



## Microendemism in Madagascar: small ranges or sampling gaps? The case of the frog *Wakea madinika*

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**Abstract.** Madagascar is one of the most biodiverse regions on Earth, with exceptionally high amphibian species richness and endemism, though increasingly threatened. Over recent decades, amphibian research efforts have intensified; however, many species remain documented from one or few localities, leading to the hypothesis that they may be micro-endemics. Among these is *Wakea madinika*, a Data Deficient mantellid frog species described in 2002 and reported only once from a single cacao plantation in the Sambirano region. We provide novel genetic and distribution data from newly discovered populations, analyse its potential distribution range, and revise its conservation status. Our findings reveal populations within the Sambirano River valley and beyond, significantly expanding its range from one to five localities, covering a minimum convex polygon of 1600 km<sup>2</sup> in northwestern Madagascar. Distribution models identified the Sambirano basin as highly suitable for the presence of the species, with additional potential habitats extending northward and southward, highlighting areas that may host undiscovered populations. The discovery of populations in unexpected localities, including Réserve Spéciale d'Ankarana and Sorobe, challenges its previous micro-endemic classification and confirms the species' presence south of the Sambirano River and much further north. Genetic data revealed unexpectedly low intraspecific divergence (0.66%) considering the geographical range and small body size, suggesting population level dispersal greater than previously thought. Populations on both sides of the Sambirano River shared identical mitochondrial sequences, indicating recent gene flow. This suggests that the river, long considered a barrier, may not have recently hindered gene flow as previously thought. Except for Ankarana, the species is only known from cacao plantations, suggesting it may be a forest dweller persisting in suboptimal habitats. We recommend reclassifying *W. madinika* as Endangered on the IUCN Red List based on our findings. Our study challenges the generalization of micro-endemism and underscores the importance of exploring Madagascar's lesser-sampled secondary habitats to understand species distributions better, address the Wallacean shortfall, and inform conservation strategies.

Key words. Amphibia, Anura, Mantellidae, Wallacean shortfall, micro-endemism, distributions, conservation, Madagascar.

### Introduction

Tropical regions harbour most of the world's biodiversity while experiencing the highest rates of decline and ex-

tinction (TRACEWSKI et al. 2016, MOURA & JETZ 2021, CEBALLOS et al. 2017, FINN et al. 2023). They are also the least explored and scientifically understood (MOURA & JETZ 2021, ŠMÍD 2022). Among them, Madagascar is one of the

regions with the highest biodiversity on Earth, with exceptionally high levels of species richness and endemism (GOODMAN 2022). It ranks among the top biodiversity hotspots for conservation priority (MYERS et al. 2000), partly because of the severe reduction and fragmentation of the pristine habitats that harbour this exceptional biodiversity, mainly rainforests (HARPER et al. 2007, VIELLEDENT et al. 2018). Despite being considered one of the best-explored and studied tropical biodiversity hotspots, especially for amphibians (NORI et al. 2020), many regions of the island remain largely unexplored, and the Linnean and Wallacean shortfalls are still remarkable (VIEITES et al. 2008, ANDRIAMALISOA & LANGRAND 2022, CARNÉ & VIEITES 2024). The island represents only 0.11% of the Earth's surface but holds ca. 5.4% of the world's frog species richness (425 species; FROST 2024). Moreover, current rates of frog species descriptions are exponential, with no signals of slowing down (ANTONELLI et al. 2022), and there is a significant undescribed diversity, likely doubling those currently described, still waiting for a taxonomic assessment (CARNÉ & VIEITES 2024).

Despite the increased sampling effort in Madagascar during the last three decades, many species are still known from only one or a few localities (GLAW & VENCES 2007, VIEITES et al. 2008, BROWN et al. 2016, ANTONELLI et al. 2022). Together with the taxonomic uncertainty that compels us to revisit and split the distribution records of many species complexes, the distribution ranges of most species are largely unknown. This gap in distributional knowledge and population trends resulted in 12 and 104 of the 313 evaluated Malagasy frog species being categorized as Data Deficient (DD) and Not Evaluated (NE), respectively, following the IUCN Red List guidelines during the Second Global Amphibian Assessment (GAA2) (LUEDKE et al. 2023, IUCN 2024a).

