

## RESEARCH NOTE

# A surprising haven: The biodiversity of an old-growth forest amidst a scorched landscape in Madagascar

Beatriz Otero Jimenez<sup>1,2</sup>  | Ren Montaña<sup>3,4</sup>  | Ryan S. Rothman<sup>1,5</sup>  | Rachel C. Williams<sup>6</sup>  | Patricia C. Wright<sup>1,7</sup>

<sup>1</sup>Department of Anthropology, Institute for the Conservation of Tropical Environments, Stony Brook University, Stony Brook, New York, USA

<sup>2</sup>Burnett Honors College, University of Central Florida, Orlando, Florida, USA

<sup>3</sup>Department of Environmental Science and Public Policy, College of Science, George Mason University, Fairfax, Virginia, USA

<sup>4</sup>National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC, USA

<sup>5</sup>Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, New York, USA

<sup>6</sup>Centre for Environmental Biotechnology, School of Natural Sciences, Bangor University, Bangor, Gwynedd, UK

<sup>7</sup>Department of Anthropology, Stony Brook University, Stony Brook, New York, USA

## Correspondence

Beatriz Otero Jimenez, Department of Anthropology, Institute for the Conservation of Tropical Environments, Stony Brook University, Stony Brook, NY 11794, USA.

Email: [beatriz.oterjimenez@gmail.com](mailto:beatriz.oterjimenez@gmail.com)

## Funding information

James Xavier Purcell; Missouri Botanical Garden; National Geographic Society, Grant/Award Number: 9929-16; Primate Conservation Inc.; Rainforest Trust, Grant/Award Number: 1-MG-331-16-4-a; National Science Foundation, Grant/Award Number: DEB-1354610; Duke University Research Funds

## Abstract

For the endemic wildlife of Madagascar, the risk of extinction increases as the island's forest cover decreases. Many of the remaining forests are isolated fragments serving as important refugia for biodiversity. In this research note, we describe the biodiversity of the Ivohiboro Humid Forest (IHF), and its conservation importance in Madagascar. Located in a region dominated by wooded savannah, the IHF represents a very rare vegetation type. We conducted six biological surveys to explore the diversity of vertebrates and vascular plants in this isolated forest. Our results show that the IHF maintains a diverse ecosystem and harbors species of conservation significance. Thirty-four of the identified species are categorized as Threatened by the IUCN, such as the ring-tailed lemur (*Lemur catta*) and Isalo Madagascar frog (*Gephyromantis corvus*). Furthermore, we inventoried species distant from their known IUCN-reported geographic ranges such as a species of blue-nosed chameleon (*Calumma* sp. aff. *boettgeri*, *linotum*) and the Lavaso dwarf lemur (*Cheirogaleus lavasoensis*).

## KEYWORDS

biodiversity, conservation, fragmented forest, Madagascar, protected area

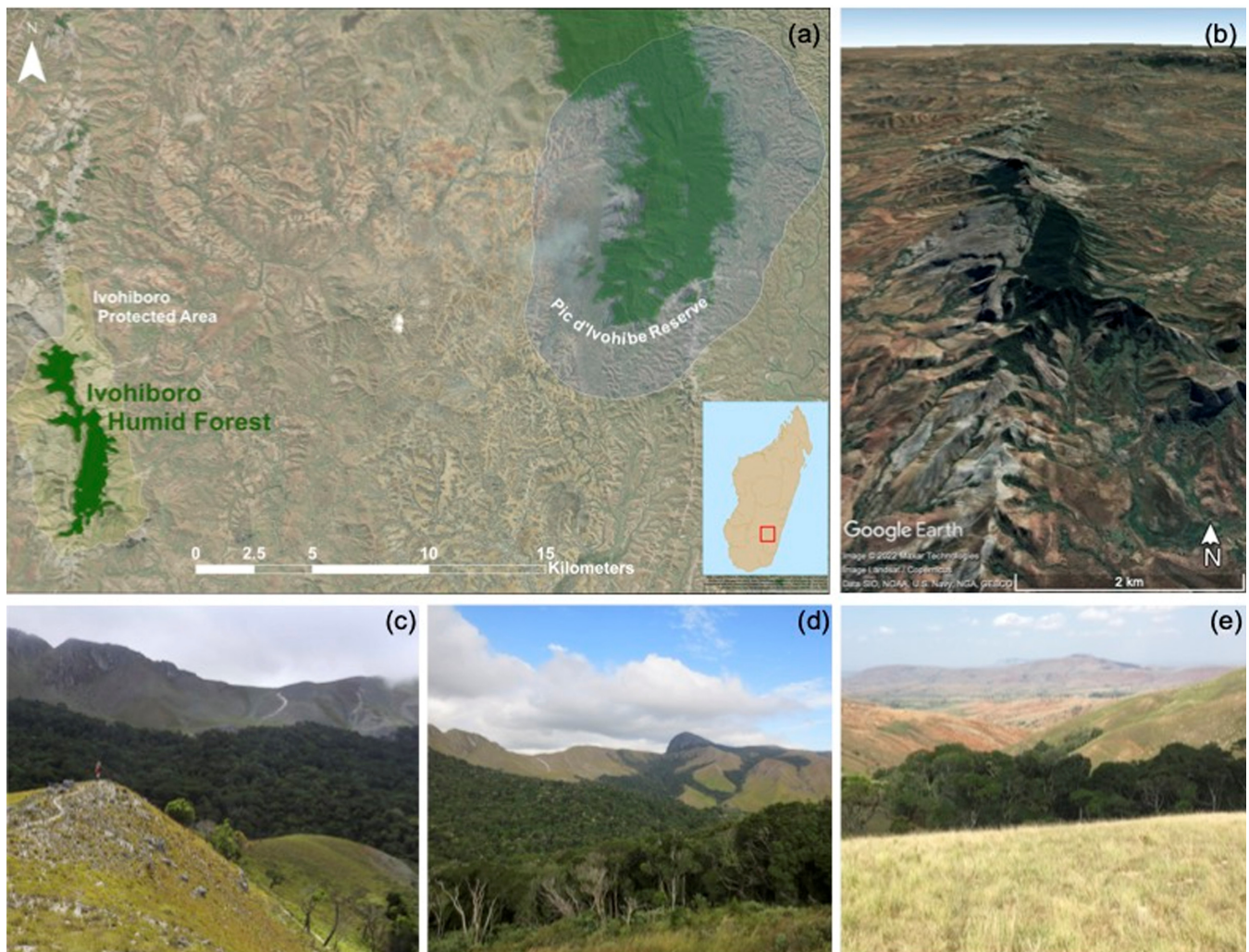
## 1 | INTRODUCTION

To prevent extinction events and the loss of critical ecosystem services, we must understand how habitat loss

and fragmentation affect wildlife. Forested habitats harbor about 80% of the world's terrestrial biodiversity of which 50% inhabit tropical forests (Dirzo & Raven, 2003; FAO & UNEP, 2020). In the last 30 years, 1.7% of Earth's

