



The Anuran Community in the Mahimborondro Protected Area in the Northern Highlands of Madagascar

Riariot Aurélien Rabenandrasana^{1*}, Angelinah Rene de Roland¹, Evianne François Haingonimonja¹, Tsiresy Maminiaina Razafimanantsoa², Lily-Arison Rene de Roland³, Gilbert Razafimanjato³, Marius Paul Hubert Rakotondratsima³, Achille Philippe Raselimanana^{2,4}, and Séraphin Fabrice³

¹Ecole Doctorale de la Biodiversité et Environnements Tropicaux, Université de Toliara, BP 304, Toliara 601, Madagascar

²Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar

³The Peregrine Fund Madagascar Program, BP 4113, Antananarivo 101, Madagascar

⁴Association Vahatra, BP 3972, Antananarivo 101, Madagascar

*Corresponding author (email: rabenandrasanaaurelien@gmail.com)

Abstract.—We conducted biological inventories of anurans during two consecutive rainy seasons, from November to December 2019 and in November 2020, at the Mahimborondro Protected Area (MPA) in the Northern Highlands of Madagascar. We employed three complementary methods: direct counts along 15 permanent transects, examination of refugia, and pitfalls along drift fences. We recorded a total of 33 species in 13 genera and four families. Four of the species are included in threatened categories of the IUCN Red List. The endemism rate is extremely high with 100% of species endemic to Madagascar. Of these, 16 (48.4%) are restricted to the Northern Highlands. Six species were classified as abundant, 11 as common, 10 as infrequent, and six species as rare at the MPA. Similarity indices show that the anuran community in the MPA differs distinctly from those in three nearby Protected Areas (Tsaratanana Reserve, Bemanevika Harmonious Landscape, and COMATSA Nord Reserve). Further investigations during various seasons and at other sites are recommended in order to learn more about anuran diversity in the MPA and to establish an effective monitoring system and conservation plan.

Madagascar is home to at least 443 anuran species in six families (Bufonidae, Dicroglossidae, Hyperoliidae, Mantellidae, Microhylidae, and Ptychadenidae) with an extremely high endemism rate of 99.3% (AmphibiaWeb 2026). According to the IUCN Red List, 34% (n = 147) of Malagasy's anuran species are threatened, 21 classified as critically endangered (CR), 82 as endangered (EN), and 44 species as vulnerable (VU) (IUCN 2025). Anurans of Madagascar exhibit a spatial distribution influenced by ecological gradients, humidity, and elevation (Nussbaum et al. 1999; Ramanamanjato 2007; Andreone et al. 2018). In addition, some species are specialists and require particular ecological conditions and habitats for their survival (Raxworthy and Nussbaum 1997; Wilmé et al. 2012; Brown et al. 2016). Also, anurans occupy different niches, with species being diurnally or nocturnally active and exploiting terrestrial, semiaquatic, or arboreal habitats (Glaw and Vences 2007; Randriamoria 2011; Andreone et al. 2018).

The Northern Highlands of Madagascar are characterized by a high specific richness and diversity of anurans mainly due to the wide variety of ecological conditions and

topography in the region, including several mountains such as Tsaratanana, Marojejy, and Anjanaharibe-Sud, which represent biogeographic refuges and centers of endemism, as well as supporting a rich variety of habitats (Andreone et al. 2018). The Mahimborondro Protected Area (MPA) covers an area of 75,472 ha of mid-elevation evergreen rainforest at elevations of 800–1,800 m. It has a wide variety of wetlands, including lakes, streams, swamps, and marshes, with the ecosystem complex of marshland and swamp vegetation serving as an important water reservoir for surrounding watersheds. In addition, volcanic lakes temporarily filled with water add to the complexity of ecological niches, which clearly indicates that the MPA is faunistically rich (Goodman et al. 2018).

MPA provides habitat for at least 23 species of anurans. However, little information is available on the anuran species richness in this area and many more species are likely to be discovered. Goodman et al. (2018) suggested that documenting more species and gathering more information on anuran species richness and diversity, abundance, endemism rate, distribution, ecology, and natural history is crucial for developing conservation and management plans. We herein

seek to enhance the available data on the anuran community, especially natural habitat requirements for conservation.

Methods

Study Sites.—The Mahimborondro Protected Area (officially Réserve de Ressources Naturelles de Mahimborondro or Category VI of IUCN) is located in the Northern Highlands of Madagascar (−14.16667– −14.50000; 48.58333–49.00000). MPA was established in 2015 according to decree no. 2015–782 of 28 April 2015. The Mahimborondro Forest forms a corridor linking the Bemanevika Protected Area (protected landscape) and the Tsaratanana Protected Area (strict nature reserve) and is part of Madagascar’s largest northern protected landscape named CAPAM (Complexe des Aires Protégées d’Ambohimirahavy-Marivorahona). The MPA is managed by The Peregrine Fund, which has had an active presence in the management of the Bemanevika PA since 2006 (Mittermeier et al. 2020).

The Mahimborondro Forest is situated on metamorphic rock dating from the Paleoproterozoic and Neorchean Eras. The flora includes typical elements and species endemic to the Sambirano Domain in northern Madagascar (Goodman et al. 2018). The MPA comprises 75,472 ha of montane

humid forests, savannah, and wetlands that include streams and swamps. It is dominated by a sub-humid climate with annual rainfall averaging 1,583 mm (in 1981–2017), of which 79% falls between November and April. The coldest season between June and August has temperatures dropping as low as 3.5 °C; the warmest season between December and February has peak temperatures above 28.5 °C (Goodman et al. 2018).

We visited five sites in the MPA at elevations of 1,455–2,000 m asl: Andohan’Ambondrona (site 1), Ambendrambe (site 2), Bekavahy (site 3), Andohan’Agnalila (site 4) and Andohan’Agnadabo (site 5) (Fig. 1). We scheduled fieldwork to coincide with the rainy season, during which most anurans mate and breed and activity is highest (Andreone 1994, 1996). Due to logistical challenges accessing our study sites, we collected data during two successive rainy seasons. During the first season from 26 November to 17 December 2019, we explored three sites (Andohan’Ambondrona, Ambendrambe, Bekavahy) in the middle to the southern parts of the MPA. During the second season from 10–23 November 2020, we surveyed two sites (Andohan’Agnalila and Andohan’Agnadabo), which are in the northern part of the MPA. Characteristics of each site are detailed in Table 1.

