, and Montagne des Français.

many species known in Ankarana have not yet been found in Andrafiamena-Andavakoera. The ecological landscape of Ankarana is much more heterogeneous and with different environmental conditions than Andrafiamena-Andavakoera, thus offering greater habitat diversity. Also of importance, Ankarana has been the subject of diverse herpetological surveys over the past decades, while the 2023 work in Andrafiamena-Andavakoera, was the first focused work on this location.

Discussion

Specific richness patterns in northern Madagascar

In Goodman *et al*. (2018), six species of amphibians and 21 reptiles are recorded from the Andrafiamena-Andavakoera and these lists are based on unpublished data and information from the literature. The results of our late 2023 biological inventory of the site almost double these estimates, with a total of 52 herpetofauna species, including 13 amphibians and 39 reptiles. Notably, nine of the 26 species cited in Goodman *et al*. (2018) were not recorded during this survey, including two amphibians (*Gephyromantis pseudoasper* and *Stumpffia* sp.) and seven reptiles (*Geckolepis maculata*, *Flexiseps melanurus*, *Madascincus stumpffi*, *Trachylepis tavaratra*, *Lycodryas granuliceps*, and *Pseudoxyrhopus microps*). In many cases we can now infer the unidentified species presented by Goodman *et al*. (2018). For example, *Gephyromantis pseudoasper*, *G. atsingy*, and *G. corvus* are morphologically similar (Crottini *et al*., 2011; Scherz *et al*., 2024). The species *G. pseudoasper* cited in Goodman *et al*. (2018) is largely terrestrial and found in the leaf litter or perched on leaves in humid and intact forest habitat (Glaw & Vences, 2007). The name "*atsingy*" refers to the type of habitat (karst formation) frequented by this species, first described in Bemaraha National Park (Crottini *et al*., 2011). The individuals attributed to *G*. cf. *atsingy* in the present study also frequent dry karst forests and were found active on *tsingy* rock in the evening after a light rain. A molecular analysis would be interesting to investigate the status of the *G*. cf. *atsingy* from this study with respect to the *G. corvus* are described recently by Sherz *et al*. (2024) from the north of Madagascar. Alternatively, it is possible that both species are not related but display convergent morphology associated with similar ecological adaptations. Given our limited sample sizes for morphological examination, molecular verification of our samples could help resolve this potential discrepancy given the considerable distance between Andrafiamena-Andavakoera and Tsingy de Bemaraha. There are no known records of *Stumpffia* in Andrafiamena-Andavakoera (Goodman *et al*., 2018). However, several new species of *Stumpffia* have recently been described from the Réserve Spéciale d'Ankarana (Rakotoarison *et al*., 2017). Based on the diagnostic morphological characters presented in these descriptions, the individuals we captured at Site 3 most likely correspond to *S. larinki*. It is highly probable that the *Stumpffia* sp. mentioned in Goodman *et al*. (2018) is *S. larinki* given the similar ecology of these two protected areas and their close proximity.

The reptiles listed in Goodman *et al*. (2018) for Andrafiamena-Andavakoera that we did not observe during our survey, such as *Flexiseps melanurus*, *Trachylepis tavaratra*, *Lycodryas granuliceps*, and *Pseudoxyrhopus microps*, are widespread in northern Madagascar. It is likely that their absence during our inventory are associated with their secretive natures and habitat preferences, and perhaps the stochastic nature of detecting animals during brief inventories. For example, *T. tavaratra* is a common species in northern Madagascar, known from Montagne d'Ambre, Ankarana, and Analamerana (Ramanamanjato *et al*., 1999). The

present survey only covered three forest parcels of Andrafiamena-Andavakoera over a limited period and during a single season and it is possible that this species was simply missed. Other discrepancies likely originate from recent taxonomic revisions. These include *Geckolepis megalepis* (Scherz *et al*., 2017b) vs *G. maculata*, *Uroplatus garamaso* (Glaw *et al*., 2023) vs *U*. sp. aff. *henkeli*, *U. fetsy* (Ratsoavina *et al*., 2019) vs *U. ebenaui,* and *Madascincus miafina* (Miralles *et al*., 2016) vs *M. stumpffi*. Linking these updated taxonomic changes to previous survey records is important to accurately represent herpetofaunal diversity over time for use in protected area management. We are able to remediate many of these records through recent literature surveys and direct comparison of specimens housed in the University of Antananarivo collections. Many of these uncertainties can be resolved with additional data (e.g., molecular), given the list presented in Goodman *et al*. (2018) is a compilation of previously published data, and no targeted herpetofaunal surveys have been conducted in this area until this expedition.