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Conservation Science and Practice* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.



**FIGURE 1** Map images of the Ivohiboro Humid Forest (IHF). (a) Map showing the Ivohiboro Protected Area (IPA; yellow), the IHF in green, and the Pic d'Ivohibe Reserve (blue polygon) with its humid forest shown in green. (b) Relief map showing elevation of the IHF, (c–e) landscape photographs of the IPA. Photo Credit: Noel Rowe (c), Ryan Rothman (d), Ren Montaña (e).

remaining forests have been lost to deforestation (FAO & UNEP, 2020). The highest rates of deforestation occur in tropical regions, making forest loss the greatest threat to biodiversity (Ehrlich & Pringle, 2008). As a result, Earth's remaining tropical biodiversity hotspots are fragments located within anthropogenic matrices (Fischer et al., 2021; Haddad et al., 2015; Perfecto & Vandermeer, 2008).

The tropical island of Madagascar is one of Earth's top biodiversity hotspots (Antonelli et al., 2022; Goodman & Benstead, 2005; Myers et al., 2000), home to 5% of the planet's biodiversity, and 90% of its species endemic to the island (Burgess et al., 2004; Ganzhorn et al., 2001; Morelli et al., 2019). Yet, Madagascar has one of the highest rates of deforestation in the world, losing more than 44% of its forested land cover between 1953 and 2014 (Vieilledent et al., 2018). The remaining forests are heavily fragmented due to human-caused fires and

deforestation (Burns et al., 2016; Ralimanana et al., 2022). Currently, humid forests on Madagascar are restricted to the eastern escarpment (Brown et al., 2015; Moat & Smith, 2007). However, the historical land cover history of central Madagascar and the western extent of humid forests remains undetermined (Harper et al., 2007; Sussman et al., 1994; Vieilledent et al., 2018).

In 2016, we encountered a forest fragment in south-central Madagascar, surrounded by wooded savannah and hereafter called the Ivohiboro Humid Forest (IHF). This forest, located within the Ivohiboro Protected Area (IPA), is classified as an IUCN Category V Protected Landscape (Dudley et al., 2013; Figure 1a–e), and managed by a committee of representatives from the surrounding villages, local NGOs, and the Madagascar Ministry for the Environment. The last recorded scientific exploration near the IPA was in 1924 (Mission H. Humbert—Plantes de Madagascar [2nd voyage],

1924). In this research note, we present our findings from six biological surveys of vertebrates and vascular plants within the IHF and highlight its potential scientific and conservation importance.

## 2 | METHODS

### 2.1 | Study site

The IPA occupies approximately 3782 ha, of which 858 hectares are classified as Humid Forest (Moat & Smith, 2007; Figure 1a–e). The IHF is centered around 22.8° S and 46.9° E, with an elevational gradient range from 650 to 1460 m above sea-level (Farr et al., 2007). Temperature data collected within the IHF (>100 m from the forest edge) shows that the mean yearly temperature is 17.7°C ± 0.54 SE (Max 21.4°C, Min 13.3°C).

The IHF is situated within the Moat and Smith (2007)-defined class “Wooded Savannah” that dominates Madagascar’s south-central highlands (Figure 1a). The area surrounding the IPA has been continuously maintained as rangeland for cattle grazing, through a practice of intentional burning (Kiener, 1963; Styger, 2004; Figure 1c–e). The IHF is shielded from fire within a sunken valley, characteristic of the island’s fault structures (Figure 1b–e). The nearest humid forest to the IHF is located approximately 20 km to the northeast in the Pic d’Ivohibe Reserve and is part of the eastern escarpment of Madagascar’s moist forests (Figure 1a). Decades of satellite-observed deforestation in the region (Sussman et al., 1994; Tucker & Townshend, 2000; Zhang et al., 2022), along with proximity to Humid Forest, indicate that the IHF may once have been part of a continuous moist forest and is now isolated by deforestation and fire. The IHF offers an opportunity to increase our understanding of the effects of isolation on populations and ecological communities to inform conservation planning and action.

### 2.2 | Biological surveys

We conducted biological inventories within the IHF to sample vertebrates (volant and non-volant) and vascular plants over 3 years across six expeditions (each lasting between 10 and 20 days), in October 2016, December 2016, April 2017, July 2017, July 2019, and November 2019. From these surveys, we created a taxonomic inventory of species of four classes of vertebrates (i.e., amphibians, birds, mammals, and reptiles) and vascular plants. We conducted specimen sampling and collection following guidelines from the Institutional

Animal Care and Use Committee (IACUC) at Stony Brook University (#1601283). We obtained local permits for each biodiversity survey from the Malagasy Ministry of Environment and Forestry (242/16/; 41/17/; 122/17/; 152/19/; 290/19/MEEF/SG/DGF/DSAP/SCB.Re).

We performed inventories of reptiles and amphibians by establishing nine transects within the forest and along streams. Each transect was approximately 200 × 20 m in size, located >100 m from the forest edge, and >200 m from each other. Within each transect, both diurnal and nocturnal surveys were conducted. All individuals observed along these transects were documented and identified to species or genera.

For the bird census, we conducted point-counts (25 points censused for 20 min each day) at stations separated by at least 200 m. We documented all birds detected visually or audibly during each of these 20-min intervals.