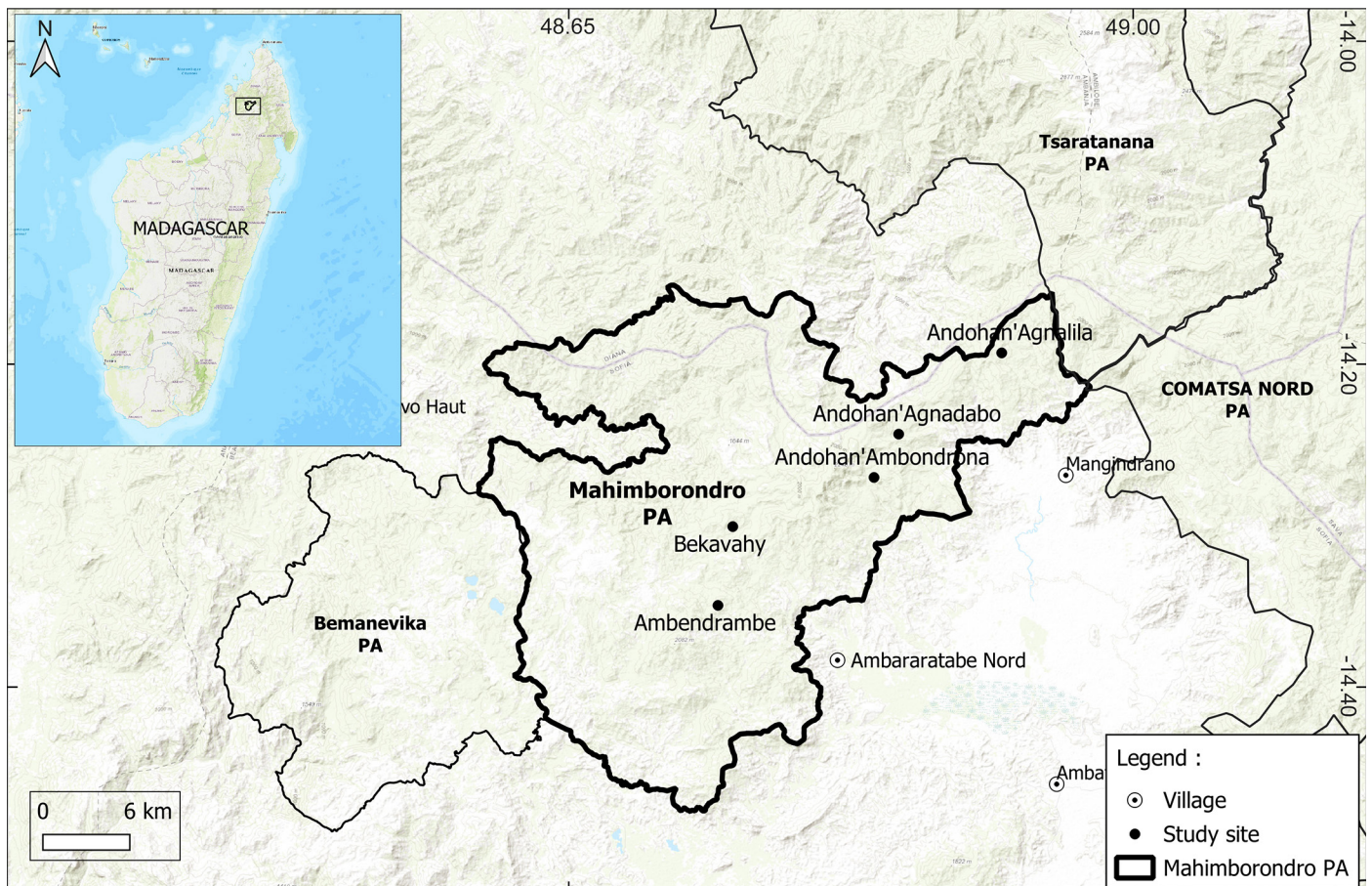


Figure 1. Map of the Mahimborondro Protected Area showing the locations of the five study sites in the Northern Highlands of Madagascar.

Table 1. Site localities surveyed in Mahimborondro Protected Area, Northern Madagascar, 25 November to 16 December 2019 and 10–23 November 2020.

Site (coordinates; elevation [m asl])	Forest type	Wetland
Site 1 (-14.27014, 48.83931; 1455–1720 m)	Continuous dense humid forest, less degraded and disturbed	Streams, temporary lakes
Site 2 (-14.34939, 48.74253; 1475–1640 m)	Continuous dense humid forest, quite degraded and disturbed	Streams, swamps
Site 3 (-14.30058, 48.75172; 1570–1730 m)	Continuous dense humid forest, relatively intact	Streams
Site 4 (-14.19300, 48.91850; 1665–1800 m)	Continuous dense humid forest, mosaic and intact	Streams, temporary lakes
Site 5 (-14.24331, 48.85461; 1640–1750 m)	Continuous dense moist and disturbed forest	Streams, temporary lakes, swamps

Biological Inventories.—We used three complementary survey methods: Direct counts, examination of refugia, and pitfall traps. Five persons conducted direct counts by day and night along three line transects 800–1,500 m in length over a period of 12 hours per day for six days at each study site (i.e., 72 h/site). Diurnal counts were during the hottest time of the morning (0800–1200 h) and when temperatures began to drop in the afternoon (1400–1600 h) (Raherilalao et al. 2022). Nocturnal visits using headlamps spanned six hours (1800–2400 h). Observers walked slowly (~1 km/h), detecting anurans by sight (in headlamp beams at night) or locating them by tracking the vocalization of calling males.

Examination of refugia involved using a stump ripper to examine various microhabitats once along each transect. This facilitated the detection of secretive and cryptic species, especially those that seek shelter under tree bark, sheathing leaves of palm trees, dead wood, and cracks in rocks. Pitfall traps consisted of buckets (275 mm deep, 290 mm diameter at the top) sunk in the ground at 10-m intervals along a 100-m-long drift fence. Small holes 2 mm in diameter in the bottom of each bucket allowed water to drain. The fence (0.5 m high) of plastic sheeting stapled to thin wooden stakes was buried 50 mm deep and positioned to traverse the middle of each pitfall trap (Raxworthy and Nussbaum 1994). Three trap lines were installed at each study site, one in the valley, one on the slope, and one on the ridge. Trap lines were checked in the morning and in the afternoon over five successive days at each site.

We identified all species encountered using two field guides (Glaw and Vences 2007; Andreone et al. 2018) and recent articles (Rakotoarison et al. 2017, 2024; Scherz et al. 2017, 2019, 2022; Rancilhac et al. 2020; Vences et al. 2022, 2023, 2024; Koppetsch et al. 2023; Rabibisoa et al. 2023). For all individuals encountered, we recorded date and time, GPS coordinates, macro- and microhabitat, and abundance. Some were collected for subsequent identification and analy-

sis. Each collected specimen was photographed to document the natural color prior to preservation (Randriamoria 2011). Collected specimens were euthanized by immersion in chlorobutanol, fixed in 4% formalin, subsequently transferred to 70% ethanol, and accessioned in the Zoology and Animal Biodiversity (ZBA) laboratory collection at the University of Antananarivo, Madagascar.

Data Analysis.—We classified abundance of species using the system developed by D’Cruze et al. (2006, 2007): Abundant (large numbers encountered on a regular basis), common (encountered on a regular basis), infrequent (unpredictable, few individuals seen), or rare (rarely seen). We also compared the species composition of the MPA with that of surrounding Protected Areas (Bemanevika Protected landscape, COMATSA Nord Protected landscape, and Tsaratanana Strict Nature Reserve) according to Goodman et al. (2018). The choice of these areas is based on two criteria: (1) these are decreed protected areas located in the Northern Highlands of Madagascar; and (2) the inventory techniques used by researchers at the other three sites were the same as those used in this study. We assessed biogeographic affinity between these protected areas by using the Jaccard similarity index and visualized the results with a dendrogram. These analyses were performed in R software using the *vegan* (2.7-3) (Oksanen et al. 2025) and *dendextend* (1.18.1) (Galili 2015) packages. For that, we calculated a Bray-Curtis distance matrix (Bray and Curtis 1957) using presence/absence data. We performed hierarchical clustering by applying Ward’s algorithm (using the method *ward.D2*) (Murtagh and Legendre 2014).