The Andrafiamena-Andavakoera protected area represents a significant refuge for biodiversity representative of the northern part of Madagascar. As our species accumulation curves (Figure 5) did not reach a plateau towards the end of each site, inventory strongly suggests that other species were not found. Major weather fluctuations has an important influence on the activity patterns of amphibians and reptiles. A light rain towards the end of the afternoon at Site 2, for example, enabled us to find frog species that we had not been seen before despite several days of surveying. These included *Blommersia wittei*, *Stumpffia mamitika*, and *Boophis* cf. *occidentalis*. We expect that multiple surveys of a given site, particularly during different seasons, are needed to document the majority of reptile and amphibian species.

At least 56 species of reptiles and amphibians are present in the Andrafiamena-Andavakoera protected area. This site has one of the highest herpetofauna measures of species diversity for any protected area in the north of Madagascar with dry forest formations. Compared to Analamerana and Ankarana, only Montagne des Français exceeds Andrafiamena-Andavakoera in terms of herpetofaunal richness with 69 species comprised of 19 amphibians and 50 reptiles (Radonirina *et al*., 2023).

Species composition and interaction

The composition of species in a given biological community might be informative about possible interspecific interactions between species (Raselimanana, 2008). Indeed, the diversity of prey species such as amphibians and lizards, including geckos, skinks, and chameleons, would correspond to the proliferation of predators such as snakes. We have seen a few cases, such as the tree snake