For terrestrial and arboreal mammal identification, we conducted diurnal and nocturnal surveys along three 2 km walking transects. Along these walking transects, we placed four Sherman live traps baited with mashed banana to capture small mammals every 25 m (i.e., rodents and nocturnal primates). We recorded the GPS location of all traps and labeled them based on transect location. For individuals observed or trapped, we recorded species taxonomy, number of individuals, GPS coordinates, and position along the transect. Transects were located at >10 m from the forest edge and >500 m apart. Additionally, we set 16 camera traps in the forest along animal trails, with an approximate density of one camera every 250 m<sup>2</sup>, placed 0.3 m from the ground. As the objective was to detect the maximum number of species during these expeditions, each camera trap was baited both with mashed banana to attract frugivores and smoked zebu meat to attract carnivores.

To survey the arboreal and troglomorphic bat fauna, we employed four different survey methods: (1) hand-held bat detectors, (2) automatic recording stations of bat vocalizations, (3) tree and cave daytime observations, and (4) mist-netting. Mist-netting was performed with special bat nylon mist nets of 3, 6, 9, and 12 m in length. Two 9 × 12-m high nets along the edges of the forest. Each night, we set four to eight single or double nets across streams, paths, or forest openings. Other surveying methods were employed within the 2 km walking transects mentioned above.

We confirmed the species assignment *Cheirogaleus* using mtDNA barcoding since we were unable to identify *Cheirogaleus* species in the field. We extracted DNA from tissue samples (ear clippings) using the Qiagen DNeasy Blood & Tissue Kit and sequenced a region of cytochrome c oxidase subunit II (*COII*). We used NCBI



**TABLE 1** Taxonomic summary of Ivoihoboro Humid Forest surveys including number of species categorized as threatened by the IUCN Red List.

Taxonomic group	Class	Order	Families	Genera	Species	Unidentified species	Total species (identified and unidentified)	IUCN threatened
Reptiles	1	1	7	14	23	4	27	5
Amphibians	1	1	2	5	22	3	25	5
Birds	1	14	34	55	63	0	63	1
Mammals	1	6	11	18	18	2	21	4
All Vertebrates	4	22	54	92	107	9	117	15
Vascular Plants	4	51	107	256	210	98	308	19

Genbank to access a subset of *COII* sequences from across the *Cheirogaleus* clade for comparison. We aligned sequences using MAFFT v7.017 (Kato et al., 2002), totaling 153 sequences of 684 nucleotide sites. We estimated a maximum likelihood (ML) phylogenetic tree for the aligned sequences using ModelFinder (Kalyaanamoorthy et al., 2017), as implemented in IQ-TREE v1.6.6 (Nguyen et al., 2015) to assess relative model fit. The phylogeny was rooted on the outgroup *Microcebus murinus* and significance was assessed using 500,000 ultrafast bootstrap replicates.

We surveyed the vascular flora inside the IHF across six 0.1 ha (50 × 20 m) plots, as established and managed by Tropical Ecological Assessment and Monitoring Network. Plots were located >100 m from forest edge and >500 m from each other. We identified all trees within these plots (>10 cm DBH), and all vascular plants collected along vertebrate sampling transects, to the levels of genus or species in collaboration with botanists from the Tsimbazaza Herbarium in Antananarivo and the Missouri Botanical Garden (for detailed sampling methods, see Fegraus, 2012). We collected plant specimens from all species or morphospecies (e.g., leaves, roots, flowers, fruit) along and visible from the transects, and these specimens were deposited in the Centre ValBio Research Station Herbarium.

### 3 | RESULTS

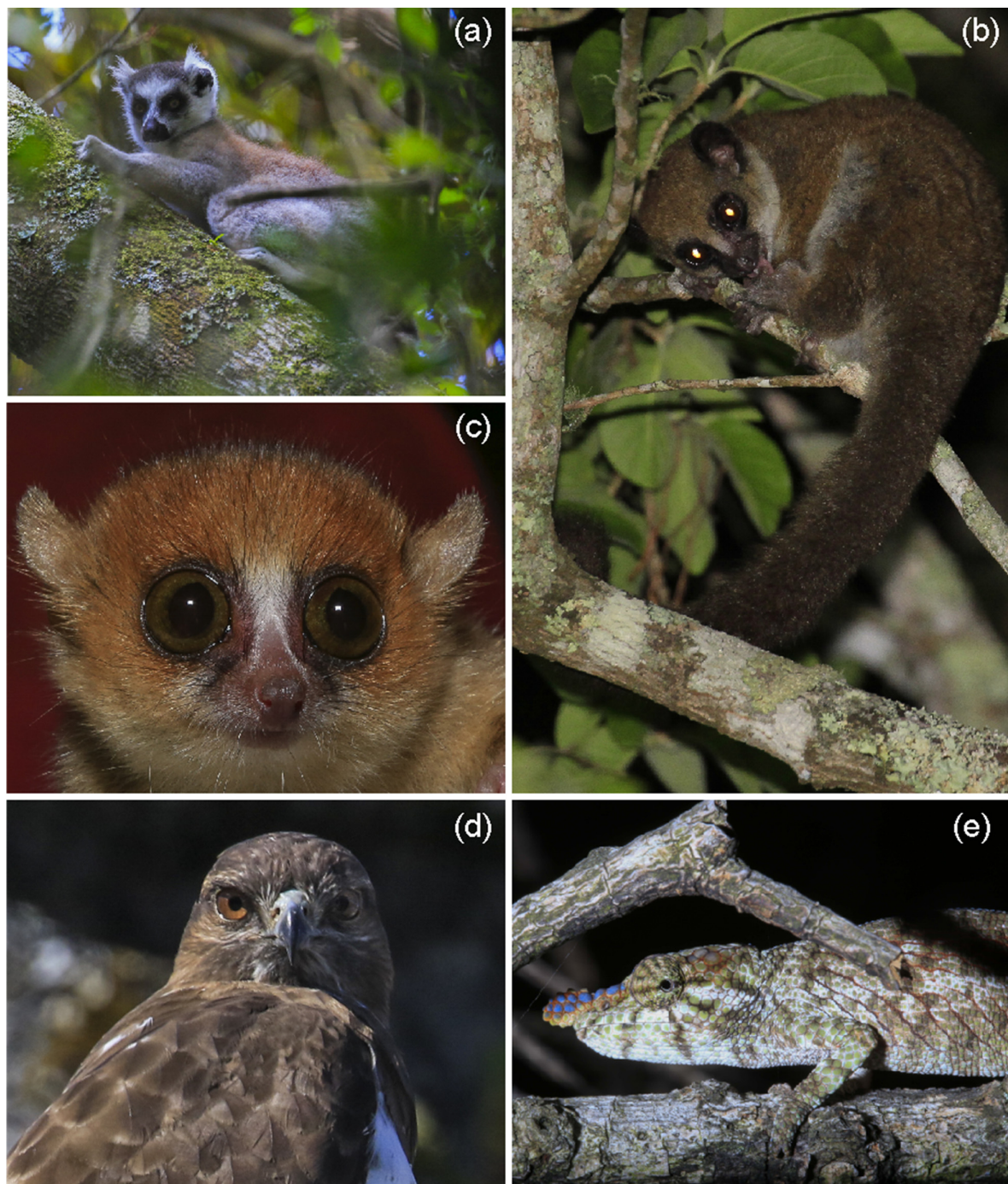
Our surveys identified 107 species of vertebrates and 219 species of vascular plants (Table 1, see Supplementary Table S1 for complete list). We identified taxa to the species-level for 92% of the vertebrates and 68% of the vascular plants (Table 1). The remaining specimens were identified to the genus-level (Table 1). Of the species identified 34, 15 vertebrate and 19 vascular plant species, were listed under the IUCN Red List threatened (i.e., vulnerable, or endangered; Table 1).