Results

Species Richness and Abundance.—We recorded a total of 33 anuran species in 13 genera and four families (Mantellidae, Microhylidae, Hyperoliidae, Ptychadenidae) (Table 2; Fig. 2), with the highest richness of 25 species found at Bekavahy.

Table 2. Species richness, conservation status, and endemism of species recorded from November–December 2019 and November 2020 in the Mahimborondro Protected Area, Madagascar. + = present, – = absent. **Activity:** D = diurnal, N = nocturnal. **Microhabitat:** A = arboreal, T = terrestrial, B = burrowing, S = semiaquatic, U = ubiquitous. **Macrohabitat:** F = forest, E = edge. **Sites:** S1 = Andohan'Ambondrona, S2 = Ambendrambe, S3 = Bekavahy, S4 = Andohan'Aganila, S5 = Andohan'Agnadabo. **Abundance:** A = abundant (large numbers encountered on a regular basis), C = common (encountered on a regular basis), I = infrequent (unpredictable, few individuals seen), R = rare (rarely seen). **IUCN Red List Status:** CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near threatened, LC = Least concern, DD = Data deficient, NE = not evaluated. **Endemism:** E = endemic to Madagascar, E* = observed only in the Northern Highlands of Madagascar, E** = observed only in the Mahimborondro Forest.

Taxon	Activity/ Microhabitat/ Macrohabitat	S1	S2	S3	S4	S5	Abundance	IUCN	Status Endemism
Family Hyperoliidae									
<i>Heterixalus carbonei</i>	N, A/S, E	–	+	–	+	–	C	LC	E
Family Mantellidae (Laliostominae)									
<i>Aglyptodactylus madagascariensis</i>	D/N, T, F/E	+	+	+	+	+	A	LC	E
Family Mantellidae (Boophinae)									
<i>Boophis cf. entingae</i>	N, A, F	+	+	+	+	+	I	NE	E**
<i>Boophis madagascariensis</i>	N, A, F	+	–	+	–	+	I	LC	E
<i>Boophis axelmeyeri</i>	N, A, F	–	–	+	–	–	I	LC	E*
<i>Boophis cf. guibei</i>	N, A, F	+	–	–	–	–	R	NE	E**
<i>Boophis idae</i>	N, A, F	+	+	+	+	–	I	LC	E
<i>Boophis siskoi</i>	N, A, F	–	–	+	–	–	C	NE	E*
<i>Boophis tampoka</i>	N, A, F	–	–	+	–	+	R	LC	E
Family Mantellidae (Mantellinae)									
<i>Blommersia blommersae</i>	N, A/T, F/E	+	+	+	+	+	A	LC	E
<i>Blommersia wittei</i>	N, A/T, F/E	+	–	+	+	–	C	LC	E*
<i>Gephyromantis angano</i>	D/N, T/A, F	+	+	+	+	+	C	NE	E**
<i>Gephyromantis ranjomavo</i>	D, T, F	–	–	–	–	+	R	NE	E*
<i>Gephyromantis granulatus</i>	N, A, F	+	+	+	+	–	I	LC	E*
<i>Gephyromantis salegy</i>	N, A, F	+	+	–	+	+	I	VU	E*
<i>Gephyromantis tahotra</i>	N, T/A, F	+	+	–	+	+	I	VU	E*
<i>Gephyromantis saturnini</i>	N, A, F	–	–	+	–	+	I	NE	E**
<i>Guibemantis depressiceps</i>	N, A, F	–	+	–	–	+	I	LC	E
<i>Guibemantis pulcherrimus</i>	D/N, A, F	+	+	+	–	–	A	NE	E*
<i>Guibemantis razandry</i>	D/N, A, F	+	+	+	+	+	C	NE	E*
<i>Guibemantis razoky</i>	D/N, A, F	+	+	+	+	+	C	NE	E*
<i>Mantidactylus danieli</i>	N/D, T, F	–	–	+	+	+	C	NE	E*
<i>Mantidactylus jonasi</i>	D/N, S, F	–	+	–	–	+	A	NE	E*
<i>Mantidactylus zipperi</i>	D/N, T, F	+	–	+	+	+	C	LC	E
<i>Mantidactylus radaka</i>	N, S/U, F	+	–	+	+	+	A	NE	E*
<i>Spinomantis peraccae</i>	N, A, F	+	–	+	+	–	I	LC	E
Family Microhylidae (Cophylinae)									
<i>Platypelis grandis</i>	N, A, F	+	–	+	+	–	C	LC	E
<i>Platypelis saikamavo</i>	N, A, F	–	–	–	–	+	R	NE	E*
<i>Plethodontohyla guentheri</i>	N, T/B, F	–	–	+	–	–	R	EN	E*
<i>Rhombophryne laevipes</i>	N, T/B, F	–	–	+	+	–	R	LC	E
<i>Stumpffia yanniki</i>	N, T, F	–	+	+	+	+	C	NE	E*
Family Microhylidae (Scaphiophryninae)									
<i>Scaphiophryne boribory</i>	N, T/B, F	+	+	+	+	+	A	VU	E
Family Ptychadenidae									
<i>Ptychadena mascareniensis</i>	D, S, E	–	+	+	+	–	C	LC	E
Totals (n = 33 species):		19	17	25	21	20			