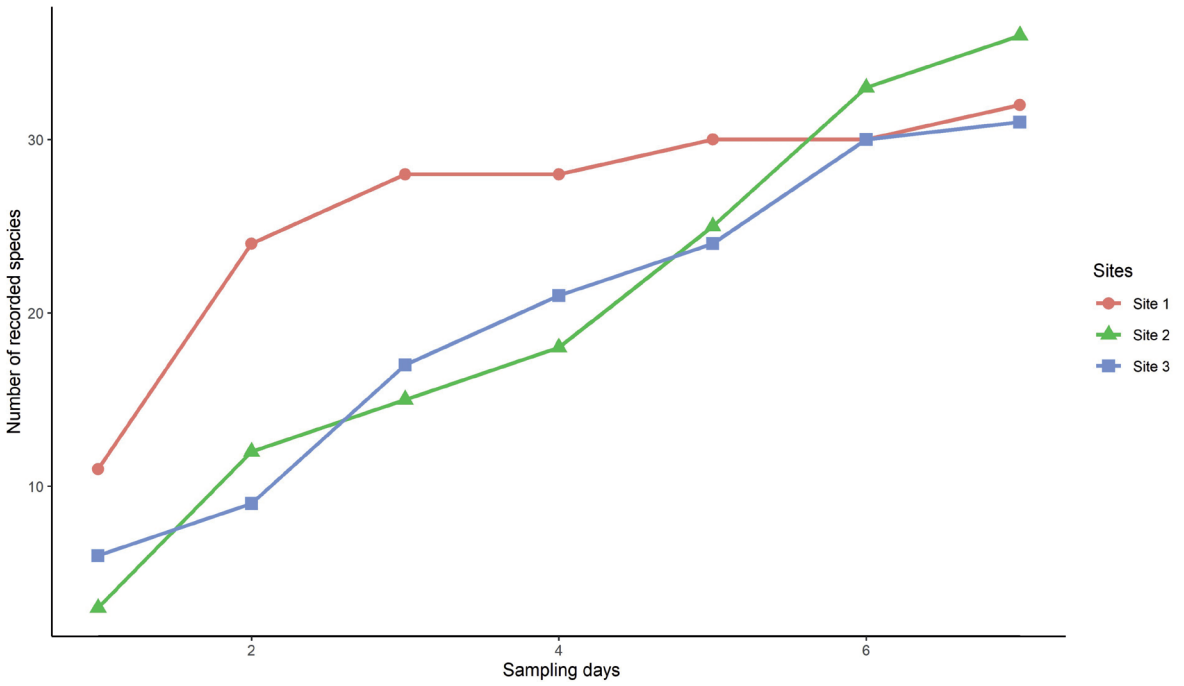

Figure 5. Species accumulation curves for both amphibians and reptiles at the three study sites in the Andrafiamena-Andavakoera protected area.

Ithycyphus miniatus regurgitating a large male chameleon, *Furcifer oustaleti.*

Extension of geographical ranges

A large number of species were recorded for the first time during the late 2023 inventory of the Andrafiamena-Andavakoera protected area. Some of the species are already known to occur in Ankarana and/or Analamerana. These include *Blaesodactylus boivini*, *Brookesia stumpffi*, *Mantella viridis,* and two species of snakes *Dromicodryas quadrilineatus* and *Madagascarophis* cf. *fuchsi*. Some species only observed in the other nearby protected areas occur at these three survey sites in Andrafiamena-Andavakoera. These include *Madascincus miafina*, previously known only from Ankarana and Montagne des Français (Miralles *et al*., 2016), *Geckolepis megalapis* (see Figure 2B) and *Uroplatus fetsy* (see Figure 2C) from Ankarana (Ratsoavina *et al*., 2019). We recorded *Phelsuma roesleri* (see Figure 2A) a day gecko described from Ankarana (Glaw *et al*., 2010) at the karstic Site 2; it was found at night resting in a *Pandanus* leaf 4 m off the ground. Our observations of these species in Andrafiamena-Andavakoera extends their ranges further north.

Conclusion

With the newly available information resulting from the late 2023 inventory of Andrafiamena-Andavakoera, we can conclude that the protected area harbors a diverse amphibian and reptile community. The species richness and composition highlight the site's specificity of the northern Madagascar ecoregion. The absence of certain expected species may be attributed to weather-associated aspects or simply by chance. Our results indicate that these species assemblages are likely excellent indicators for monitoring the ecological integrity of habitats in the Andrafiamena-Andavakoera protected area. Despite information available on the ecological distributions and habitat preferences available in the literature for these taxa, gaps in our knowledge regarding the primary ecological factors driving the diversification in Andrafiamena-Andavakoera still remain. We update these records with several geographical range extensions for reptile species as well as species-specific habitat preferences and ecological interactions.

Studies using standardized protocols to examine patterns of occurrence of reptiles and amphibians in relation to environmental gradients require robust baseline data, as Goodman *et al*. (2018) represents for this area. Increasingly important are resurveys of sites over time given the cryptic nature of these species, the number of undescribed taxa which still remain, and the rapid habitat modifications currently taking place in these forested regions. This need is clearly emphasized by the number of new species records found during our survey alone. Other questions that remain in need of additional information relate to compatibility between conservation initiatives and sustainable use of the Andrafiamena-Andavakoera protected area to leverage this interesting and endemic biodiversity to bolster ecotourism, while at the same time supporting continued infrastructural and financial support for this important natural area.

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References

Antonelli, A., Smith, R. J., Perrigo, A. L., Crottini, A., Hackel, J. *et al*. 2022. Madagascar's extraordinary biodiversity: Evolution, distribution, and use. *Science*, 378 (6623): 1-9.

AmphibiaWeb. 2025. <https://amphibiaweb.org> University of California, Berkeley. Accessed 11 March 2024.

Andreone, F., Randrianirina, J. E., Jenkins, P. D. & Aprea, G. 2000. Species diversity of Amphibia, Reptilia and Lipotyphla (Mammalia) at Ambolokopatrika, a rainforest between the Anjanaharibe-Sud and Marojejy massifs, NE Madagascar. *Biodiversity and Conservation*, 9: 1587-1622.