#### 3.1 | Reptiles

We identified one order (Squamata), 7 families, 14 genera, and 23 distinct reptile species. Four of the observed reptiles could only be identified to the genus level: two chameleons (*Calumma* sp. and *Palleon* sp.), one plated lizard (*Zonosaurus* sp.), and one Malagasy iguana (*Oplurus* sp.). The *Calumma* individual had morphological affinity to the blue-nosed species *Calumma boettgeri* and *Calumma linotum* (Figure 2e). If indeed the observed individual is either of the two known blue-nosed chameleon species (Prötzel et al., 2015), it would represent a significant range expansion since these species are endemic to areas of northern Madagascar, more than 1000 km from the IHF (Glaw et al., 2015). The Chamaeleonidae ( $N = 11$ ) and the Gekkonidae ( $N = 8$ ) families represented most of the species identified. A total of five species are categorized as threatened by the IUCN Red List (Supplementary Table S2) with the Hillebrand's chameleon (*Calumma hillebrandi*) and the malahelo leaf-tailed gecko (*U. malahelo*) classified as endangered.

#### 3.2 | Amphibians

We identified one order (Anura), two families (Mantellidae and Microhylidae), five genera (*Boophis*, *Mantidactylus*, *Gephyromantis*, *Anodonthyla*, and *Aglyptodactylus*), and 22 species of amphibians. However, we were unable to identify the species level of three *Mantidactylus* specimens. Of the observed species, five are categorized as threatened by the IUCN Red List (Supplementary Table S2). Two of them are classified as endangered: the Isalo Madagascar frog (*Gephyromantis corvus*) and the slow climbing frog (*Anodonthyla moramora*). The presence of these species represents a range expansion from their known distributions. *G. corvus* is endemic to the Isalo region 150 km west of the IHF (IUCN SSC Amphibian Specialist Group, 2016b), and *An. moramora* to the Ranomafana region approximately 150 km northeast of the IHF (IUCN SSC Amphibian Specialist Group, 2016a).



**FIGURE 2** Images of selected species in the Ivohiboro Humid Forest (IHF). (a) *Lemur catta* (ring-tailed lemur), (b) *Cheriogaleus* sp. (dwarf lemur), (c) *Microcebus* sp. (mouse lemur), (d) *Buteo brachypterus* (Madagascar buzzard), (e) *Calumma* sp. aff. *boettgeri* (unidentified species with phenotypic affinity to blue-nosed chameleon). Photo Credit: Noel Rowe.

### 3.3 | Birds

We identified all specimens, which included 14 orders, 34 families, 55 genera, and 63 species of birds. The most common bird families recorded include Vangidae ( $N = 10$ ), Bernieridae ( $N = 6$ ), and Accipitridae ( $N = 4$ ). Of the observed species, one is categorized as threatened by the IUCN Red List

(Supplementary Table S2), the red-tailed Newtonia (*Newtonia fanovanae*).

### 3.4 | Mammals

We identified 6 orders, 11 families, 18 genera, and 18 species of mammals. Two of the observed specimens, all