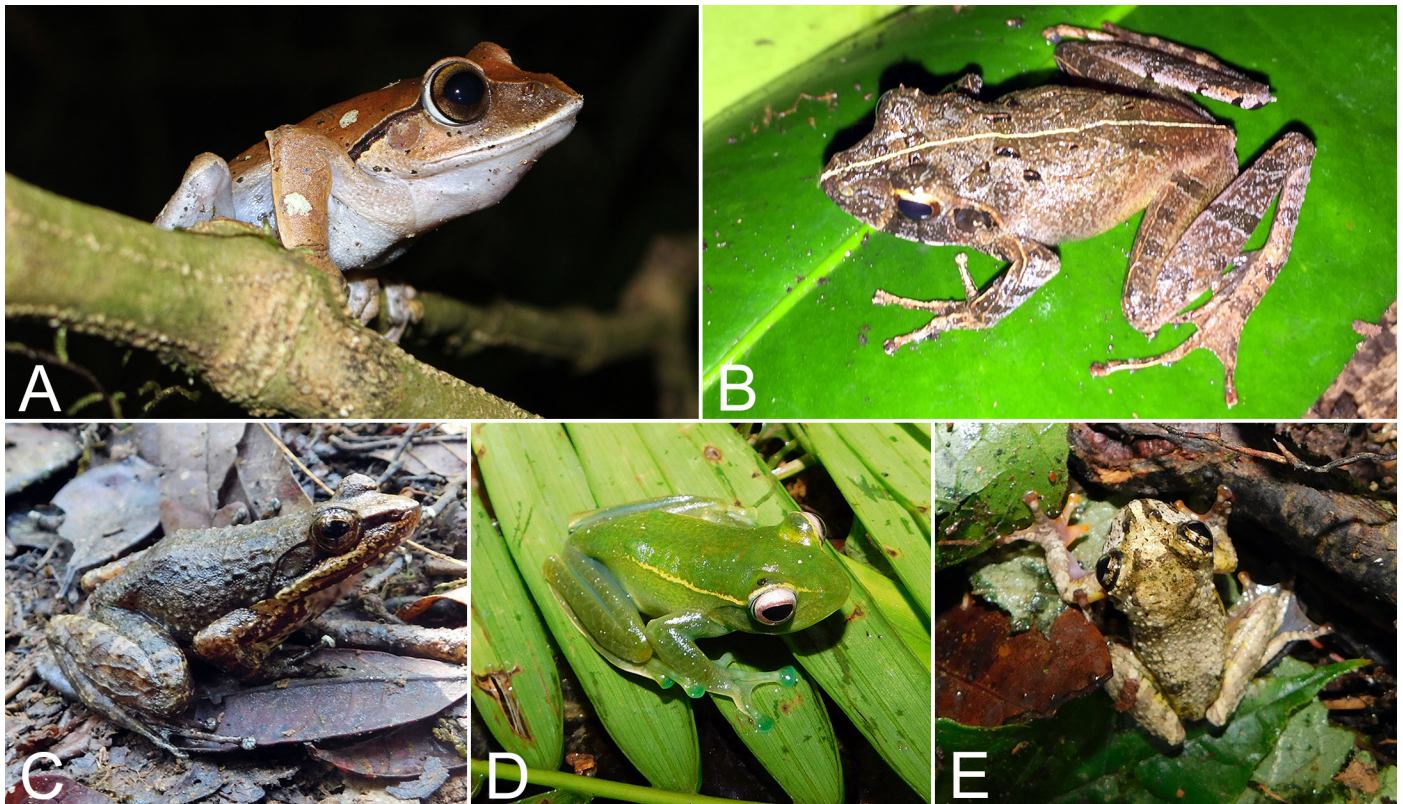


Figure 2. Representative anuran species encountered in the Mahimborondro Protected Area: *Boophis* cf. *entingae* (A), *Gephyromantis angano* (B), *Mantidactylus danieli* (C), *Boophis tampoka* (D), and *Boophis* cf. *guibei* (E).

All are endemic to Madagascar, 16 (48.4%) are only known from the Northern Highlands of Madagascar, and four (12%) are found only at the MPA. Four species (12%) are threatened according to the IUCN Red List (IUCN 2025); one (*Plethodontohyla guentheri*) is Endangered and three (*Gephyromantis salegi*, *G. tahotra*, *Scaphiophryne boribory*) are Vulnerable. Among the species inventoried, two (*Boophis* cf. *entingae* and *B. cf. guibei*) have yet to be definitively identified.

We classified six (18.2%) species as abundant, 11 (33.3%) as common, 10 (30.3%) as infrequent, and six (18.2%) as

rare (Table 2). Five species (*Platypelis grandis*, *P. saikamavo*, *Plethodontohyla guentheri*, *Boophis* cf. *guibei*, *Gephyromantis ranjomavo*) were represented by only one individual.

Macro- and Microhabitats.—Most species ($n = 28$) were found only in forest habitat, two species (*Heterixalus carbonei* and *Ptychadena mascareniensis*) exclusively along forest edges, and three (*Aglyptodactylus madagascariensis*, *Blommersia blommersae*, *B. wittei*) were found in both forest and forest edge habitats (Table 2; Fig. 3). In terms of microhabitats, 17 (51.5%) species were arboreal, five (15.15%) were terres-

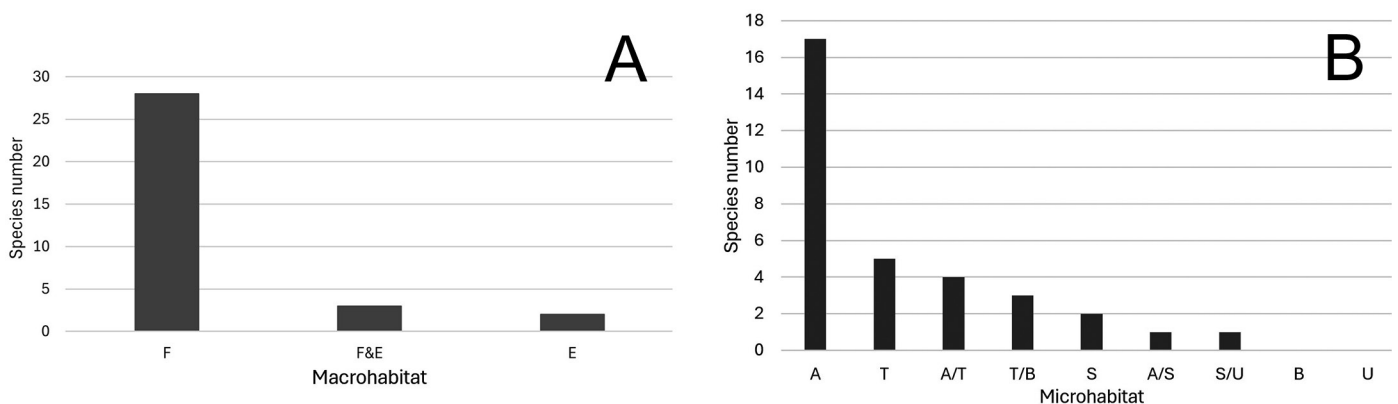


Figure 3. Histograms showing anuran species distribution related to macrohabitats (F = forest, E = forest edge) (A) and microhabitats in the Mahimborondro Forest (A = arboreal, T = terrestrial, B = burrowing, S = semiaquatic, and U = ubiquitous) (B).

trial, four (12.12%) were both arboreal and terrestrial, and two (*Mantidactylus jonasi* and *Ptychadena mascareniensis*) were semi-aquatic (Table 2; Fig. 3).

Comparisons of Species Composition.—Similarity indices of the MPA with three surrounding PAs (COMATSA Nord, Tsaratanana, and Bemanevika) ranged from 0.57 to 0.81. There is a similarity of anuran community within the three PAs (Table 3). The dendrogram (Fig. 4) shows the presence of two major groups, the first consisting of Tsaratanana, Bemanevika, and COMATSA Nord, which are very similar and have 14 species in common, whereas the second group, comprising solely Mahimborondro, a forest corridor, was characterized by 16 unique species.

Discussion

This update showing 33 species in the anuran community at the MPA dramatically increases the known number of species from the 23 reported by Goodman et al. (2018). The difference in numbers of species is likely attributable to: (1) extended effort spanning five weeks during two consecutive seasons (2019 and 2020) and (2) surveys of five sites. Comparing the results of the two studies, 14 species were included by both, seven exclusively by Goodman et al.