According to the available data, many of these species can be considered rare. The concept of rarity can be interpreted both from a distribution and abundance perspectives, with species being considered rare either because their numbers are low regardless of their distribution range, or because they occur in a small area irrespective of their abundance. MAYR (1963) distinguished two categories of rare species: highly localized and highly specialized. These highly localized species were later defined as “narrow endemics”, meaning taxa that occur in one or a few small populations and are confined to a single or a few localities (DRURY 1980, KRUCKEBERG & RABINOWITZ 1985). “Micro-endemic” has become a popular concept and is equivalent to “narrow-endemic”, yet there is no clear consensus on the size of the distribution range required to qualify as micro.

Madagascar is renowned for its high rates of micro-endemism (VENCES et al. 2009), reaching more than 37% in amphibians (BROWN et al. 2014, GOODMAN et al. 2022). The processes leading to these high levels of micro-endemism are hotly debated, and different hypotheses have been proposed: the role of large rivers (PASTORINI et al. 2003), the effects of watershed contraction during Quaternary climatic shifts (WILMÉ et al. 2006), the influence of high moun-

tains acting as refugia (WOLLENBERG et al. 2008), current climate patterns (PEARSON & RAXWORTHY 2009), body size (BROWN et al. 2016), human activities since their arrival (HELMSTETTER et al. 2021), or a combination of multiple processes (BROWN et al. 2014). Much of the current micro-endemism is likely to be genuine; however, in other cases, the species' true distribution range may be more extensive than currently believed due to incomplete field sampling or low detectability, which could imply that a species is incorrectly assigned as micro-endemic (VIEITES et al. 2008, RAKOTOARISON et al. 2017, 2020). A narrow range may also result from severe habitat destruction, leaving few remnants of a previously larger distribution.

Rainforests are the most speciose and threatened ecosystems in Madagascar (HARPER et al. 2007) and, consequently, have attracted the most scientific attention. Confined to protected areas or isolated enclave patches, they are often challenging to access and logistically demanding to sample (VIEITES et al. 2008), leading to concentrated sampling around few campsites and trails, and leaving much of the rainforests unsampled. Nevertheless, new species continue to be discovered each year, even in the most thoroughly studied localities (e.g., GABRIEL et al. 2024, CARNÉ & VIEITES 2024). This is largely due to the detection of cryptic species unveiled through molecular data (RAKOTOARISON et al. 2017, SCHERZ et al. 2022) and the seasonal patterns and secretive behaviours of certain species, which cause them to go unnoticed during many sampling campaigns (HEINERMANN et al. 2015, SCHERZ et al. 2015, DUBOS et al. 2020, RAKOTOARISON et al. 2021). Indeed, venturing beyond typical sites has led to new species discoveries and range extensions (SCHERZ et al. 2020, RAKOTOARISON et al. 2020, HUTTER et al. 2021, FULGENCE et al. 2022, RAKOTOARISON et al. 2022).

Given the ongoing deforestation and landscape transformation in Madagascar (HARPER et al. 2007, VIELLEDENT et al. 2017), agricultural forested secondary habitats (e.g., cacao, banana, or vanilla plantations) are becoming increasingly common. Many species that once dwelled in the rainforests may either perish or adapt and persist in these artificial habitats, which can still support viable populations (EVANS 2019). These habitats harbour considerable frog diversity, particularly in the leaf litter, with a notable presence of microhylids (RAKOTOARISON et al. 2017, HENDING et al. 2023). In fact, some species have been described exclusively from these habitats (e.g., VENCES et al. 2002). Partly because they are less attractive for sampling, these habitats have received much less attention (ANDRIAMALISOA & LANGRAND 2022). However, exploring these habitats could enhance our understanding of species' distribution ranges and contribute to completing the amphibian inventory of Madagascar.

Frog families native to Madagascar are Hyperoliidae, Mantellidae, Microhylidae, and Ptychadenidae. With 12 genera and currently 285 described species, Mantellidae is the most diverse by far (FROST et al. 2024). *Wakea* GLAW & VENCES 2006 is a monotypic mantellid genus described from an agricultural lowland area of northwestern Mada-

gascar, the Sambirano region. *Wakea madinika* (VENCES, ANDREONE, GLAW & MATTIOLI, 2002) is a miniaturized frog that was originally described within the genus *Mantidactylus*. Subsequent molecular evidence led to its reclassification into the newly established genus *Wakea*, which has been recovered as the sister taxon to *Mantella* (GLAW & VENCES 2006, KURABAYASHI et al. 2008, WOLLENBERG et al. 2011).