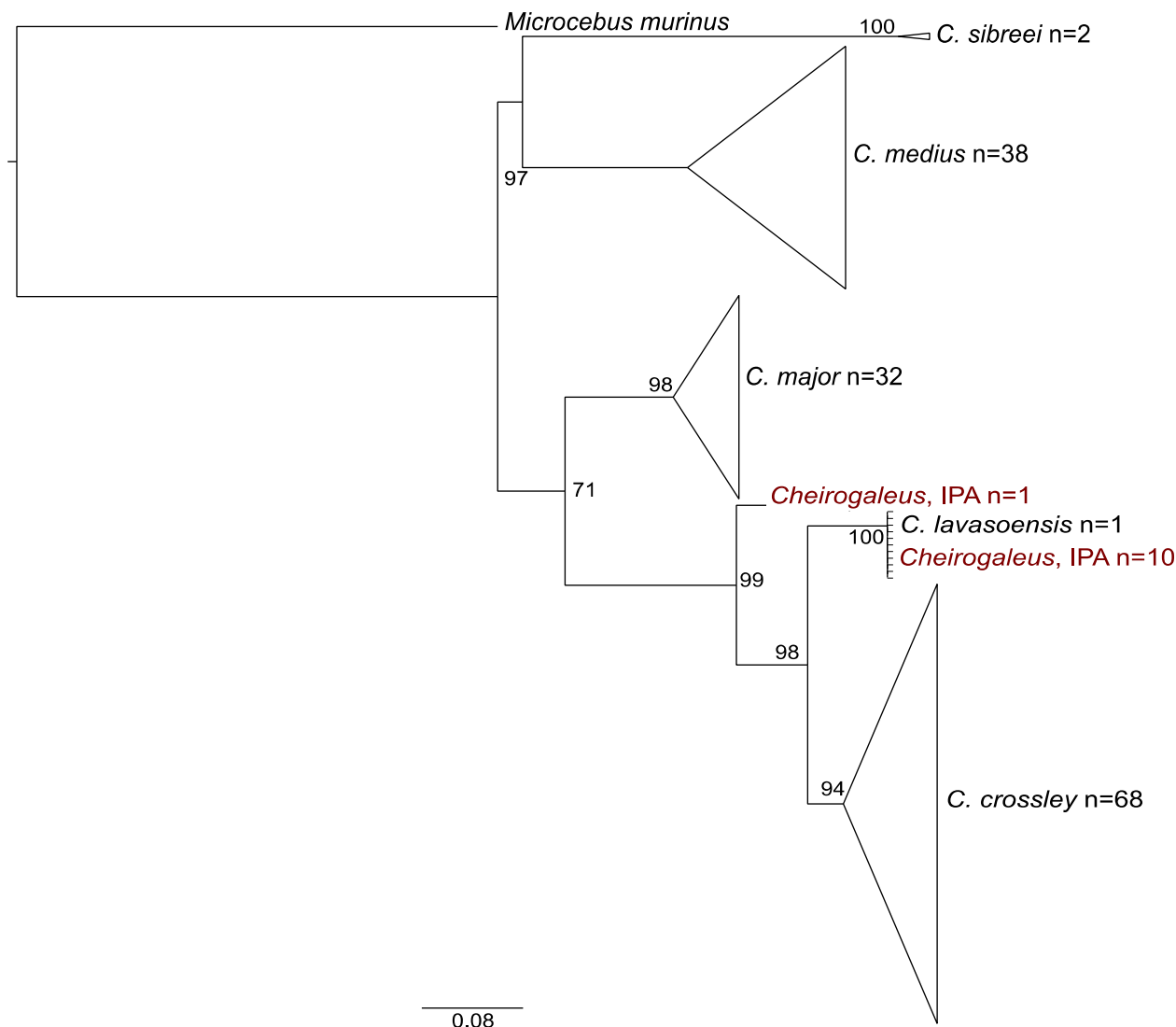


FIGURE 3 Mitochondrial DNA (*COII*) phylogenetic tree of *Cheirogaleus* specimens (red) from Ivohiboro Humid Forest.

belonging to the Cheirogaleidae family of primates, could only be identified to the genus level. The most common orders of mammals observed were Chiroptera ( $N = 5$ ), Rodentia ( $N = 5$ ), and Primates ( $N = 2$  species and  $N = 2$  morphospecies) representing 65% of observed mammal species. Within the order Primates, we documented three morphologically distinct cheirogaleids (i.e., two *Cheirogaleus* sp., and one *Microcebus* sp.; Figure 2b,c) and one lemurid (i.e., ring-tailed lemur, *Lemur catta*; Figure 2a). We conducted a preliminary analysis of mitochondrial DNA for the *Cheirogaleus* individuals to identify the species present. Our results show that there are two distinct species present, one of which is *Cheirogaleus lavasoensis* (Figure 3), the other remains unknown. In addition, we identified three species within the order Carnivora: the fossa, (*Cryptoprocta ferox*), spotted fanaloka (*Fossa fossana*), and ring-tailed vontsira (*Galidia elegans*). Of the

observed species, four are categorized as threatened by the IUCN (Supplementary Table S2), and two are classified as endangered: the ring-tailed lemur (*L. catta*), and the Lavasoa dwarf lemur (*C. lavasoensis*).

### 3.5 | Vascular plants

We documented a total of 4 taxonomic classes, 42 orders, 106 families, and 254 genera of vascular in the IHF. We identified 210 plant species, while the remaining 98 were identified at the level of genus (Supplementary Table S1). Plants of the order Malpighiales ( $N = 38$ ) and Gentianales ( $N = 35$ ) represented the greatest number of taxa found. The most abundant families of vascular plants include the Rubiaceae ( $N = 19$ ), Euphorbiaceae ( $N = 15$ ), and Apocynaceae ( $N = 12$ ). Of the observed species,



19 are categorized as threatened by the IUCN, of which 6 are classified as endangered (Supplementary Table S2).

## 4 | DISCUSSION

Despite its small size and isolation, the IHF exhibited signals of a biodiverse ecosystem. Our biological surveys yielded surprising results providing clues to the importance of the IHF in safeguarding biodiversity. The diverse species of reptiles and amphibians present in the IHF highlight the conservation value of this forest fragment. Endangered amphibians present in the IHF, both *G. corvus* and *An. Moramora*, indicate isolated, novel populations of the species, and a range expansion from their recorded range. Similarly, if the observed chameleon with affinity to *C. boettgeri* is determined to be the blue-nosed chameleon, it would suggest a range expansion, this population being more than 1000 km southwest of the species' known distribution.

The presence of predators suggests that although the IHF is a small and isolated forest, it has a biodiverse ecosystem (Sergio et al., 2008). Demonstrative of this, we recorded the presence of carnivorans (e.g., fossa, *C. ferox*, and spotted fanaloka, *F. fossana*), boa constrictors (e.g., Malagasy tree boa, *Sanzinia madagascariensis*, and Dumeril's boa, *Acrantophis dumerili*), diurnal raptors (e.g., Malagasy harrier-hawk, *Polyboroides radiatus*, and the Malagasy kestrel, *Falco newtoni*), and nocturnal raptors (e.g., Madagascar scops owl, *Otus rutilus*, and the Madagascar long-eared owl, *Asio madagascariensis*).