(2018), and 19 exclusively by this study. The seven species recorded by Goodman et al. (2018) not found during this study were *Blommersia grandisonae*, *Boophis goudotii*, *B. vittatus*, *Gephyromantis zavona*, *Mantella nigricans*, *Mantidactylus melanopleura*, and *M. mocquardi*.

Sampling effort in the MPA is illustrated as accumulation curves summarizing all recorded species (Fig. 5). Bekavahy (site 3) was the richest site with 25 species (274 individuals), whereas Ambendrambe (site 2), with 17 species (227 individuals), had the lowest diversity. This difference probably is best explained by the degree of forest degradation (e.g., Huey et al. 2009; Sinervo et al. 2010). Ambendrambe (site 2) has been more greatly affected by anthropogenic disturbance than the other sites, which probably is best explained by its greater proximity to the nearest village.

Although Mahimborondro and Bemanevika are contiguous, they appear to differ in species composition with 16 unique species at the Mahimborondro PA and five at the Bemanevika PA. A similar pattern was observed when comparing Mahimborondro to two other nearby PAs, with 13 unique species at Tsaratanana, and 15 unique species at COMATSA Nord (Goodman et al. 2018). This relatively low species overlap among sites indicates that species compo-

Table 3. Jaccard Similarity Indices comparing the anuran community in the Mahimborondro Protected Area with three other Protected Areas in the Northern Highlands of Madagascar. PA = Protected Area.

Sites	Mahimborondro PA	Bemanevika PA	COMATSA Nord PA	Tsaratanana PA
Mahimborondro PA	1	0.73	0.81	0.78
Bemanevika PA	0.73	1	0.70	0.57
COMATSA Nord PA	0.81	0.70	1	0.70
Tsaratanana PA	0.78	0.57	0.70	1

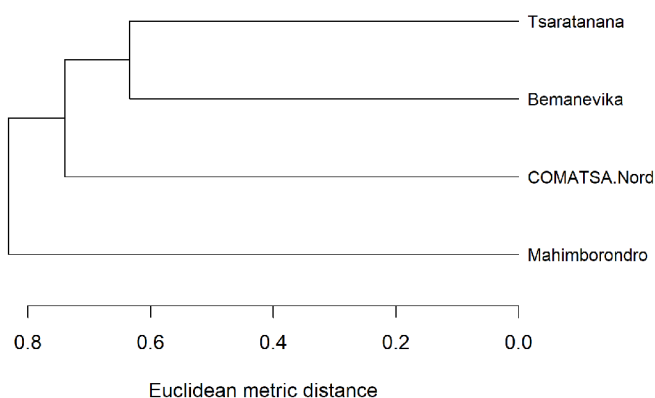


Figure 4. Dendrogram illustrating the biogeographic affinity of the anuran community of the Mahimborondro Protected Area in comparison to those of the Bemanevika, COMATSA Nord, and Tsaratanana Protected Areas.

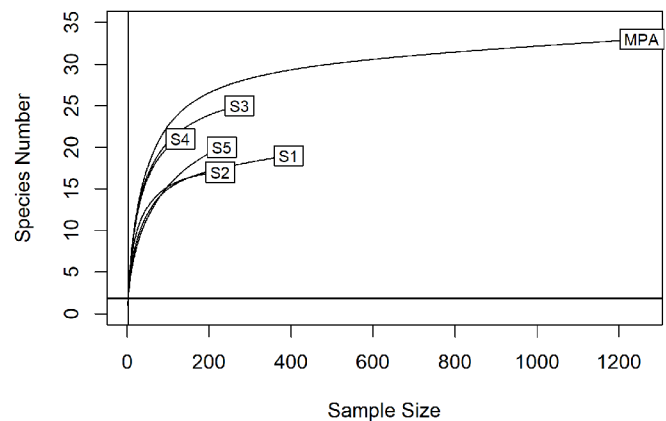


Figure 5. Accumulation curves of anuran sampling efforts in the Mahimborondro Protected Area. S1 = Andohan'Ambondrona, S2 = Ambendrambe, S3 = Bekavahy, S4 = Andohan'Agnalila, S5 = Andohan'Agnadabo.

sition varies spatially, even among areas with similar habitats and biota (Colwell 2009).

Field studies comparing some massifs (e.g., Andreone et al. 2009) clearly showed that anurans are extremely sensitive to local conditions and even minor shifts in elevation, trade wind exposure, or mean temperature can result in substantial differences in herpetofaunal species composition. Elevation at the MPA ranges from 251 m to > 2,000 m, daily temperatures vary between 10.8 °C and 20.3 °C, and average annual rainfall is about 1,583 mm (Goodman et al. 2018), whereas at the Tsaratanana PA, elevation reaches 2,876 m at Maromokotra, average temperatures are 12.4–20.8 °C, and an average annual rainfall is 1,913 mm; the Bemanevika PA has an elevational range of 501–2,000 m, average daily temperatures vary between 12.6 and 22.8 °C, and average annual rainfall is 1,677 mm; and the elevation range at the COMATSA Nord PA is 251 to > 2,000 m, average temperatures are 13–21.9 °C, and average annual rainfall is 1,863 mm. Also, the MPA is a forest corridor, which facilitates dispersal of forest-dwelling species and provides an important means of genetic exchange (Andreone et al. 2000), thus contributing to connectivity between protected areas. Another factor is the lack of herpetological surveys as few recent investigations have been conducted in the three nearby PAs, rendering the available information on anuran diversity out of date, especially considering many new anuran species recently described in Madagascar — including species found in the MPA (*Boophis siskoi*, *Guibemantis pulcherrimus*, *G. razandry*, *G. razoky*, *Gephyromantis saturnini*, *G. ranjomavo*, *Mantidactylus danieli*, *M. jonasi*, *M. radaka*, *Platypelis saikamavo*, *Stumpffia yanniki*) (Glaw and Vences 2011; Rakotoarison et al. 2017, 2024; Scherz et al. 2017, 2022; Rancilhac et al. 2020; Vences et al. 2022, 2023, 2024; Koppetsch et al. 2023; Rabibisoa et al. 2023).

The rarity of some species can usually be explained by the paucity of suitable habitats (Randriamoria 2011), but some arboreal and burrowing species could be abundant in some habitats but difficult to find. Of the species identified, *Boophis tampoka*, *Plethodontohyla guentheri*, and *Scaphiophryne boribory*, for instance, were particularly difficult to detect because of their cryptic behavior. On the other hand, species such as *Blommersia blommersae* and *Mantidactylus jonasi* were abundant, indicating that suitable habitat and ample food are available.

