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A COMPREHENSIVE ANALYSIS OF REPTILE DIVERSITY IN MADIDI NATIONAL PARK AND NATURAL INTEGRATED MANAGEMENT AREA, ONE OF THE WORLD'S MOST BIOLOGICALLY DIVERSE PROTECTED AREAS

UN ANÁLISIS COMPLETO DE LA DIVERSIDAD DE REPTILES EN EL PARQUE NACIONAL Y ÁREA NATURAL DE MANEJO INTEGRADO MADIDI, UNA DE LAS ÁREAS PROTEGIDAS CON MAYOR DIVERSIDAD BIOLÓGICA DEL MUNDO

James Aparicio[1†], Mauricio Ocampo[1,2*], Nuria Bernal-Hoverud[3,4], Enrique Domic[3] & Robert B. Wallace[3]

[1]*Red de Investigadores en Herpetología - Bolivia, Av. José Aguirre 260, Los Pinos, Zona Sur, La Paz, Bolivia.*

[2]*Unidad de Zoología - Instituto de Ecología, Universidad Mayor de San Andrés, Casilla 10077 – Correo Central, La Paz, Bolivia.*

[3]*Wildlife Conservation Society, Edificio Torre Soleil, Calle Jaime Mendoza # 987, San Miguel, La Paz, Bolivia.*

[4]*Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409, USA.*

† James Aparicio sadly passed away after this research was carried out.

** Corresponding author. E-mail: mauiocampo@gmail.com*

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Resumen.– La Amazonía es la selva tropical más grande del mundo, albergando una miríada de plantas, hongos y animales, y abarcando una gran diversidad de ecorregiones. Bolivia ha asignado el 17 % de su territorio a áreas protegidas nacionales, entre las cuales el Parque Nacional y Área Natural de Manejo Integrado Madidi cuenta con la mayor representación de ecorregiones en el país. Sin embargo, a pesar de su importancia, el conocimiento sobre la herpetofauna de Madidi sigue siendo limitado. Este estudio presenta el inventario más completo de la diversidad de reptiles dentro y alrededor de Madidi, combinando una extensa revisión de la literatura con tres años de trabajo de campo. Calculamos los índices de diversidad alfa, beta, gamma y oscura para comprender la composición de las especies de reptiles en las ecorregiones representadas dentro del área protegida. Registramos 110 especies de reptiles dentro del parque, siendo la ecorregión del Bosque Amazónico Subandino la que muestra mayor diversidad. Los índices de diversidad aplicados indican el potencial para descubrir nuevas especies en el área, y como se espera en una zona montañosa, hay un alto recambio de especies entre las ecorregiones, cada una de ellas exhibiendo una composición distintiva de especies. Recomendamos un monitoreo continuo en un área con tan alta diversidad de reptiles, especialmente considerando los impactos que el cambio climático tendrá en las comunidades de estas especies a lo largo del tiempo.

Palabras clave.– Diversidad obscura, ecorregiones, herpetofauna, reptiles amazónicos, recambio de especies.

Abstract.– The Amazon is the world's largest tropical rainforest, hosting a myriad of plants, fungi and animals, and encompassing a wide diversity of ecoregions. Bolivia has allocated 17 % of its territory to national protected areas, among which Madidi National Park and Natural Integrated Management Area boasts the largest representation of ecoregions in the country. However, despite its significance, knowledge of Madidi's herpetofauna remains limited. This study presents the most comprehensive survey of reptile diversity in and around Madidi, combining an extensive literature review with three years of fieldwork. We computed alpha, beta, gamma, and dark diversity indices to comprehend the composition of reptile species across the ecoregions represented within the protected area. We registered 110 reptile species within the park, with the Sub-Andean Amazon Forest ecoregion displaying the highest diversity. The diversity indices applied indicate the potential for discovering additional species in the area, and as expected for a mountainous area, there is a high turnover of species between ecoregions, each of them exhibiting a distinctive species composition. We recommend continuous monitoring in an area with such high reptile diversity, particularly considering the impacts that climate change will have on these species' assemblages over time.

Keywords.– Amazonian reptiles, dark diversity, ecoregions, herpetofauna, species turnover.