*Wakea madinika* was described based on eight specimens from a single locality (VENCES et al. 2002), a temporary pond in a cacao plantation 200 m upstream from Antsirasa (13.9394°S, 48.5544°E, elevation < 100 m a.s.l.; Fig. 1), in the lowlands of the northern side of the Sambirano River. Further targeted surveys at the type locality and nearby localities failed to record the species, suggesting low detectability (IUCN 2016). Since its description,

no other specimens have been reported, thus flagging this species as a micro-endemic data-deficient species. The size of the species suggests it has a limited dispersal capacity (males 11–13 mm, females 15–16 mm), yet specimens were abundant at the type locality, seemingly tolerating its human-altered status. *Wakea madinika* is believed to be confined to a small lowland area in the Sambirano River valley, since the large and wide river (100–200 m) likely acts as a southern dispersal barrier, while the steep Sambirano valley confines the species to the lowland areas.

As a result of multiple targeted field campaigns over the past decade, we present new locality records for the poorly known *W. madinika*, analyse the species' mitochondrial variation, propose a conservation status, and provide a potential distribution range inferred through species distribution modelling.

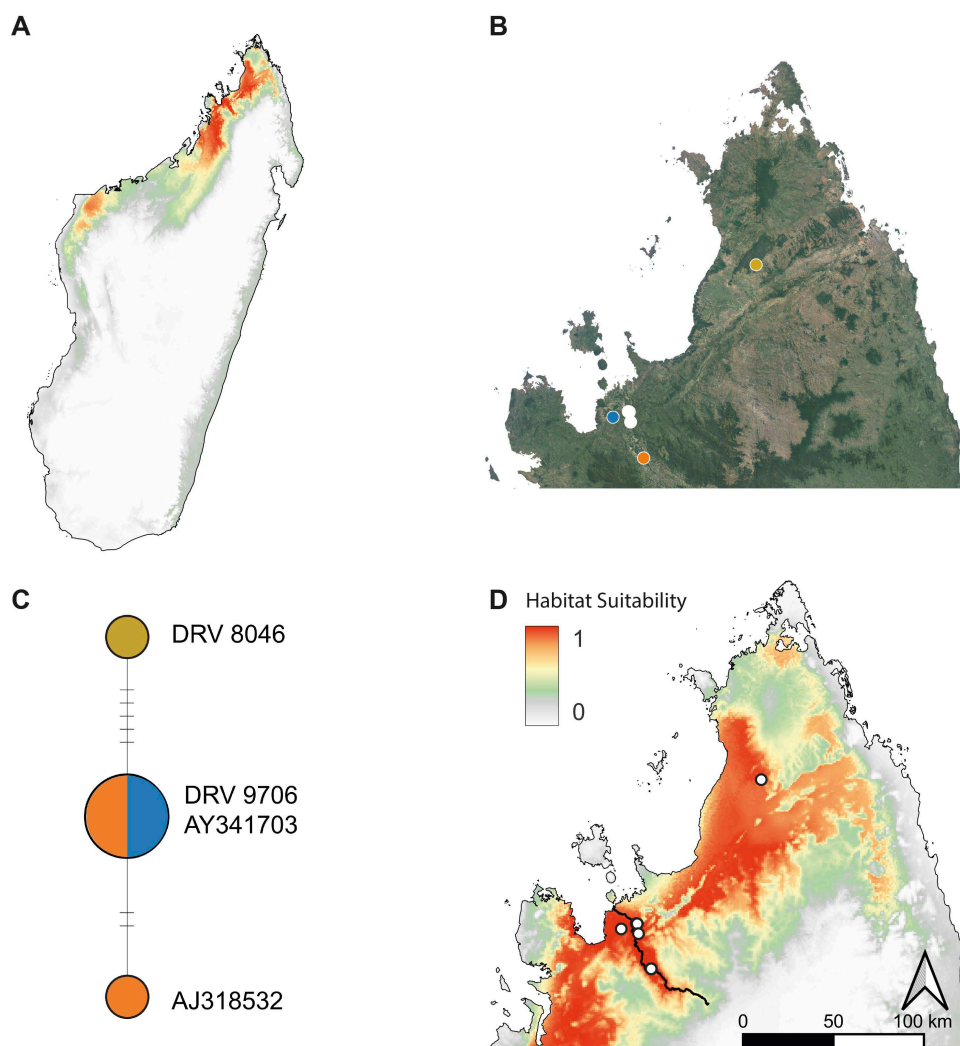


Figure 1. (A) *Wakea madinika* habitat suitability map, (B) Close-up map showing the currently known localities of *W. madinika* in northern Madagascar. The blue, brown, and white circles represent the newly discovered localities: Sorobe, Réserve Spéciale d'Ankarana, and Ambanja, respectively. The type locality, Antsirasa, is represented with an orange circle. (C) The 16S rDNA haplotype network was coloured according to the map localities. (D) Habitat suitability map obtained through ensemble modelling in 'biomod2' with occurrence records shown as white points. The Sambirano River is outlined with a black line.