The primate diversity within the IHF included one diurnal lemur species (*L. catta*) and three nocturnal lemurs (*C. lavasoensis*, *Cheirogaleus* sp., and *Microcebus* sp.). The presence of ring-tailed lemurs in the IHF was unexpected, as *L. catta* is typically distributed across dry habitats (Goodman et al., 2006; Lafleur et al., 2016; LaFleur & Gould, 2020). We observed and documented eight separate groups of *L. catta* in this forest, with group sizes ranging from 11 to 20 individuals. This species is currently listed as endangered by the IUCN Red List and is of particular conservation concern due to recent population declines and local extinctions driven by habitat loss and human activities (Gould & Sauter, 2016; LaFleur et al., 2016, 2019; Reuter & Schaefer, 2017). This suggests that *L. catta* might be using the IHF as a refuge and may reflect previously unknown habitat for the species. Thus, IHF ring-tailed lemur populations are important for conservation and provide an opportunity to study the behavior and ecology of the species in this special environment.

Madagascar's humid forests contain high lemur species diversity (Antonelli et al., 2022). For example, the

closest protected area to IHF containing humid forest, Pic d' Ivohibe Reserve (Figure 1a), has four diurnal lemur species: *Eulemur rubriventer*, *Eulemur rufifrons*, *Hapalemur meridionalis*, and *L. catta* (the latter located in the westward wooded grassland; Mittermeier et al., 2010). In contrast, we observed only one diurnal lemur species in the IHF (*L. catta*) and hypothesize that the more common diurnal may have been extirpated from the IHF by meat hunting based on field observations and regional hunting patterns. The brown lemurs (genus *Eulemur*) and bamboo lemurs (genus *Hapalemur*) are among the most common, and the most hunted lemur species (Borgerson et al., 2022; Thompson et al., 2023). During our work in the IHF, we observed lemur traps in and around the forest. Hunting is one of the main drivers of lemur population decline, and has resulted in local extinctions in different regions of Madagascar (Jenkins et al., 2011; Schwitzer et al., 2014; Thompson et al., 2023). We hope that hunting in the IHF will decrease in coming years since it is part of the IPA, which was established in 2021.

The nocturnal lemurs (i.e., *Cheirogaleids*) present in IHF were differentiated as two distinct dwarf lemur species (*C. lavasoensis* and *Cheirogaleus* sp.; Figure 3), and one mouse lemur (*Microcebus*). *C. lavasoensis* is classified as endangered by the IUCN (Blanco et al., 2018), and prior to these surveys its reported distribution was restricted to dry and moist forests in the Anosy region, about 275 km south-east of the IHF (Thiele et al., 2013). The presence of this species suggests either a potential range expansion, or that these are relictual populations of *C. lavasoensis* in the IHF. We are conducting more comprehensive genetic analysis of both *Cheirogaleus* and *Microcebus* to explore the phylogenetic history of the IHF lemurs.

In conclusion, the IHF is habitat for 34 Threatened species vertebrates and vascular plants as categorized by IUCN Red List. Our results indicate a potential expansion of the known ranges for several of these species. These findings highlight the role IHF plays as a refuge for biodiversity in the region and indicate the great value of this forest for species conservation. The IHF offers the opportunity to explore both the history of forest cover, and species ranges in central Madagascar. In addition, to allowing the study of behavioral changes of dry habitat species in humid ecosystems. Further exploration of this isolated humid forest may hold the key to illuminating the IHF's role as a relict or refuge for Malagasy flora and fauna.

## AUTHOR CONTRIBUTIONS

*Conception, data acquisition:* Beatriz Otero Jimenez, Ren Montañó, Ryan S. Rothman, and Patricia C. Wright.

*Manuscript draft:* Beatriz Otero Jimenez, Ren Montaña, Ryan S. Rothman, Rachel C. Williams, and Patricia C. Wright. *Securing funding:* Patricia C. Wright. *Data analysis:* Ren Montaña (*Biogeographical*), Rachel C. Williams (*Genetic Analysis*), and Beatriz Otero Jimenez, Ren Montaña, and Ryan S. Rothman (*Taxonomic data*).

## ACKNOWLEDGMENTS

We want to thank the Centre ValBio collection teams for conducting the biodiversity surveys and aiding in the identification of species. Special thanks to Laza H. Andrianandrianina, Dina Andrianoely, Christopher Birkinshaw, Amy E. Dunham, Andrzej Kepel, Marta Kepel, Rokiman Letsara, Christopher J. Raxworthy, Scott K. Robinson, Noel Rowe, Bekah Weatherington, Brett R. Scheffers, and Missouri Botanical Garden for aiding in the collection and identification of species. We want to thank the villages of Antanambao, Amboakitsy, and Analamary and the village elders for allowing us to travel through their lands and guiding our way. We thank the Ihosy Gendarmerie for accompanying our teams in their expeditions. We thank the Duke Lemur Center and Dr Anne Yoder for their support in the phylogenetic analysis. Finally, we thank the Madagascar Institute for the Conservation of Tropical Environments (MICET) for their technical and logistical support. Field surveys and data analysis were supported by grants from the Rainforest Foundation, National Geographic Society, Missouri Botanical Gardens, Primate Conservation Incorporated, and the National Institute of Health Institutional Research and Academic Career Development Award at Stony Brook University. DNA sequencing was funded by National Science Foundation Grant DEB-1354610 and RW salary by Duke University research funds to Anne D. Yoder. Geographic surveys and analysis by RM were supported by James Xavier Purcell. The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

All survey data are included in the Supplementary documents. Genetic sequencing data are available upon request to the corresponding author.