INTRODUCTION

The Amazon is the most biodiverse region on the planet (Antonelli et al., 2018) due to various factors. One of them has been the rapid rise of the Andes, facilitating the formation of diverse and dynamic ecosystems and acting as species pump (Hoorn et al., 2010, 2013). Through geological movements, population separations and isolations occur, driving vicariant speciation in many species (Umbrello et al., 2024). This process is orchestrated by climatic and topographic shifts, which lead to the establishment of new resources, predators, and pathogens that shape community structures throughout the Andes (Chazot et al., 2018). Other crucial factors include the origins of plants and animals during the Late Cretaceous and early Paleogene, and the global cooling of the Eocene-Oligocene and Pleistocene, which led to the contraction of tropical forests. During these glacial periods, the Amazon served as a refuge, harboring species and providing sufficient time for adaptive evolution (Haffer 1969; Garzón-Orduña et al., 2015; Rocha & Kaefer, 2019; Escobar et al., 2021). Specifically, the areas of highest species diversity in the Amazon are concentrated in the mountainous regions of the basin, where there is greater richness, as well as higher turnover of species in a smaller area (Sonne & Rahbek, 2024).

Throughout their evolutionary history, reptiles capitalized on the geological history of the Andes, undergoing a significant adaptive radiation by exploiting new ecological opportunities that became available (Gomes et al., 2013; Prates et al., 2015; Esquerré et al., 2019; Ocampo et al., 2022). Additionally, reptiles play a crucial role in the trophic chain in ecosystems due to their high ecological diversity, especially across the altitudinal gradient of the Andes, from primary consumers such as turtles to top predators such as caiman and snakes.

The Madidi National Park and Natural Integrated Management Area (hereafter Madidi National Park) in the Plurinational State of Bolivia spans one of the most diverse and extensive altitudinal gradients in the upper Amazon, safeguarding a wide diversity of ecoregions, and considered as one of the most diverse parks in the world (Salinas & Wallace, 2012; Wallace et al., 2017; Ocampo et al., 2024). Knowledge of its herpetofauna was limited and scattered across a few publications, technical reports, and incidental records (Emmons, 1991; Pérez-Bejar, 1997; MacQuarrie et al., 2001; Montambault, 2002). These sources covered only a handful of easily accessible localities, providing an incomplete understanding of the true diversity harbored within this park. Here, we report the results of a comprehensive survey of reptile diversity for Madidi National Park as part of the Identidad Madidi project (https://madidiid.org/en/) led by the Wildlife Conservation Society (WCS) during three consecutive years (2015 to 2017) of fieldwork across an altitudinal gradient that covered a range of 4,616 m a.s.l. (Identidad Madidi & SERNAP, 2017, 2019; Identidad Madidi, 2020), complemented with a thorough search of available published information on reptiles in the area and surroundings.

METHODS

Study area

Madidi National Park, spanning 18,957.4 km², is Bolivia's third largest protected area, encompassing five municipalities (San Buenaventura, Ixiamas, Guanay, Pelechuco, Apolo) and three indigenous territories (Uchupiamonas, Tacana and Lecos). The altitudinal range spans from 6,044 m a.s.l. at the peak of the Chaupi Orco mountain, to 180 m a.s.l. at its lowest point (Salinas & Wallace, 2012). Situated within the Amazon basin, Madidi includes six distinct ecoregions: Sub-Andean Amazon Forests, Pre-Andean Amazon Forests, Cerrado Paceño, Yungas, Inter-Andean Dry Forests, and High Andean Vegetation (Fig. 1) (Ibisch et al., 2003). Its strategic location and vast expanse render it as the protected area with the best representation of ecosystems and with the highest species richness in Bolivia, positioning it as one of the most significant conservation areas continentally and globally (Salinas & Wallace, 2012).

The study area was delineated using two buffers. The first buffer, set at 1 km, accounted for records located near the park boundaries and potential georeferencing inaccuracies in historical data, as well as the natural dynamics of river meanders (Seminara, 2006), which alter river courses and subsequently modify the park's boundaries. Consequently, species recorded within this 1-km buffer zone were considered as present within the park.