## Materials and methods

### Fieldwork

Since 2016, the research team led by DRV, has organized several expeditions to Ambanja and the Sambirano River valley to find *Wakea* specimens. In February 2016, we followed the road toward the type locality of *W. madinika* and found the species at two localities along the road: locality 04-2016 (19 February 2016), cacao plantation near the road, 13.70690° S, 48.47788° E, 29 m a.s.l., four specimens; and locality 07-2016, cacao plantation by the road, 13.70865° S, 48.48379° E, 33 m a.s.l., seventeen specimens found by D. R. VIEITES, F. M. RATSOAVINA, Y. RICHARD, G. PONZ-SEGRELLES and X. FERRER during the daytime. We also visited several localities between Ambanja and Antsohihy to the south with no positive results.

In 2019, we found several *W. madinika* south of the Sambirano River in Sorobe ca. 5 km by the road south of Ambanja, Diana region (28 November 2019). They were found in a cacao plantation with dense dry leaf litter, locality 15-2019, 13.73492° S, 48.40101° E, 22 m a.s.l., 10 specimens. On 29 November 2019, we found several individuals of *W. madinika* in cacao plantations along the road beside the Sambirano River: locality 16-2019, 13.70834° S, 48.48288° E, 34 m a.s.l., six specimens; locality 17-2019, cacao plantation near Ambolidimaka, 13.75903° S, 48.48930° E, 20 specimens (Fig. 2); locality 20-2019, 13.70770° S, 48.48188° E, 30 m a.s.l., one specimen, found by D. R. VIEITES, M. P. VAN DEN BURG and M. L. RAZAFIARIMANANA, during daytime. We visited several plantations south of Sorobe without finding any individuals of *W. madinika*.

In 2022, a single specimen was found during daytime on 17 March 2022 by M. P. VAN DEN BURG, A. CARNÉ, N. A. A. RAHAGALALA and S. E. RAKOTOMANGA, in a muddy forest in the Réserve Spéciale (RS) d'Ankarana, Diana Region (12.96978° S, 49.11859° E, 99 m a.s.l.; Fig. 1). This individual was active during the day in the leaf litter (Fig. 2).

### Genetic data

We PCR-amplified 16S rDNA gene fragments extracted from tissue samples of two *W. madinika* specimens, DRV 8046 from Ankarana RS and DRV 9706 from Sorobe, using primers 16Sar-L: 5'-CGCCTGTTTATCAAAAACAT-3' and 16SbrH: 5'-CCGGTCTGAACTCAGATCACGT-3' (PALUMBI et al. 1991). PCR conditions were as follows: 95 °C for 2 min, 45 cycles at 95 °C for 30 s, annealing temperature of 48 °C for 30 s, extension at 72 °C for 30 s; final extension of 5 min at 72 °C. We incorporated individual barcodes (EXP-PBC096, ONT) on a second PCR, following ONT PCR barcoding guidelines, to allow multiple samples in each sequencing run. We cleaned up the PCR products up using 0.8 × Ampure XP magnetic beads (BeckMan Coulter) and generated a library by pooling the products equimolarly. We added sequencing adaptors via ligation using the Ligation kit v14 (SQL-LSK114, ONT). We loaded the library into an ONT R10.4 flow cell for MinION sequencing on a Mk1C instrument (ONT), and the samples were run for five hours. We basecalled the fast5 resulting files using Guppy v.6.5.7 with the superior setting (high-precision basecalling) (WICK et al. 2019). We obtained 9,348 and 7,686 reads for samples DRV 8046 and DRV 9706, respectively, and exported them to Geneious Prime v. 2023.0.3 (KEARSE et al. 2012), where we aligned them using the integrated MAFFT algorithm. We repeated the process and trimmed the sequences to approximately 200 per sample, to reduce artefact-generated gaps. We removed the primers and we generated the final consensus sequence using a 65% threshold. We aligned the two available *W. madinika* GenBank sequences (AY341703 and AJ318532) and the newly sequenced individuals (PQ608560, PQ608561), in the online application MAFFT v.7 (KATO et al. 2019) with default parameters and edited the resulting alignment in Geneious. We calculated uncorrected p-distance in Mega v. 10 (KUMAR et al. 2018) using pairwise deletion and accounting for transitions and transversions. We construct-



Figure 2. Dorsolateral views of *Wakea madinika* in life: (left) from the Sambirano road, locality 17-2019; (right) from Réserve Spéciale d'Ankarana. Photographs by D. R. VIEITES & M. P. VAN DEN BURG.

ed a haplotype network in PopART using the TCS option (LEIGHT & BRYANT 2015).