The heterogeneity of the ecological environment offers a high variability of biotopes for many species and increases the presence of endemic species, which makes research on biogeographic models particularly important (Andreone et al. 2009). The endemism rate of 100% in the MPA is the same as that of other nearby PAs: 100% (n = 41) in the Tsaratanana PA, 100% (n = 37) in the Bemanevika PA, and 100% (n = 42) in the COMATSA Nord PA (Goodman et al. 2018, when considering *Ptychadena mascareniensis* as a Malagasy endemic fide Zimkus et al. 2016; Kopij 2026). Anurans are influ-

enced by the suitability of particular macro- or microhabitats, as well as their ability to cope with changes in the natural environment (Raxworthy and Nussbaum 1997). Ecological requirements and tolerance of changes in the environment vary from species to species (Irwin et al. 2010). Most of the species recorded in the present study occupy forests, whereas the others were found either on forest edges or in both forests and along edges. Most available ecological niches appear to be exploited by anurans. Indeed, arboreal species are most frequently observed, followed respectively by terrestrial, terrestrial and arboreal, terrestrial and burrowing, semi-aquatic, and semi-aquatic and ubiquitous species. The predominance of arboreal species seems to be linked to the structure of the study sites. Trees provide important refuges for many species, as well as breeding and development sites for tadpoles.

Our study found that the MPA is home to several species previously considered rare and limited to specific areas, effectively extending the known ranges of these species. For instance, *Boophis tampoka*, previously known only from the Tsingy de Bemaraha PA (Glaw and Vences 2007; Andreone et al. 2018), later was reported by Vences et al. (2011) to occur in Antambato, Sahaovy, Antsatramidola, and at the bridge on the road between Antsohihy and Befandriana Nord 123 km from the Mahimborondro Forest, and at the Makira PA (Goodman et al. 2018). Our specimen (RDR 135) (36.6 mm SVL) had a green dorsum with small scattered yellowish dots and small red dots on the dorsum and head and a golden iris with an irregularly shaped brown inner ring and a blue periphery, characteristics that correspond to descriptions in Glaw and Vences (2007). *Heterixalus carbonei* was thought to be restricted to three locations, the Tsingy de Bemaraha, Kirindy, and Montagne d'Ambre PAs (Glaw and Vences 2007), but the Association Vahatra team identified some individuals in the Bemanevika PA in 2018 (Goodman et al. 2018). Our specimen (RDR 020) (22 mm SVL) had a yellow-brown dorsum with yellow dorsolateral stripes extending onto the shanks. Glaw and Vences (2007) reported *Plethodontohyla guentheri* only in the forests of the Marojejy PA but Goodman et al. (2018) recorded some individuals in the Masoala PA. Our specimen (RDR 048) (26.3 mm SVL) has adpressed tibiotarsal articulations that reached the posterior edges of the eyes, fingertips distinctly enlarged, finger 2 slightly shorter than finger 4, an almost smooth greenish dorsum with an irregular pattern of shorter light-brown lines and spots, very dark head and flanks, and distinct dorsolateral borders running from the tip of the snout to the inguinal region. *Scaphiophryne boribory* was known only from Fierenana and Marotandrano (Glaw and Vences 2007) until Rabearivony et al. (2010) confirmed its presence in the Bemanevika PA and Goodman et al. (2018) found some individuals in the COMATSA Sud and Ankeniheny-Zahamena PAs. Our specimens (RDR 013) (50–57 mm SVL) have rather smooth skin with numerous

large granules, a green dorsum with symmetrical brown markings, a contrasting black venter with rounded white spots of various sizes. *Stumpffia yanniki* was known only from a forest fragment beside National Road 31, between Bealanana and Antsohihy Districts (Rakotoarison et al. 2017). Our specimens (RDR 096) (9.5–10.7 mm SVL) had manus with four fingers (first moderately reduced in length) and pes with five toes (first distinctly reduced in length), terminal phalanges without enlarged discs, a smooth dorsum with a large contrasting central dark marking, light head and dorsolateral parts, and a grayish venter with very little light pigmentation.

Of the unidentified specimens, RDR 023 was identified as *Boophis* cf. *guibei* but differed from the original description in the color of the iris; *B. guibei* typically has a red iris (Glaw and Vences 2007; AmphibiaWeb 2026), whereas that of our specimen was black. We identified RDR 107 as *Boophis* cf. *entingae*, but the only difference with *B. entingae* were dermal spines on its heels that were much longer than those usually seen in the species. However, *Boophis entingae* is known from the Montagne d'Ambre PA, Tsaratanana, Manongarivo PA, Benavony, Masoala PA, and south within the forest corridor at Anjozorobe (Glaw et al. 2010; IUCN 2025). Although we have tentatively treated these individuals as separate taxa, definitive identification will require DNA analyses.

The presence of two species only found at Mahimborondro Forest (*Gephyromantis angano* and *G. saturnini*), four that are classified as threatened species, and the high anuran species richness emphasizes the importance of the Mahimborondro PA for anuran community conservation. Despite efforts of The Peregrine Fund, the official manager of the MPA, existing conservation measures need to be strengthened to minimize the impact of anthropogenic disturbance on anurans, especially at the Ambendrambe site, the forest block nearest to surrounding villages.

Conclusion

This biological survey conducted in the Mahimborondro Forest has provided substantial new data on the diversity and composition of the anuran communities in the Northern Highlands of Madagascar, revealing high species richness and abundance, and documenting range extensions for several species known previously from only a few localities. Our findings identify the Mahimborondro Forest as one of the highest anuran-rich sub-humid forest blocks in the nation. Furthermore, this Protected Area serves as an important refuge for at least four threatened species, all of which are conservation priorities due to their endemism, restricted ranges, and rarity. This study also reinforces the key role that habitat heterogeneity plays. However, we strongly recommend further investigations across different seasons and at additional sites and the use of molecular analyses to confirm provisional species identifications.

Acknowledgements

We thank the Ministry of Environment and Sustainable Development (MEDD) for granting permission for this research referred to the authorization 142/19/MEDD/SG/DGEF/DGRNE and for its collaboration with The Peregrine Fund - Madagascar Program. Thanks to Mr. Razafimahatratra Bertrand for his comments on the preliminary version of this manuscript. Our sincere thanks go to the University of Toliara, The Peregrine Fund - Madagascar Program and Association Vahatra Madagascar for their support and helpfulness.