The second buffer extended 50 km beyond the park's boundaries and was used to assemble species communities that facilitated the calculation of dark diversity across ecoregions. Dark diversity is estimated based on the co-occurrence frequency of species within communities, providing a complementary list of species potentially present in ecoregions where they were not recorded. By analyzing co-occurrence patterns with other species, this method predicts species presence with a reasonable degree of accuracy (Lewis et al., 2017). The list estimated through the dark diversity analysis, is presented as complementary information in the results. However, it is not included in the calculations of alpha or beta diversity. Expanding the study area by 50-km beyond the strict limits of the park introduced three

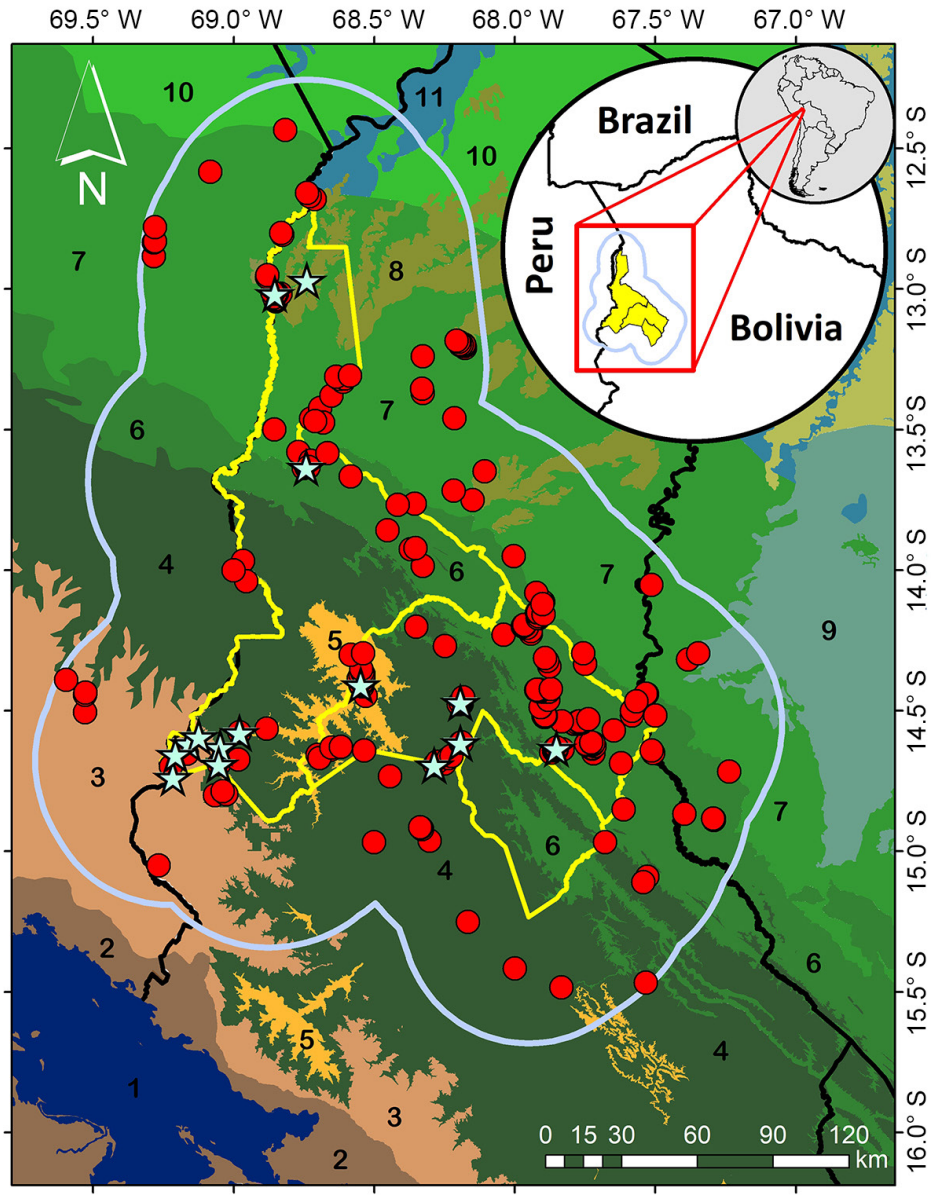

Figura 1. Mapa del área de estudio, con el Parque Nacional y el Área Natural de Manejo Integrado Madidi delineados en amarillo, una línea azul claro que representa la zona de amortiguamiento de 50 km, estrellas azules claras que indican los campamentos de trabajo de campo, y puntos rojos que denotan los registros de reptiles tanto de la base de datos como del trabajo de campo. Los números en negro corresponden a las ecorregiones, donde 1 es el Lago Titicaca, 2 Puna Húmeda, 3 Vegetación Altoandina, 4 Yungas, 5 Bosques Secos Interandinos, 6 Bosques Amazónicos Subandinos, 7 Bosques Amazónicos Preandinos, 8 Cerrado Paceño, 9 Sabana Inundable de los Llanos de Moxos, 10 Bosque Amazónico de Pando, 11 Bosque Inundable Amazónico.