### Species distribution modelling

We downloaded current bioclimatic data and variables at 30 arc sec (~1 km) from CHELSA (KARGER et al. 2017). Our initial dataset contained 22 variables, including 19 climatic variables (bio1 to bio19; see KARGER et al. 2017), net primary productivity, growing season length, and digital elevation model (DEM; NASA, 2024). We excluded tightly correlated variables (Pearson's correlation coefficient > 0.7) and, given the reduced occurrence dataset (N = 6), retained only three explanatory variables: digital elevation model (DEM), net primary productivity (npp), and isothermality (bio3).

We conducted all analyses in R (R Core Team 2023) using the 'biomod2' package (THULLER et al. 2024). We ran the models using six algorithms: two Regression-based methods: Generalized Linear Model (GLM), Generalized Additive Model (GAM), three Tree-based methods: Random Forests (RF), Classification Tree Analysis (CTA), Generalized Boosting Model (GBM), and one Machine-learning-based method: Maximum Entropy (MAXNET).

We ran the models keeping only one occurrence per pixel, splitting the occurrence dataset into 70% of data for training and 30% data for the evaluation, tuning algorithm parameters with the 'bigboss' option, and using 20 randomly selected datasets of pseudoabsences, each containing a number of pseudoabsences equal to the number of occurrences. We run 10 replicates per model to account for algorithm, pseudoabsence dataset, and dataset split variabilities (N = 200 models per algorithm). We evaluated variable importance using three permutations and each independent run using four metrics: TSS, Kappa, ROC, and accuracy. We ensembled the models using 'all models' with a True Skill Statistics (TSS; ALLOUCHE et al. 2006) greater than 0.7 to obtain the consensus model through the mean of probabilities over the selected models (EMmean). We evaluated the resulting ensembled model with AUC-ROC and TSS. We generated the final habitat suitability map using QGIS version 3.22.26 (<http://www.qgis.org>).

## Results

### Mitochondrial diversity

By analysing the four sequenced individuals (529 bp, 7 segregating sites; 0 parsimony-informative sites, Tajima's D: -0.817, non-significant) we identified a new mitochondrial haplotype in Ankarana RS. The Sorobe specimen nested within the same haplotype as the previously sequenced holotype. The mean intraspecific genetic diversity of the 16S rDNA gene fragment of the four included individuals is 0.66%. The genetic divergence of the furthest sample, the Ankarana RS population in the north (DRV 8046; Fig. 1C), against the most divergent individual (AJ318532;

a paratype from the type locality) is 1.32%, despite ca. 125 aerial km between both populations. We observed greater divergence (two mutations; 0.37%) between the two type specimens (Holotype = ZSM 601/2001; AJ318532 and Paratype = MRSN A2066; AY341703) compared to the absence of mutations between the paratype and the newly discovered Sorobe locality (DRV 9706), despite the 30 aerial km that separate them and the fact that Sorobe is on the other side of the Sambirano River.

### Species distribution models

We were able to produce a good model for *W. madinika* (AUC: 0.99; TSS: 0.99) with 100% of the observed presences correctly predicted to be present (sensitivity) and 99% of absences correctly predicted to be absent (specificity). Isothermality is the most important variable explaining the distribution of the species (48%), followed by DEM (29%), and npp (20%) (Fig. 3). The habitat of *W. madinika* becomes more suitable with higher isothermality (i.e., when the temperature stability throughout the year is greater), at lower elevations, and with increasing net primary productivity (Fig. 3).

Our SDM analysis identifies the Sambirano River basin as highly suitable for *W. madinika*, from the coastline up to ca. 200 m a.s.l. (Fig. 1D). The suitable habitat expands northward, reaching Ambilobe, Ankarana RS, and the southwestern limits of Montagne d'Ambre National Park, bordering the western coastline and extending to the surroundings of Analamerana SR in the east. To the south, the suitable habitat extends about 50 km south of Antoshihy. Additionally, our SDM results predict a completely disconnected suitable patch of habitat to the southwest, extending from the Tsingy de Namoroka National Park to Besalamy (Fig. 1A).