Andreone, F., Cadle, J. E., Cox, N., Glaw, F., Nussbaum, R. A., Raxworthy, C. J., Stuart, S. Vallan, D. & Vences, M. 2005. Species review of amphibian extinction risks in Madagascar: Conclusions from the global amphibian assessment. *Conservation Biology*, 19 (6): 1790-1802.

Brown, J. L., Sillero, N., Glaw, F., Bora, P., Vieites, D. R. & Vences, M. 2016. Spatial biodiversity patterns of Madagascar's amphibians and reptiles. *PLoS ONE*, 11 (1): e0144076. doi:10.1371/journal.pone.0144076

Carné, A. & Vieites, D. R. 2024. A race against extinction: The challenge to overcome the Linnean amphibian shortfall in tropical biodiversity hotspots. *Diversity and Distributions*, 00: e13912.

Crottini, A., Glaw, F., Casiraghi, M., Jenkins, R. K. B., Mercurio, V., Randrianantoandro, C. J., Randrianirina, J. E. & Andreone, A. 2011. A new *Gephyromantis* (*Phylacomantis*) frog species from the pinnacle karst of Bemaraha, western Madagascar. *ZooKeys*, 81: 51-71.

D'Cruze, N. & Kumar, S. 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. *Animal Conservation*, 14: 542-552.

D'Cruze, N., Green, K. E., Robinson, J. E. & Gardner, C. J. 2006. A rapid assessment of the amphibians and reptiles of an unprotected area of dry deciduous forest in north Madagascar. *Herpetological Bulletin*, 96: 17-25.

D'Cruze, N., Sabela, J., Green, K., Dawnson, J., Gardner, C., Robinson, J., Starkie, G., Vences, M. & Glaw, F. 2007. The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. *Herpetological Conservation and Biology*, 2 (2): 87-99.

D'Cruze, N., Köhler, J., Franzen, M. & Glaw, F. 2008. A conservation assessment of the amphibians and reptiles of the Forêt d'Ambre Special Reserve, north Madagascar. *Madagascar Conservation & Development*, 3 (1): 144-54.

D'Cruze, N., Henson, D. Olsson, A. & Emmet, D. 2009. The importance of herpetological survey work in conserving Malagasy biodiversity: Are we doing enough? *Herpetological Review*, 40 (1): 19-25.

Defries, R., Hansen, A., Turner, B. L., Reid, R. & Liu, J. 2007. Land use change around protected areas: Management to balance human needs and ecological function. *Ecological Applications*, 17 (4): 1031-1038.

Durkin, L., Steer, M. D. & Belle, E. M. S. 2011. Herpetological surveys of forest fragments between Montagne d'Ambre and Ankarana Special Reserve, northern Madagascar. *Herpetological Conservation and Biology*, 6 (1): 114-126.

Glaw, F. & Vences, M. 2007. *A field guide to the amphibians and reptiles of Madagascar*, 3rd edition. Vences & Glaw Verlag, Cologne.

Glaw, F., Vences, M. & Schmidt, K. 2001. A new species of *Paroedura* Günther from northern Madagascar (Reptilia, Squamata, Gekkonidae). *Spixiana*, 24 (3): 249-256.

Glaw, F., Vences, M. & Nussbaum, R. A. 2005a. A new species of *Heteroliodon* (Reptilia: Squamata: Colubridae) from Montagne des Français, far northern Madagascar. *Herpetologica*, 61 (3): 275-280.

Glaw, F., Franzen, M. & Vences, M. 2005b. New species of colubrid snake (*Liopholidophis*) from northern Madagascar. *Salamandra*, 41 (1/2): 83-90.

Glaw, F., Simone, H. & Vences, M. 2006. Discovery of a new basal relict lineage of Madagascan frogs and its implications for mantellid evolution. *Zootaxa*, 1334: 27-43.

Glaw, F., Gehring, P.-S., Köhler, J., Franzen, M. & Vences, M. 2010. A new dwarf species of day gecko, genus *Phelsuma*, from the Ankarana pinnacle karst in northern Madagascar. *Salamandra*, 46 (2): 83-92.