Figure 1. Map of the study area, with the Madidi National Park and Natural Integrated Management Area outlined in yellow, a light blue line representing the 50-km buffer area, light blue stars indicating fieldwork camps, and red dots denoting reptilian records from both the database and fieldwork. Black numbers correspond to ecoregions, where 1 is Titicaca Lake, 2 Wet Puna, 3 High Andean Vegetation, 4 Yungas, 5 Inter-Andean Dry Forests, 6 Sub-Andean Amazon Forests, 7 Pre-Andean Amazon Forests, 8 Cerrado Paceño, 9 Llanos de Moxos Flooded Savannahs, 10 Pando Amazon Forest, 11 Amazonian Floodplain Forest.

additional ecoregions to the study: Amazonian Flood Forest, Pando Amazon Forest, and Llanos de Moxos Flooded Savannahs.

Baseline

A herpetological database was organized, compiling the largest possible number of records. Unfortunately, scientific publications available online are limited, with the majority of documented records within the park derived from local technical reports (Cortez & Tejada, 2002; Domic et al., 2012), official catalogs from the Colección Boliviana de Fauna (CBF), and photographic records from the WCS database. This information was further supplemented with data published in online databases, such as GBIF.org (GBIF 2014), Geo-Vertebrados from the Museo de Historia Natural Noel Kempff Mercado, and the identification and verification of photographs from the iNaturalist.net platform. The study boundaries were delimited by the 50-km buffer zones mentioned above.

Field work

With the objective of increasing the number of reported species within Madidi, fifteen distinct sites were surveyed, spanning the full altitudinal gradient of the park, as well as all ecoregions present within the park (Fig. 1, Appendix S1). We applied the visual and auditory encounter survey technique through exhaustive searches across all sites to document the maximum

reptilian diversity during our surveys (Dodd, 2016). This involved meticulous diurnal and nocturnal searches around potential shelters such as under rocks, logs, and leaf litter, as well as in streams and swamps (Simmons, 2002), with the objective of completing 36 man-hours per day. Straight-line drift fences with pitfall traps were deployed at seven of the fifteen sites (Dodd, 2016), but not in the higher elevation sites where this technique was impractical due to the predominantly rocky substrate (Appendix S1).

We conducted scientific collections of some species whose identification was considered uncertain. Euthanasia was performed using an overdose of sodium thiopental anaesthetic, followed by fixation in formalin and preservation in 70 % ethanol (Dodd, 2016; Leary et al., 2020). Subsequently, specimens were deposited at the Colección Boliviana de Fauna (CBF) in La Paz, Bolivia (Appendix S2). Taxonomic identification was conducted in the laboratory, involving comparisons with reference collections for validation, as well as the necessary taxonomic keys for the different taxonomic groups (Avila-Pires, 1995; Harvey et al., 2003; Doan & Castoe, 2005; Harvey et al., 2005; Rueda-Almonacid et al., 2007; Torres-Carvajal, 2007; Kok, 2010; Ascenso et al., 2019). These voucher specimens represent a crucial resource for prospective taxonomic revisions in the future.

Data Analyses

Alpha diversity was computed based on field-sampled data. Rarefaction curves for both samples and individuals were generated, and nonparametric species richness estimators (i.e., Chao, ACE, Jackknife) were calculated and compared with the overall species richness. R Studio software, along with the vegan package and functions such as rarefy were employed to calculate individual-based rarefaction curves, specaccum for sample-based rarefaction curves, estimateR to compute ACE values, and specpool to estimate species richness using Chao 2 and Jackknife 2 indices were employed for analysis (R Core Team, 2022).

For beta diversity analysis, we quantified dissimilarity between ecoregions using the Whittaker index, utilizing fieldwork data and the betadiver function from the BiodiversityR package in R Studio software. A dendrogram and a ternary diagram were built to visualize dissimilarities among the different ecoregions represented in the park. Gamma diversity encompassed all recorded species in the study, both inside and outside the park limits (records within a 1-km and 50-km buffers) representing the regional species pool.