## ORCID

Beatriz Otero Jimenez  <https://orcid.org/0000-0002-9686-9493>

Ren Montaña  <https://orcid.org/0000-0002-4382-9316>

Ryan S. Rothman  <https://orcid.org/0000-0002-8985-6168>

6168

Rachel C. Williams  <https://orcid.org/0000-0002-7158-4117>

## REFERENCES

- Antonelli, A., Smith, R. J., Perrigo, A. L., Crottini, A., Hackel, J., Testo, W., Farooq, H., Torres Jiménez, M. F., Andela, N., Andermann, T., Andriamanohera, A. M., Andriambololona, S., Bachman, S. P., Bacon, C. D., Baker, W. J., Belluardo, F., Birkinshaw, C., Borrell, J. S., Cable, S., ... Ralimanana, H. (2022). Madagascar's extraordinary biodiversity: Evolution, distribution, and use. *Science*, 378(6623), eabf0869. <https://doi.org/10.1126/science.abf0869>
- Blanco, M. B., Dolch, R., Donati, G., Ganzhorn, J. U., Greene, L. K., LePors, B., Lewis, R., Louis, E. E., Rafalinirina, H. A., Raharivololona, B., Rakotoarisoa, G., Ralison, J., Randriaingy, H. N. T., Rasoloarison, R., Razafindrasolo, M., Sgarlata, G. M., Wright, P. C., & Zaonarivelo, J. R. (2018). *IUCN red list of threatened species: Cheirogaleus lavasoensis*. IUCN Red List of Threatened Species <https://www.iucnredlist.org/fr>
- Borgerson, C., Johnson, S. E., Hall, E., Brown, K. A., Narváez-Torres, P. R., Rasolofoniaina, B. J. R., Razafindrapaoly, B. N., Merson, S. D., Thompson, K. E. T., Holmes, S. M., Louis, E. E., & Golden, C. D. (2022). A national-level assessment of lemur hunting pressure in Madagascar. *International Journal of Primatology*, 43(1), 92–113. <https://doi.org/10.1007/s10764-021-00215-5>
- Brown, K. A., Parks, K. E., Bethell, C. A., Johnson, S. E., & Mulligan, M. (2015). Predicting plant diversity patterns in Madagascar: Understanding the effects of climate and land cover change in a biodiversity hotspot. *PLoS One*, 10(4), e0122721. <https://doi.org/10.1371/journal.pone.0122721>
- Burgess, N., Hales, J. D., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T., & Newman, K. (2004). Terrestrial ecoregions of Africa and Madagascar: A conservation assessment. <https://www.cabdirect.org/cabdirect/abstract/20073287118>
- Burns, S. J., Godfrey, L. R., Faina, P., McGee, D., Hardt, B., Ranivoharimanana, L., & Randrianasy, J. (2016). Rapid human-induced landscape transformation in Madagascar at the end of the first millennium of the common era. *Quaternary Science Reviews*, 134, 92–99. <https://doi.org/10.1016/j.quascirev.2016.01.007>
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, 28(1), 137–167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- Dudley, N., Shadie, P., & Stolton, S. (2013). Guidelines for applying protected area management categories including IUCN WCPA best practice guidance on Recognising Protected Areas and Assigning Management Categories and Governance Types. Best Practice Protected Area Guidelines Series, No. 21. <https://www.cabdirect.org/cabdirect/abstract/20193172820>
- Ehrlich, P. R., & Pringle, R. M. (2008). Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. *Proceedings of the National Academy of Sciences of the United States of America*, 105(Supplement 1), 11579–11586. <https://doi.org/10.1073/PNAS.0801911105>



- FAO and UNEP. (2020). The State of the World's Forests (2020). Forests, biodiversity and people. <https://doi.org/10.4060/ca8642en>
- Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, 45(2), 1–33. <https://doi.org/10.1029/2005RG000183>
- Fegraus, E. (2012). Tropical ecology assessment and monitoring network (TEAM network). *Biodiversity & Ecology*, 4, 287. <https://doi.org/10.7809/b-e.00085>
- Fischer, R., Taubert, F., Müller, M. S., Groeneveld, J., Lehmann, S., Wiegand, T., & Huth, A. (2021). Accelerated forest fragmentation leads to critical increase in tropical forest edge area. *Science Advances*, 7(37), eabg7012. <https://doi.org/10.1126/sciadv.abg7012>
- Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., & Sommer, S. (2001). The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx*, 35(4), 346–348. <https://doi.org/10.1046/j.1365-3008.2001.00201.x>
- Glaw, F., Jenkins, R. K. B., Prötzel, D., & Tolley, K. (2015). IUCN red list of threatened species: *Calumma boettgeri*. IUCN Red List of Threatened Species. <https://www.iucnredlist.org/en>
- Goodman, S. M., & Benstead, J. P. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39(1), 73–77. <https://doi.org/10.1017/S0030605305000128>
- Goodman, S. M., Rakotoarisoa, S. V., & Wilmé, L. (2006). The distribution and biogeography of the ringtailed lemur (*Lemur catta*) in Madagascar. In *Ringtailed lemur biology: Lemur catta in Madagascar* (pp. 3–15). Boston, MA: Springer US.
- Gould, L., & Sauther, M. (2016). Going, going, gone. Is the iconic ring-tailed lemur (*Lemur catta*) headed for imminent extirpation? *Primate Conservation*, 30, 89–101.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), e1500052. <https://doi.org/10.1126/sciadv.1500052>
- 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(4), 325–333. <https://doi.org/10.1017/S0376892907004262>
- IUCN SSC Amphibian Specialist Group. (2016a). *Anodonthyla moramora*. The IUCN Red List of Threatened Species 2016: e.T136055A517485. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136055A517485.en>
- IUCN SSC Amphibian Specialist Group. (2016b). *Gephyromantis corvus*. The IUCN Red List of Threatened Species 2016: e.T57473A84170678. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T57473A84170678.en>
- Jenkins, R. K. B., Keane, A., Rakotoarivelo, A. R., Rakotomboavonjy, V., Randrianandrianina, F. H., Razafimanahaka, H. J., Ralaarimalala, S. R., & Jones, J. P. G. (2011). Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLoS One*, 6(12), e27570. <https://doi.org/10.1371/JOURNAL.PONE.0027570>
- Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., & Jermin, L. S. (2017). ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14(6) Article 6, 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh, K., Misawa, K., Kuma, K., & Miyata, T. (2002). MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30(14), 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Kiener, A. (1963). Le «Tavy» à Madagascar: Ses différentes formes et dénominations. Bilan du tavy et problèmes humains. Moyens de lutte. *Revue Bois et Forêts Des Tropiques*, 90, 9–16.
- LaFleur, M., Clarke, T. A., Reuter, K., & Schaeffer, T. (2016). Rapid decrease in populations of wild ring-tailed lemurs (*Lemur catta*) in Madagascar. *Folia Primatologica*, 87(5), 320–330. <https://doi.org/10.1159/000455121>
- LaFleur, M., Clarke, T. A., Reuter, K. E., Schaefer, M. S., & terHorst, C. (2019). Illegal trade of wild-captured *Lemur catta* within Madagascar. *Folia Primatologica*, 90(4), 199–214. <https://doi.org/10.1159/000496970>
- LaFleur, M., & Gould, L. (2020). *Lemur catta*. The IUCN Red List of Threatened Species 2020: e.T11496A115565760. <https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T11496A115565760.en>. Accessed on 05 July 2023.
- Mittermeier, R. A., Louis, E. E., Jr., Richardson, M. J., Schwitzer, C., Langrand, O., Rylands, A. B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., & Roos, C. (2010). *Lemurs of Madagascar*. Conservation International.
- Moat, J., & Smith, P. (2007). *Atlas of the vegetation of Madagascar*. Royal Botanic Gardens, Kew <https://press.uchicago.edu/ucp/books/book/distributed/A/bo9854791.html>
- Morelli, T. L., Smith, A. B., Mancini, A. N., Balko, E. A., Borgerson, C., Dolch, R., Farris, Z., Federman, S., Golden, C. D., Holmes, S. M., Irwin, M., Jacobs, R. L., Johnson, S., King, T., Lehman, S. M., Louis, E. E., Murphy, A., Randriahaingo, H. N. T., Randrianarimanana, H. L. L., ... Baden, A. L. (2019). The fate of Madagascar's rainforest habitat. *Nature Climate Change*, 10(1), 89–96. <https://doi.org/10.1038/s41558-019-0647-x>
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Nguyen, L.-T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32(1), 268–274. <https://doi.org/10.1093/molbev/msu300>
- Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems—A new conservation paradigm. *Year in Ecology and Conservation Biology*, 2008(1134), 173–200. <https://doi.org/10.1196/annals.1439.011>
- Prötzel, D., Ruthensteiner, B., Scherz, M., & Glaw, F. (2015). Systematic revision of the Malagasy chameleons *Calumma boettgeri* and *C. linotum* (Squamata: Chamaeleonidae). *Zootaxa*, 4048, 211–231. <https://doi.org/10.11646/zootaxa.4048.2.4>
- Ralimanana, H., Perrigo, A. L., Smith, R. J., Borrell, J. S., Faurby, S., Rajaonah, M. T., Randriamboavonjy, T.,