Glaw, F., Rösler, H., Ineich, I., Gehring, P.-S., Köhler, J. & Vences, M. 2014. A new species of nocturnal gecko (*Paroedura*) from karstic limestone in northern Madagascar. *Zoosystematic and Evolution*, 90 (2): 249-259.

Glaw, F., Vences, M. & Raxworthy, C. J. 2022. Diversity and exploration of the Malagasy reptile fauna. In *The new natural history of Madagascar*, ed. S. M. Goodman, pp. 1423-1442. Princeton University Press, Princeton.

Glaw, F., Köhler, J., Ratsoavina, F. M., Raselimanana, A. P., Crottini, A., Gehring, P.-S., Böhme, W. Scherz, M. D. & Vences, M. 2023. A new species of *Uroplatus* (Gekkonidae) from Ankarana National Park, Madagascar, of remarkably high genetic divergence. *Salamandra*, 59 (3): 239-261.

Goodman, S. M. (ed.). 2022. *The new natural history of Madagascar*. Princeton University Press, Princeton.

Goodman, S. M., Raherilalao, M. J. & Wohlhauser, S. (eds**.). 2018.** *Les aires protégées terrestres de Madagascar : Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota*. Association Vahatra, Antananarivo.

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D. & Hawkins, F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, 34: 325-333.

Hawkins, A. F. A., Chapman, P., Ganzhorn, J. U., Bloxam, Q. M. C., Barlow, S. C. & Tonge, S. J. 1990. Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. *Biological Conservation*, 54 (2): 83-110.

Hawlitschek, O., Scherz, M. D., Ruthensteiner, B., Crottini, A. & Glaw, F. 2018. Computational molecular species delimitation and taxonomic revision of the gecko genus *Ebenavia* Boettger, 1878. *The Science of Nature*, 105: 49.

IUCN. 2024. The IUCN Red List of Threatened Species. Version 2024-1. https://www.iucnredlist.org. Accessed on [August 2024].

Jenkins, R. K. B., Tognelli, M. F., Bowles, P., Cox, N., Brown, J. L., Chan, L., Andreone, F., Andriamazava, A., Andriantsimanarilafy, R. R., Anjeriniaina, M., Bora, P., Brady, L. D., Hantalalaina, E. F., Glaw, F., Griffiths, R. A., Taylor, G. H., Hoffmann, M.,

Katariya, V., Rabibisoa, N. H., Rafanomezantsoa, J., Rakotomalala, D. R., Rakotondravony, H., Rakotondrazafy, N. A., Ralambonirainy, J., Ramanamanjato, J.-B., Randriamahazo, H., Randrianantoandro, J. C., Randrianasolo, H. H., Randrianirina, J. E., Randrianizahana, H., Raselimanana, A. P., Rasolohery, A., Ratsoavina, F. M., Raxworthy, C. J., Robsomanitrandrasana, E., Finoana, R., Van Dijk, P. P., Yoder, A. D. & Vences, M. 2014. Extinction risks and the conservation of Madagascar's reptiles. *PLoS ONE*, 9 (8): e100173.

Jono, T., Bauer, A. M., Brennan, I. & Mori, A. 2015. New species of *Blaesodactylus* (Squamata: Gekkonidae) from Tsingy karstic outcrops in Ankarana National Park, northern Madagascar. *Zootaxa*, 3980 (3): 406-416.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., Dransfield, J., Fisher, L., Glaw, F., Good, T. C., Harper, G. J., Hijmans, R. J., Lees, D. C., Louis Jr., E., Nussbaum, R. A., Raxworthy, C. J., Razafimpahanana, A., Schatz, G. E., Vences, M., Vieites, D. R., Wright, P. C. & Zjhra, M. L. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, 320 (5873): 222-225.

Köhler, J., Vences, M., D'Cruze, N. & Glaw, F. 2010. Giant dwarfs: Discovery of a radiation of large-bodied 'stump-toed frogs' from karstic cave environments of northern Madagascar. *Journal of Zoology*, 282: 21-38.

Magurran, A. E. 1988. *Ecological diversity and its measurements*. Princeton University Press, Princeton.