We assessed dark diversity using the Beals index on species co-occurrence likelihood with 95 % confidence (Lewis et al., 2016). This method estimates dark diversity by calculating the probability that a species occurs in a plot based on its co-occurrence with the observed species in the rest of the dataset. A species is thus considered to be part of the dark diversity of a plot if it is absent in the plot, but regularly co-occurs with species that are present in the plot. This index provides complementary information about the species expected in an ecoregion but, for some reason was not recorded. The analysis was conducted using the beals function in the vegan package in R (R Core Team, 2022). Lists of species were compiled for each ecoregion inside and outside the protected area, resulting in 13 ecoregions for comparison (6 inside and 7 outside), and the probability of species co-occurrence was estimated.

RESULTS

Baseline

From a total of 655 individual records (270 individuals inside Madidi, and 385 individuals outside Madidi), the total number species recorded was 116, 85 species confirmed inside Madidi, 99 species outside Madidi, with 68 species shared between both areas (Table 1).

Field work

In the 15 sites surveyed we captured 147 individuals, corresponding to 69 species (Table 1), 25 of which represent new records for the park, of which one of them is a new record for Bolivia, and six of them are potential candidate species new to science (Table 2).

Alpha diversity

Over 209 days of effective sampling, and previous extensive literature review, we documented a total of 110 species confirmed inside the park (Table 1). The Sub-Andean Amazon Forest, Pre-Andean Amazon Forest, and the Yungas emerged as the three ecoregions with the highest diversity, with 71, 55 and 40 species, respectively. Notably, no reptile species had previously been documented in Cerrado Paceño and High Andean Vegetation in Madidi, and now we report three species for Cerrado Paceño and four species for High Andean Vegetation. Fieldwork efforts documented 61 % of the species diversity present in the park. Accumulation and rarefaction curves indicate that an asymptote has not yet been reached, suggesting the likelihood of recording additional species in the future (Fig. 2). Of the 110 species now known for Madidi National Park, the Chao 2 and Jackknife 2 species richness estimators overestimated their predictions (116 and 125, respectively); however, Chao 2 was the closest to this value.

Tabla 1. Número total de especies encontradas en cada una de las ecorregiones en este estudio y esfuerzo de muestreo; "Days" se refiere al número de días efectivos de muestreo en cada ecorregión. Número de especies registradas de: FW Trabajo de campo, BLI Línea base dentro de Madidi, BLO Línea base fuera de Madidi. Los guiones indican que la ecorregión no está representada en la columna respectiva.

Table 1. Total number of species found in each of the ecoregions in this study and sampling effort; "Days" refers to the number of effective days surveyed in each ecoregion. Number of species recorded from: FW Field work, BLI Baseline inside Madidi, BLO Baseline outside Madidi. Dashes indicate that the ecoregion is not represented in the respective column.

Ecoregions	Days	FW	BLI	BLO	Total Madidi	Total Gamma
Sub-Andean Amazon Forests	44	18	65	39	71	80
Pre-Andean Amazon Forests	44	37	35	73	55	87
Pando Amazon Forests	-	-	-	1	-	1
Cerrado Paceño	22	3	0	11	3	13
Llanos de Moxos Flooded Savannahs	-	-	-	7	-	7
Yungas	72	23	21	20	40	53
Inter-Andean Dry Forests	15	14	9	-	20	20
High Andean Vegetation	12	4	0	2	4	5
Total	**209**	**69**	**85**	**99**	**110**	**133**

Tabla 2. Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

Table 2. Checklist of reptilian species registered in Madidi National Park and Natural Integrated Management Area for this study. Species that are potentially new to science but have not yet been formally described are listed as "sp.". Rec = Type of record, which can be fw = from field work, bl = from baseline database, or bo = both; CS = Conservation Status, categories according to the IUCN; Ecoregions which can be in = inside the park, ou = outside the park, or bo = both: AFF = Amazonian Floodplain Forest, SAF = Sub-Andean Amazon Forests, PAF = Pre-Andean Amazon Forests, PNF = Pando Amazon Forests, CP = Cerrado Paceño, FSM = Llanos de Moxos Flooded Savannah, YU = Yungas, IDF = Inter-Andean Dry Forests, HAV = High Andean Vegetation; values in bold represent the estimated presence based on the probability from Beals' index in the dark diversity analysis.; * = new record for the park, ** = new record for Bolivia.

Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Testudines														
Chelidae	*Mesoclemmys gibba*	bl				ou							178	205
	Mesoclemmys nasuta	bl			ou								454	454
	Phrynops geoffroanus	bo			in	bo							214	314
	Platemys platycephala	bl			ou	ou				in			205	1086
Kinosternidae	*Kinosternon scorpioides*	bl			in								1064	1064
Podocnemididae	*Podocnemis unifilis*	bo	VU		in	bo							185	386
Testudinidae	*Chelonoidis carbonarius*	bl			in								282	282
	Chelonoidis denticulatus	bo			bo	bo	ou	**bo**	**ou**	**bo**	**in**		174	454

Tabla 2 (cont.). Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

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Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Crocodylia														
Alligatoridae	*Caiman crocodilus**	fw	LC			in							214	214
	Caiman yacare	bo	LC		bo	bo	**ou**						161	454
	Melanosuchus niger	bo			in	bo							190	305
	Paleosuchus palpebrosus	bl	LC		bo	bo	**ou**						205	454
	Paleosuchus trigonatus	bo	LC		in	in							264	340
Squamata (Sauria)														
Alopoglossidae	*Alopoglossus andeanus*	bl	LC		ou	bo	**ou**						256	269
	*Alopoglossus brevifrontalis**	bo				bo							205	214
Amphisbaenidae	*Amphisbaena alba*	bl	LC		in	ou				ou			205	1533
	*Amphisbaena fuliginosa**	fw	LC		in								292	292
Anolidae	*Anolis fuscoauratus*	bo	LC		bo	bo				ou			190	1326
	Anolis ortonii	bl	LC		in	ou				in			205	929
	Anolis punctatus	bo	LC		bo	bo		ou		bo			187	1602
Diploglossidae	*Diploglossus fasciatus*	bl	LC		bo					ou			232	574
Gymnophthalmidae	*Bachia dorbignyi*	bo	LC		bo	bo			ou		in		182	1068
	Bachia trisanale	bl	LC			ou							205	205
	Cercosaura argulus	bo	LC			bo				in			205	1124
	Cercosaura bassleri	bo	LC		bo	ou		in					198	1068
	*Cercosaura eigenmanni**	bo	LC			ou		ou		bo			199	2210
	Cercosaura manicata boliviana	bl	LC		in								540	540
	Cercosaura schreibersii	bo	LC		in	bo				in	in		212	1919
	Euspondylus sp.*/**	fw								in			1783	1783
	Potamites ecpleopus	bl	LC		bo					in			272	929
	Potamites ocellatus	bo	VU		bo	ou		in					540	1326
	*Proctoporus bolivianus**	bo	LC							bo		bo	1148	4510
	Proctoporus guentheri	bl	LC							ou			1494	1513
Hoplocercidae	*Enyalioides palpebralis*	bl	LC		in	ou				in			269	929

Tabla 2 (cont.). Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

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Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Liolaemidae	*Liolaemus multiformis*	bl										ou	4340	4340
	Liolaemus sp. 1*	fw										in	4181	4181
	Liolaemus sp. 2*	fw										in	5059	5059
Phyllodactylidae	*Thecadactylus solimoensis*	bo	LC		bo	bo				in	in		197	1068
Polychrotidae	*Polychrus liogaster*	bl	LC		bo	bo	**ou**						205	540
Scincidae	*Copeoglossum nigropunctatum*	bo	LC		bo	bo		ou			in		200	785
	Exila nigropalmata	bl	LC							ou			1148	1148
	Varzea altamazonica	bl	LC			bo							205	218
Teiidae	*Ameiva ameiva*	bo	LC		bo	bo		bo	ou	bo	in		182	1510
	Kentropyx altamazonica	bl	LC		ou	ou				in			269	1124
	Kentropyx pelviceps	bo	LC		bo	bo		ou		in			199	1170
	Kentropyx sp.*	fw						in					198	198
	Tupinambis teguixin	bl	LC			bo		ou					183	540
Tropiduridae	*Plica plica*	bl				ou							205	205
	Plica umbra	bo	LC		bo	bo				in			205	1124
	Stenocercus caducus	bo	LC		bo	in		ou	ou		in		182	1068
	Stenocercus roseiventris	bo	LC		bo	ou				in	in		205	1919
	Stenocercus sp.*	fw								in			1170	1170
	Tropidurus etheridgei	bl	LC		ou								340	340
	Tropidurus melanopleurus	bo	LC		bo								225	686
	Tropidurus sp.*	fw								in			1783	1783
Sphaerodactylidae	*Gonatodes hasemani*	bl	LC			ou							205	205
	Gonatodes humeralis	bo	LC		bo	bo	**ou**						175	454
Squamata (Serpentes)														
Boidae	*Boa constrictor**	bo	LC			ou					in		205	715
	Corallus batesii	bl	LC							in	in		830	1616
	Corallus hortulana				in	bo				bo	in		190	819
	Epicrates cenchria	bo	LC		in	bo							264	351