## Discussion

### Changing the paradigm, from micro-endemism to regional endemic

We are amid a global biodiversity crisis (WAKE & VREDENBURG 2008, COWIE et al. 2022), affecting all biodiversity hotspots to varying degrees (COSTELLO et al. 2022). Any step towards reducing the Wallacean shortfall contributes to more effective conservation measures to minimize biodiversity loss. This is especially important in tropical regions where unparalleled high biological diversity faces significant threats, but economic resources and knowledge of species distributions remain limited (MOURA & JETZ 2021).

We present new distributional data for the poorly known *W. madinika*, a mantellid described in 2002, previously known only from its type locality and has been overlooked despite targeted sampling efforts (IUCN 2016). Our records show *W. madinika* should no longer be considered a micro-endemic species confined to a single locality. We

significantly expand the species' distributional range from one to five localities, covering a minimum convex polygon area of 1600 km<sup>2</sup>.

After several expeditions to northwestern Madagascar, we found *W. madinika* in two unexpected localities outside the Sambirano River valley, where it was supposed to be endemic (IUCN 2016). Sorobe is ca. 5 km south of Ambanja town and south of the Sambirano River, while all the other localities lie north of this river. At low elevations, where *W. madinika* is projected to occur (Fig. 3), the Sambirano is a large river, 100–200 m wide and with a high-water volume ranging from 9 m<sup>3</sup>s<sup>-1</sup> in one dry season to over 700 m<sup>3</sup>s<sup>-1</sup>, averaging 140 m<sup>3</sup>/s between 1953 and 1983 (Global Runoff Data Centre 2024). It is very unlikely that miniature frogs like *W. madinika* can cross such a barrier. Still, we found populations on both sides with identical mtDNA sequences. This suggests that the species can disperse more than expected by its size, or that its distribution range and population size are much larger than we thought. It also suggests that the Sambirano River has not always been a barrier for dispersal. The Sambirano River was previously hypothesized to have acted as a physical barrier for several groups that show phylogeographic breaks between northern and southern populations (PABIJAN et al. 2015, and references therein). It has also been proposed as a retreat-dispersion watershed region, contributing to centres of endemism due to sequential forest retreats and expansions during cold, dry periods (GANZHORN et al. 2014). This is partly supported by the presence of centres of endemism north of the Sambirano River (BROWN et al. 2014). How-

ever, our findings suggest that the Sambirano River is not a permanent barrier for *W. madinika*. It is possible that during severe droughts the river dried out, as has happened these years with the southwestern rivers from Madagascar, allowing dispersal between both riverbanks. Additionally, although it has never been found, the species could also occur in the upper course of the river, where the barrier effect is weaker, allowing for continuous gene flow.

The other unexpected locality where we found *W. madinika*, the Ankarana RS, is geographically distant from all other known localities (Fig. 1). The genetic divergence between the Ankarana and southern populations is low, especially when compared to the higher divergence typically observed among Malagasy amphibians, even between closer populations (CARNÉ & VIEITES 2024). This locality confirms that the species has a much broader distribution than previously expected, contradicting its prior classification as micro-endemic and suggesting greater environmental tolerance. The low mitochondrial variability observed suggests recent population connectivity, which could be achieved through large and connected widely distributed populations or high dispersal capacities at individual or population levels.

Our ensemble *W. madinika* distribution model provides a potential distribution area to guide future survey efforts. Given the limited number of available localities, this model needs to be interpreted cautiously; still, it can identify areas with environmental conditions similar to the known localities. The model predicts new potentially suitable areas where the species might occur, including an iso-