Megson, S., Mitchell, P. & D'Cruze, N. 2009a. Notes on geographic distribution Reptilia, Serpentes, Colubridae, *Heteroliodon fohy*: Distribution extension. *Check List*, 5 (3): 692-694.

Megson, S., Mitchell, P., Köhler, J., Marsh, C., Franzen, M., Glaw, F. & D'Cruze, N. 2009b. A comprehensive survey of amphibians and reptiles in the extreme north of Madagascar. *Herpetology Notes*, 2: 31-44.

Miralles, A., Köhler, J., Glaw, F. & Vences, M. 2016. Species delimitation methods put into taxonomic practice: Two new *Madascincus* species formerly allocated to historical species names (Squamata, Scincidae). *Zoosystematics & Evolution*, 92 (2): 257-275.

Pabijan, M., Brown, J. L., Chan, L. M., Rakotondravony, H. A., Raselimanana, A. P., Yoder, A. D., Glaw, F. & Vences, M. 2015. Phylogeography of the arid-adapted Malagasy bullfrog, *Laliostoma labrosum*, influenced by past connectivity and habitat stability. *Molecular Phylogenetics and Evolution*, 92: 11-24.

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Rabearivony, J. & Raselimanana, A. P. 2022. Chameleons (Squamata: Chamaeleonidae) as bio-Indicators. *European Modern Studies Journal*, 6 (6): 282-298.

Radonirina, H. O., Randriamahatantsoa, B., Rabibisoa, N. H. C. & Raxworthy, C. J. 2023. Amphibians and reptiles of the Montagne des Français: An update of the distribution and regional endemicity. *Animals*, 13: 3361. https://doi.org/10.3390/ani13213361.

Raherilalao, M. J., Soarimalala, V., Raselimanana, A. P., Radasimalala, V. Goodman, S. M. & Tahinarivony, J. A. 2022. Evaluation éco-biologique de la faune et de la flore de l'Aire Protégée d'Ambohitr'Antsingy (Montagne des Français), au Nord de Madagascar. *Malagasy Nature*, 16: 1-78.

Rakotoarison, A., Scherz, M. D., Glaw, F., Köhler, J., Andreone, F., Franzen, M., Glos, J., Hawlitschek, O., Jono, T., Mori, A., Ndriantsoa, S. H., Raminosoa, N. R., Riemann, J. C., Rödel, M. O., Rosa, G. M., Vieites, D. R., Crottini, A. & Vences, M. 2017. Describing the smaller majority: Integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. *Vertebrate Zoology*, 67 (3): 271-398.

Rakotoarison, A., Glaw, F., Rasolonjatovo, S. M., Razafindraibe, J. H., Vences, M. & Scherz, M. D. 2022. Discovery of frogs of the *Stumpffia hara* species group (Microhylidae, Cophylinae) on Montagne d'Ambre in northern Madagascar, with description of a new species. *Evolutionary Systematics*, 6: 21-33.

Rakotondravony, H. A. 2006. Aspects de la conservation des reptiles et des amphibiens dans la région de Daraina. *Madagascar Conservation & Development*, 1: 15-18.

Ramanamanjato, J.-B., Nussbaum, R. A. & Raxworthy, C. J. 1999. A new species of *Mabuya* Fitzinger (Squamata: Scincidae: Lygosominae) from northern Madagascar. *Occasional Papers of The University of Michigan Museum of Zoology*, 728: 1-22.

Randriamialisoa, Andriantsimanarilafy, R. R., Rakotondrina, A. J. V., Rakotoarisoa, J. A., Ranaivoson T. N., Rabearivony, J. & Raselimanana, A. P. 2023. Overview of reptile diversity from Bobaomby complex, northern tip of Madagascar. *Animals*, 3396: 1-13.

Raselimanana, A. P. 2008. Herpétofaune des forêts sèches malgaches. Dans Les forêts sèches de Madagascar, eds. S. M. Goodman & L. Wilmé. *Malagasy Nature*, 1: 46-75.

Ratsoavina, F. M., Scherz, M. D., Tolley, K. A., Raselimanana, A. P., Glaw, F. & Vences, M. 2019. A new species of *Uroplatus* (Gekkonidae) from Ankarana National Park, Madagascar, of remarkably high genetic divergence. *Zootaxa*, 4683 (1): 84-96.