Literature Cited

- AmphibiaWeb. 2026. University of California, Berkeley, California, USA. <<https://amphibiaweb.org>>.
- Andreone, F. 1994. The amphibians of Ranomafana rain forest, Madagascar – preliminary community analysis and conservation considerations. *Oryx* 28: 207–214. <http://dx.doi.org/10.1017/S003060530002857X>.
- Andreone, F. 1996. Seasonal variations of the amphibian communities in two rainforests of Madagascar, pp. 397–402. In: W.R. Lourenço (ed.), *Biogéographie de Madagascar*. Editions de l'Orstom, Paris, France.
- Andreone, F., J.E. Randrianirina, P.D. Jenkins, and G. Aprea. 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. <http://dx.doi.org/10.1023/A:1026559728808>.
- Andreone, F., F. Glaw, F. Mattioli, R. Jesu, G. Schimmenti, J.E. Randrianirina, and M. Vences. 2009. The peculiar herpetofauna of some Tsaratanana rainforests and its affinities with Manongarivo and other massifs and forests of northern Madagascar. *Italian Journal of Zoology* 76: 92–110. <http://dx.doi.org/10.1080/11250000802088603>.
- Andreone, F., A. Crottini, M.R. Goncalo, and A.P. Raselimanana. 2018. *Les Amphibiens du Nord de Madagascar*. Association Vahatra, Antananarivo, Madagascar.
- Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325–349. <http://doi.org/10.2307/1942268>.
- Brown, J.L., N. Sillero, F. Glaw, P. Bora, D.R. Vieites, and M. Vences. 2016. Spatial biodiversity patterns of Madagascar's amphibians and reptiles. *PLoS ONE* 11: e0144076. <https://doi.org/10.1371/journal.pone.0144076>.
- Colwell, R.K. 2009. Biodiversity: concepts, patterns, and measurement, pp. 258–263. In: S.A. Levin (ed.), *The Princeton Guide to Ecology*. Princeton University Press, Princeton, New Jersey, USA. <https://doi.org/10.1515/9781400833023.257>.
- D'Cruze, N., K.E. Green, J.E. Robinson, and C.J. Gardner. 2006. A rapid assessment of the amphibians and reptiles of an unprotected area of dry deciduous forest in north Madagascar. *Herpetological Bulletin* 96: 17–26.
- D'Cruze, N., J. Sabel, K. Green, J. Dawson, C. Gardner, J. Robinson, G. Starkie, M. Vences, and F. Glaw. 2007. The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. *Herpetological Conservation and Biology* 2: 87–99. <https://doi.org/10.3390/ani13213361>.
- Galili, T. 2015. dendextend: an R package for visualizing, adjusting, and comparing trees of hierarchical clustering. *Bioinformatics*. <http://doi.org/10.1093/bioinformatics/btv428>. <<https://www.rdocumentation.org/packages/dendextend/versions/1.19.1#how-to-cite-the-dendextend-package>>.
- Glaw, F. and M. Vences. 2007. *A Field Guide to the Amphibians and Reptiles of Madagascar*. Third edition. Vences & Glaw Verlag, Köln (Cologne), Germany.
- Glaw, F. and M. Vences. 2011. Description of a new frog species of *Gephyromantis* (subgenus *Laurentomantis*) with tibial glands from Madagascar (Amphibia, Mantellidae). *Spixiana*, 34 (1): 121–127.
- Glaw, F., J. Köhler, I. de la Riva, D.R. Vieites, and M. Vences. 2010. Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*. *Zootaxa* 2383: 182. <http://doi.org/10.11646/zootaxa.2383.1.1>.