- Vorontsova, M. S., Cooke, R. S. C., Phelps, L. N., Sayol, F., Andela, N., Andermann, T., Andriamanohera, A. M., Andriambololonera, S., Bachman, S. P., Bacon, C. D., Baker, W. J., Belluardo, F., ... Antonelli, A. (2022). Madagascar's extraordinary biodiversity: Threats and opportunities. *Science*, 378(6623), eadf1466. <https://doi.org/10.1126/science.adf1466>
- Reuter, K. E., & Schaefer, M. S. (2017). Illegal captive lemurs in Madagascar: Comparing the use of online and in-person data collection methods. *American Journal of Primatology*, 79(11), e22541. <https://doi.org/10.1002/ajp.22541>
- Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343(6173), 842–843. <https://doi.org/10.1126/science.1245783>
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., & Hiraldo, F. (2008). Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics*, 39, 1–19. <https://doi.org/10.1146/ANNUREV.ECOLSYS.39.110707.173545>
- Styger, E. (2004). *Fire-less alternatives to slash-and-burn agriculture (tavy) in the rainforest region of Madagascar—ProQuest* [PhD dissertation, Cornell University]. <https://www.proquest.com/docview/305212791?pq-origsite=gscholar&fromopenview=true>
- Sussman, R. W., Green, G. M., & Sussman, L. K. (1994). Satellite imagery, human ecology, anthropology, and deforestation in Madagascar. *Human Ecology*, 22(3), 333–354.
- Thiele, D., Razafimahatratra, E., & Hapke, A. (2013). Discrepant partitioning of genetic diversity in mouse lemurs and dwarf lemurs—Biological reality or taxonomic bias? *Molecular Phylogenetics and Evolution*, 69(3), 593–609. <https://doi.org/10.1016/J.YMPEV.2013.07.019>
- Thompson, K. E. T., Borgerson, C., Wright, P. C., Randriamanetsy, J. M., Andrianantenaina, M. Y., Andriamavosoloarisoa, N. N. M., Razafindrahasy, T. A., Rothman, R. S., Surkis, C., Bankoff, R. J., Daniels, C., & Twiss, K. C. (2023). A coupled humanitarian and biodiversity crisis in Western Madagascar. *International Journal of Primatology*, 1–28. <https://doi.org/10.1007/s10764-022-00338-3>
- Tucker, C. J., & Townshend, J. R. G. (2000). Strategies for monitoring tropical deforestation using satellite data. *International Journal of Remote Sensing*, 21(6–7), 1461–1471. <https://doi.org/10.1080/014311600210263>
- Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J. R., Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222, 189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>
- Zhang, L., Ameca, E. I., Otero-Jimenez, B., Montaña, S. K., Shea, A., Kelly, T., Andrianoely, D., & Wright, P. C. (2022). Human-induced deforestation increases extinction risk faster than climate pressures: Evidence from long-term monitoring of the globally endangered Milne-Edward's sifaka. *Biological Conservation*, 274, 109716. <https://doi.org/10.1016/j.biocon.2022.109716>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Otero Jimenez, B., Montaña, R., Rothman, R. S., Williams, R. C., & Wright, P. C. (2023). A surprising haven: The biodiversity of an old-growth forest amidst a scorched landscape in Madagascar. *Conservation Science and Practice*, 5(9), e12993. <https://doi.org/10.1111/csp2.12993>

© 2023. This work is published under  
<http://creativecommons.org/licenses/by/4.0/>(the “License”). Notwithstanding  
the ProQuest Terms and Conditions, you may use this content in accordance  
with the terms of the License.