Raxworthy, C. J. & Nussbaum, R. A. 1994. A rain-forest survey of amphibians, reptiles and small mammals at Montagne d'Ambre Madagascar. *Biological Conservation*, 69 (1): 65-73.

Raxworthy, C. J. & Nussbaum, R. A. 1995. Systematics, speciation, and biogeography of the dwarf chameleons *Brookesia* Gray (Reptilia; Sauria; Chamaeleontidae) of northern Madagascar. *Journal of Zoology*, 235: 525-558.

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.

Ruane, S., Burbrink, F. T., Randriamahatantsoa, B. & Raxworthy, C. J. 2016. The cat-eyed snakes of Madagascar: Phylogeny and description of a new species of *Madagascarophis* (Serpentes: Lamprophiidae) from the Tsingy of Ankarana. *Copeia*, 104 (3): 711-721.

Ruane, S., Myers, E. A., Lo, K., Yuen, S., Welt, R. S., Juman, M., Futterman, I., Nussbaum, R. A., Schneider, G., Burbrink, F. T. & Raxworthy, C. J. 2018. Unrecognized species diversity and new insights into colour pattern polymorphism within the widespread Malagasy snake *Mimophis* (Serpentes: Lamprophiidae). *Systematics and Biodiversity*, 16 (3): 229-244.

Scherz, M. D., Glaw, F., Köhler, J., Andreone, F., Franzen, M., Glos, J., Hawlitschek, O., Jono, T., Mori, A., Ndriantsoa, S. H., Raminosoa, N., Riemann, J.C., Rödel, M.-O., Rosa, G.M., Vieites, D. R., Crottini, A. & Vences, M. 2017a. Describing the smaller majority: Integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. *Vertebrate Zoology*, 67 (3): 271-398.

Scherz, M. D., Daza, J. D., Köhler, J. Vences, M. & Glaw, F. 2017b. Off the scale: A new species of fish-scale gecko (Squamata: Gekkonidae: *Geckolepis*) with exceptionally large scales. *PeerJ*, 5: e2955. DOI 10.7717/peerj.2955

Scherz, M. D., Schmidt, R., Brown, J. L., Glos, J., Lattenkamp, E. Z., Rakotomalala, Z., Rakotoarison, A., Rakotonindrina, R. T., Randriamalala, O., Raselimanana, A. P., Rasolonjatovo, S. M., Ratsoavina, F. M., Razafindraibe, J. H., Glaw, F. & Vences, M. 2023. Repeated divergence of amphibians and reptiles across an elevational gradient in northern Madagascar. *Ecology and Evolution*, 13 (3), e9914.

Scherz, M. D., Rudolph, J., Rakotondratsima, M., Ratsoavina, F. M., Crottini, A., Andreone, F., Glaw F. & Vences, M. 2024. Molecular systematics of the subgenus *Gephyromantis* (Phylacomantis) with description of a new subspecies. *Zootaxa*, 5446: 205-220.

Scott, D. M., Brown, D., Mahood, S., Denton, B., Silburn, A. & Rakotondraparany, F. 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation*, 127: 72-87.

Uetz, P., Freed, P, Aguilar, R., Reyes, F., Kudera, J. & Hošek, J. (eds.). 2024. The Reptile Database. http://www.reptile-database.org, accessed [February 26].

Vallan, D. 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation*, 96: 31-43.

Vallan, D., Andreone, F., Raherisoa, V. H. & Dolch, R. 2004. Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar. *Oryx*, 38 (4): 410-417.

Vences, M., Glaw, F. & Márquez, R. 2006. The calls of the frogs of Madagascar. Alosa, sons de la natura, FonoZoo. Barcelona, Spain. [audio CD].

Vieites, D. R., Nieto-Roman, S. & Vences, M. 2008. Towards understanding the spatial pattern of amphibian diversity in Madagascar. *Monografie del Museo Regionale di* Scienze *Naturali di Torino*, 45: 397-410.