- Goodman, S.M., M.J. Raherilalao, and S. Wohlhauser. 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, Madagascar.
- Huey, R.B., C.A. Deutsch, J.J. Tewksbury, L.J. Vitt, P.E. Hertz, A.H. Perez, and T.J. Garland. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceeding of the Royal Society of London B* 276: 1939–1948. <http://dx.doi.org/10.1098/rspb.2008.1957>.
- Irwin, M.T., P.C. Wright, C. Birkinshaw, B.L. Fisher, C.J. Gardner, J. Glos, S.M. Goodman, P. Loiselle, P. Rabeson, J.-L. Raharison, M.J. Raherilalao, D. Rakotondravony, A.P. Raselimanana, J. Ratsimbazafy, J.S. Sparks, L. Wilmé, and J.U. Ganzhorn. 2010. Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation* 143: 2351–2362. <https://doi.org/10.1016/j.biocon.2010.01.023>.
- IUCN [International Union for Conservation of Nature] 2025: *The IUCN Red List of Threatened Species* (version 2025-1). < <https://www.iucnredlist.org> >.
- Kopij, G. 2026. Herping the African continent: Alien amphibians and reptiles in sub-Saharan Africa. *Biology* 15: 1–27. <https://doi.org/10.3390/biology15080639>.
- Koppetsch, T., M. Pabijan, C.R. Hutter, J. Köhler, P.-S. Gehring, A. Rakotoarison, F.M. Ratsoavina, M.D. Scherz, D.R. Vieites, F. Glaw, and M. Vences. 2023. An initial molecular resolution of the mantellid frogs of the *Guibemantis* *liber* complex reveals three new species from northern Madagascar. *Vertebrate Zoology* 73: 397–432. <http://dx.doi.org/10.3897/vz.73.e94063>.
- Mittermeier, J.C., D.R. Wright, A. Benjara, R. Colyn, B. Gardner, M. Jocque, L. Kemp, A. Rene de Roland, D. Sloomackers, and L.-A. Rene de Roland. 2020. A rapid avifaunal survey of the Mahimborondro Protected Area, northern Madagascar. *Malagasy Nature* 14: 44–56.
- Murtagh, F. and P. Legendre. 2014. Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion? *Journal of Classification* 31: 274–295. <https://doi.org/10.1007/s00357-014-9161-z>.
- Nussbaum, R.A., C.J. Raxworthy, and J.B. Ramanamanjato. 1999. Additional species of *Mabuya* Fitzinger (Reptilia: Squamata: Scincidae) from western Madagascar. *Journal of Herpetology* 33: 264–280. <https://doi.org/10.2307/1565724>.
- Oksanen, J., G.L. Simpson, F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, P. Solymos, M.H.H. Stevens, E. Szocs, H. Wagner, M. Barbour, M. De Bedward, B. Bolker, D. Borcard, T. Borman, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H.B. Antoniazzi Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M.O. Hill, L. Lahti, C. Martino, D. McGlinn, M.-H. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C.J.F. Ter Braak, and J. Weedon. 2025. *vegan: Community Ecology Package*. R Package Version 2.6-8. <http://doi.org/10.32614/CRAN.package.vegan>. <<https://vegandevs.github.io/vegan/>>.
- Rabearyvony, J., A.P. Raselimanana, M.A. Andriamazava, R. Thorstrom, and L.-A. Rene de Roland. 2010. A new locality for the endangered microhylid frog *Scaphiophrynne boribory* from northern Madagascar and a rapid survey of other amphibians of the Bemanevika region. *Herpetology Notes* 3: 105–109.
- Rabibisoa, N.H.C., R.S. Welt and C.J. Raxworthy. 2023. Revision of the subgenus *Oechthomantis* frogs from Madagascar (Amphibia: Mantellidae) with the description of four species and resurrection of *Mantidactylus catalai* and *M. poissoni*. *Animals* 13: 2800. <https://doi.org/10.3390/ani13172800>.
- Raherilalao, M.J., V. Soarimalala, A.P. Raselimanana, V. Radasimalala, S.M. Goodman, and J.A. Tahinarivony. 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., M.D. Scherz, F. Glaw, J. Köhler, F. Andreone, M. Franzen, J. Glos, O. Hawlitschek, T. Jono, A. Mori, S.H. Ndirantsoa, N.R. Raminosoa, J.C. Riemann, M.-O. Rödel, G.M. Rosa, D.R. Vieites, A. Crottini, and M. Vences. 2017. Describing the smaller majority: integrative taxonomy reveals twenty-six new species of tiny microhylid frogs (genus *Stumpffia*) from Madagascar. *Vertebrate Zoology* 67: 271–398. <https://doi.org/10.3897/vz.67.e31595>.
- Rakotoarison, A., M. Vences, F. Andreone, A. Crottini, F. Glaw, M.D. Scherz, and A.P. Raselimanana. 2024. A new species of colorful *Platypelis* (Amphibia: Microhylidae) from the Tsaratanàna and Bemanevika Massifs in northern Madagascar. *Zootaxa* 5501: 171–180 <https://doi.org/10.11646/zootaxa.5501.1.8>.
- Ramanamanjato, J.-B. 2007. Reptile and amphibian communities along the humidity gradient and fragmentation effects in the littoral forests of southeastern Madagascar, pp. 167–179. In: J.U. Ganzhorn, S.M. Goodman, and M. Vincelette (eds.), *Biodiversity, Ecology and Conservation of Littoral Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin)*. Series editor A. Alonso. SI/MAB Series #11. Smithsonian Institution, Washington, D.C., USA.
- Rancilhac, L., T. Bruy, M.D. Scherz, E.A. Pereira, M. Preick, N. Straube, M.L. Lyra, A. Ohler, J. W. Streicher, F. Andreone, A. Crottini, C.R. Hutter, J.C. Randrianantoandro, A. Rakotoarison, F. Glaw, M. Hofreiter, and M. Vences. 2020. Target-enriched DNA sequencing from historical type material enables a partial revision of the Madagascar giant stream frogs (genus *Mantidactylus*). *Journal of Natural History* 54: 87–118. <https://doi.org/10.1080/00222933.2020.1748243>.
- Randriamoria, T.M. 2011. Un premier aperçu de la diversité herpétofaunique d'un bloc forestier isolé, la forêt sèche de Beanka, dans la partie Ouest de Madagascar. *Malagasy Nature* 5: 75–88.
- Raxworthy, C.J. and R.A. Nussbaum. 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Conservation Biology* 69: 65–73. [https://doi.org/10.1016/0006-3207\(94\)90329-8](https://doi.org/10.1016/0006-3207(94)90329-8).
- Raxworthy, C.J. and R.A. Nussbaum. 1997. Biogeographic patterns of reptiles in eastern Madagascar, pp. 124–141. In: S.M. Goodman and B. Patterson (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D.C., USA.
- Scherz, M.D., M. Vences, J. Borrell, L. Ball, D.H. Nomenjanahary, D. Parker, M. Rakotondratsima, E. Razafimandimby, T. Starnes, J. Rabearyvony, and F. Glaw. 2017. A new frog species of the subgenus *Asperomantis* (Anura, Mantellidae, *Gephyromantis*) from the Bealanana District of northern Madagascar. *Zoosystematics and Evolution* 93: 451–466. <https://doi.org/10.3897/zse.93.14906>.
- Scherz, M.D., J. Köhler, M. Vences, and F. Glaw. 2019. A new yellow-toed *Platypelis* species (Anura, Microhylidae, Cophylinae) from the Maroantsetra region, northeastern Madagascar. *Evolutionary Systematics* 3: 75–83. <http://dx.doi.org/10.3897/evolsyst.3.33417>.
- Scherz, M.D., A. Crottini, C.R. Hutter, A. Hildenbrand, F. Andreone, T.R. Fulgence, G. Köhler, S.H. Ndirantsoa, A. Ohler, M. Preick, A. Rakotoarison, L. Rancilhac, A.P. Raselimanana, J.C. Riemann, M.-O. Rödel, G.M. Rosa, J.W. Streicher, D.R. Vieites, J. Köhler, M. Hofreiter, F. Glaw, and M. Vences. 2022. An inordinate fondness for inconspicuous brown frogs: integration of phylogenomics, archival DNA analysis, morphology, and bioacoustics yields 24 new taxa in the subgenus *Brygomantis* (genus *Mantidactylus*) from Madagascar. *Megataxa* 7: 113–311. <https://doi.org/10.11646/megataxa.7.2.1>.
- Sinervo, B., F. Méndez-de-la-Cruz, D.B. Miles, B. Heulin, E. Bastiaens, M.V.-S. Cruz, R. Lara-Resendiz, N. Martínez-Méndez, M.L. Calderón-Espinosa, R.N. Meza-Lázaro, H. Gadsden, L.J. Avila, M. Morando, I.J. de la Riva, P.V. Sepúlveda, C.F.D. Rocha, N. Ibargüengoytia, C.A. Puntriano, M. Massot, V. Lepetz, T.A. Oksanen, D.G. Chapple, A.M. Bauer, W.M. Branch, J. Clobert, and J.W. Sites, Jr.. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899. <https://doi.org/10.1126/science.1184695>.
- Vences, M., J. Köhler, D.R. Vieites, and F. Glaw. 2011. Molecular and bioacoustic differentiation of deep conspecific lineages of the Malagasy tree frogs *Boophis tampoka* and *B. luteus*. *Herpetology Notes* 4: 239–246.
- Vences, M., J. Köhler, A. Crottini, M. Hofreiter, C.R. Hutter, L. du Preez, M. Preick, A. Rakotoarison, L. Rancilhac, A.P. Raselimanana, G.M. Rosa, M.D. Scherz, and F. Glaw. 2022. An integrative taxonomic revision and redefinition of *Gephyromantis* (*Laurentomantis*) *malagasy* based on archival DNA analysis reveals four new mantellid frog species from Madagascar. *Vertebrate Zoology* 72: 271–309. <http://dx.doi.org/10.3897/vz.72.e78830>.
- Vences, M., C.R. Hutter, F. Glaw, A. Rakotoarison, A.P. Raselimanana, and M.D. Scherz. 2023. A new species of *Pandanus*-dwelling frog from northern Madagascar related to *Guibemantis pulcher*. *Zootaxa* 5306: 97–115. <https://doi.org/10.11646/zootaxa.5306.1>.
- Vences, M., J. Köhler, C.R. Hutter, M. Preick, A. Petzold, A. Rakotoarison, F.M. Ratsoavina, F. Glaw, and M.D. Scherz. 2024. Communicator whistles: a trek through the taxonomy of the *Boophis marojejensis* complex reveals seven new, morphologically cryptic treefrogs from Madagascar (Amphibia: Anura: Mantellidae). *Vertebrate Zoology* 74: 643–681. <https://doi.org/10.3897/vz.74.e121110>.
- Wilmé, L., M. Ravokatra, R. Dolch, D. Schurman, E. Mathieu, H. Schuetz, and P.O. Waerber. 2012. Toponyms for centers of endemism in Madagascar. *Madagascar Conservation and Development* 7: 30–40.
- Zimkus, B.M., L.P. Lawson, M.F. Barej, C.D. Barratt, A. Channing, K.M. Dash, J.M. Dehling, L.H. Du Preez, P.S. Gehring, E. Greenbaum, V. Gvoždík, J. Harvey, J. Kielgast, Z.K. Chifundera, Z.T. Nagy, M. Pabijan, J. Penner, M.O. Rödel, M. Vences, and S. Lötters. 2016. Leapfrogging into new territory: How Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. *Molecular Phylogenetics and Evolution* 106: 254–269. <https://doi.org/10.1016/j.ympev.2016.09.018>.