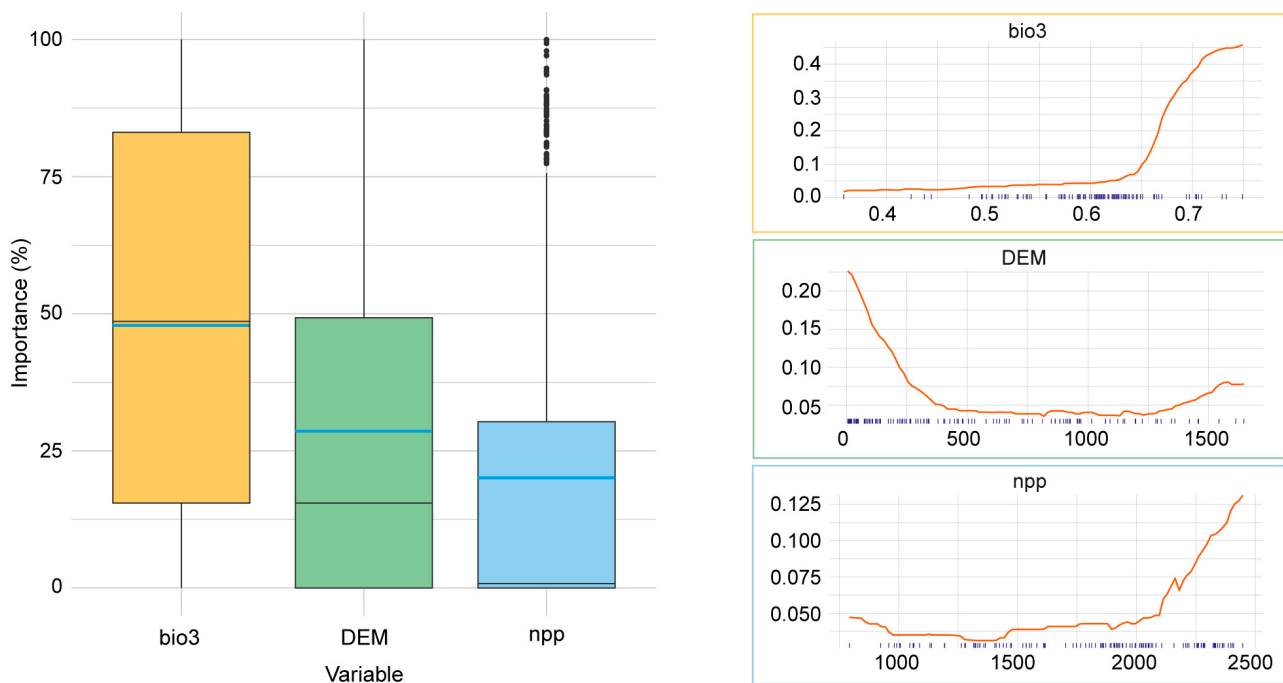


Figure 3. Variable contribution boxplot (left) and response curves (right) for the three variables included in the ensemble species distribution model of *Wakea madinika*. The blue line in the boxplot represents the mean value of each variable; digital elevation model (DEM), net primary productivity (npp), and isothermality (bio3).

lated patch of suitable habitat in the southwest (Fig. 1A). We surveyed several localities with suitable conditions from Sorobe to Ankarafantsika, without detecting the species. However, given the lack of records since 2002, these potentially suitable areas could harbour undiscovered populations, providing valuable insights into the species' habitat and ecology, and increasing the occurrence dataset to develop more informative and robust distributional models.

In niche-based modelling, species are seen as entities responding uniformly to climatic conditions, with static spatiotemporal climatic tolerances. This approach assumes that any area with conditions outside a species' current ecological niche limits is unsuitable (THOMAS et al. 2004, GUISSAN & THULLER 2005). Our model defines the current ecological niche limits of *W. madinika* based on all known records since 2002; 6 cell grids of ca.  $1 \times 1$  km. Therefore, the actual ecological limits of the species could be greater, meaning that we might underestimate the species' real distribution.

*Wakea madinika* is an excellent example of a species previously considered micro-endemic that unexpectedly has a much larger distribution range. Numerous species of miniature frogs and reptiles from Madagascar are currently considered to be micro-endemics (e.g., *Stumpffia*, *Mini* and other microhylid frogs, or *Brookesia* chameleons). *Wakea madinika*, as a miniature frog with an unexpectedly large range, highlights the need for increased spatial sampling across Madagascar to understand species ranges better and to clarify whether the level of micro-endemism is real or an artefact due to a lack of sampling.

#### Low mitochondrial divergence

The low mitochondrial divergence found within *W. madinika* between distant populations is in sharp contrast with the widespread pattern found in other Malagasy amphibians (CARNÉ & VIEITES 2024), where higher divergence values are often observed even between geographically closer populations (e.g., SCHERZ et al. 2022). This low variation is particularly striking given the involved geographical area, the miniaturized body size, and the presumed philopatry of the species.

The observed low genetic differentiation suggests recent gene flow between distant populations or a recent expansion. More data are needed to assess its genetic diversity and spatial structure. However, *Wakea* seems to be a good model for comparing other miniaturized frogs to understand dispersal capacities in amphibians constrained by body size. Rarity can refer to both limited geographic distributions and/or lower abundances despite the range. The species is abundant in the localities where it is found, with many specimens present in the leaf litter. We found the species active from November to February, suggesting that it is at least active throughout the rainy season. Such low genetic divergence between distant populations may result from large populations occupying the territory, with high connectivity between them, but likely a low effective popu-

lation size resulting from a recent population expansion. Alternatively, it could stem from a once-abundant, widespread, and connected distribution that has since been reduced to fragmented populations, which can still be locally abundant. The latter could explain the observed genetic variation and why *W. madinika* has remained unnoticed despite targeted sampling. More population genomic data and demographic analyses are needed to disentangle its biogeographical history.

The reproductive ecology of the species remains largely unknown. Although a tadpole stage has not been documented, its existence has been hypothesised based on the species' phylogenetic relationships and the presence of eggs in a collected female (VENCES et al. 2002, GLAW & VENCES 2002). The sister genus *Mantella* typically deposits eggs outside water, with tadpoles later washed by rain into swamps or streams. The observed activity of *Wakea madinika* during the rainy season, along with its potential tadpole stage, could explain the low mitochondrial divergence observed between the two Sambirano riverbanks through storm-driven flooding events that flush tadpoles into the river, resulting in dispersal.

All known *W. madinika* localities are cacao plantations, except for Ankarana. Cacao trees require shade to grow, so tall rainforest trees are retained while cacao trees are planted underneath them. As such, cacao plantations are found at previously forested sites. The Ankarana locality is a protected muddy, deciduous rainforest, which is arguably the typical habitat for this species. However, it has never been found so far in this reserve. The species seems to persist in potentially suboptimal altered environments, which may indicate a certain degree of resilience and ecological plasticity (PULLIAM 2000). The combination of inhabiting unattractive-to-sample habitats, the existing sampling bias towards rainforests and protected areas, and the highly fragmentary herpetological sampling in Madagascar may also explain why the species has been overlooked since 2002 (ANDRIAMIALISOA & LANGRAND 2022). Current rates of deforestation and habitat transformation are especially high in lowland areas and may have significantly reduced both local population sizes and the number of existing populations. Such niche flexibility could be crucial for the species' survival amid ongoing habitat degradation and future climate change.

The possibility of deliberate or accidental introduction of specimens is unlikely. First, this species is small and not particularly attractive, making intentional introduction improbable. Second, unintentional introduction through plants is also improbable, as there are no cacao plantations in Ankarana RS, and plant import/export from the protected area is prohibited.

#### Conservation status

*Wakea madinika* was categorized as Data Deficient (DD) for being known from only one locality (IUCN 2016). Data on population trends are lacking. However, based on its

extent of occurrence (EOO) being less than 5000 km<sup>2</sup> and the fact that there are fewer than five known, fragmented localities, we propose reclassifying the species as Endangered (EN) according to the IUCN Red List Criteria B1a (IUCN 2024b). Furthermore, all but one of the known localities (i.e., Ankarana RS) are anthropogenic habitats where the species persists in currently present leaf litter. This situation could change drastically if these forested plantations are converted into herbaceous agricultural habitats (e.g., rice fields). Future sampling may lead to the discovery of new populations, potentially filling its range or increasing it.

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## Appendix

Initial list of variables considered for the modeling analysis. The variables highlighted in bold were selected to generate the model.

Name	Description	Source
bio1	mean annual air temperature	KARGER et al. 2017
bio2	mean diurnal air temperature range	KARGER et al. 2017
<b>bio3</b>	<b>isothermality</b>	<b>KARGER et al. 2017</b>
bio4	temperature seasonality	KARGER et al. 2017
bio5	mean daily maximum air temperature of the warmest month	KARGER et al. 2017
bio6	mean daily minimum air temperature of the coldest month	KARGER et al. 2017
bio7	annual range of air temperature	KARGER et al. 2017
bio8	mean daily mean air temperatures of the wettest quarter	KARGER et al. 2017
bio9	mean daily mean air temperatures of the driest quarter	KARGER et al. 2017
bio10	mean daily mean air temperatures of the warmest quarter	KARGER et al. 2017
bio11	mean daily mean air temperatures of the coldest quarter	KARGER et al. 2017
bio12	annual precipitation amount	KARGER et al. 2017
bio13	precipitation amount of the wettest month	KARGER et al. 2017
bio14	precipitation amount of the driest month	KARGER et al. 2017
bio15	precipitation seasonality	KARGER et al. 2017
bio16	mean monthly precipitation amount of the wettest quarter	KARGER et al. 2017
bio17	mean monthly precipitation amount of the driest quarter	KARGER et al. 2017
bio18	mean monthly precipitation amount of the warmest quarter	KARGER et al. 2017
bio19	mean monthly precipitation amount of the coldest quarter	KARGER et al. 2017
<b>npp</b>	<b>net primary productivity</b>	<b>KARGER et al. 2017</b>
gsl	growing season length	KARGER et al. 2017
<b>DEM</b>	<b>digital elevation model</b>	<b>NASA, 2024</b>