Tabla 2 (cont.). Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

Table 2 (cont.). Checklist of reptilian species registered in Madidi National Park and Natural Integrated Management Area for this study. Species that are potentially new to science but have not yet been formally described are listed as "sp.". Rec = Type of record, which can be fw = from field work, bl = from baseline database, or bo = both; CS = Conservation Status, categories according to the IUCN; Ecoregions which can be in = inside the park, ou = outside the park, or bo = both: AFF = Amazonian Floodplain Forest, SAF = Sub-Andean Amazon Forests, PAF = Pre-Andean Amazon Forests, PNF = Pando Amazon Forests, CP = Cerrado Paceño, FSM = Llanos de Moxos Flooded Savannah, YU = Yungas, IDF = Inter-Andean Dry Forests, HAV = High Andean Vegetation; values in bold represent the estimated presence based on the probability from Beals' index in the dark diversity analysis.; * = new record for the park, ** = new record for Bolivia.

Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Boidae (Cont.)	*Eunectes beniensis*	bl	LC			in		ou					203	232
	Eunectes murinus	bl	LC		in	bo							190	270
Colubridae	*Atractus elaps*	bl	LC			ou							178	178
	Atractus emmeli	bl	LC							ou			809	809
	Atractus major	bl	LC			ou							205	210
	Chironius exoletus	bl	LC		bo	ou							203	540
	Chironius fuscus	bo	LC		bo	bo				bo			205	1644
	Chironius multiventris	bl	LC		in	bo							205	318
	Chironius scurrulus	bl	LC		in								270	270
	*Chironius whipala**	fw								in			1635	1635
	Chlorosoma viridissimum	bl	LC			ou							205	205
	Clelia clelia	bo	LC		ou	in			ou	in	in		182	1602
	Dendrophidion dendrophis	bl	LC			ou							269	269
	*Dipsas bucephala**	fw	LC							in			2337	2337
	Dipsas catesbyi	bo	LC		in	bo					in		205	1068
	Dipsas pavonina	bl	LC		in								552	552
	Dipsas sp.*	fw								in			1170	1170
	Dipsas variegata	bl	LC		in					ou			322	537
	Drepanoides anomalus	bo	LC		in	bo							218	322
	*Drymarchon corais**	bo	LC			bo		ou			in		183	737
	Drymobius rhombifer	bo	LC		ou	ou							205	382
	Drymoluber dichrous	bo	LC		in	bo				in			205	1590
	Erythrolamprus aesculapii	bo	LC		in	ou				in			262	1471
	Erythrolamprus miliaris	bo	LC			in				in			205	1535
	Erythrolamprus poecilogyrus	bl	LC		in	ou			ou				182	270
	Erythrolamprus reginae	bl	LC		bo	in							205	546
	Erythrolamprus taeniogaster	bl	LC		in								286	286
	*Erythrolamprus typhlus**	bo	LC			bo							262	269

Tabla 2 (cont.). Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

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Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Colubridae (Cont.)	*Helicops angulatus*	bl	LC					ou					194	194
	Helicops leopardinus	bl	LC			ou							205	205
	Helicops polylepis	bo	LC		bo	bo	**ou**						206	293
	Imantodes cenchoa	bo	LC		in	bo		ou		in			190	929
	Imantodes lentiferus	bo	LC		in	bo							205	373
	Leptodeira annulata	bo	LC		bo	bo	**ou**						205	499
	Leptophis bolivianus	bl			in	in							230	283
	*Mastigodryas boddaerti**	fw	LC								in		823	823
	Oxybelis fulgidus	bl	LC		in								322	520
	*Oxybelis inkaterra**	fw	LC								in		882	882
	Oxyrhopus formosus	bl	LC			ou							205	205
	Oxyrhopus melanogenys	bo	LC		in	bo				in			205	1569
	Oxyrhopus petolarius	bo	LC		in	ou				in			205	1619
	Philodryas olfersii	bl	LC		bo								270	454
	Phrynonax sexcarinatus	bl	LC							in			1569	1569
	*Pseudablabes patagoniensis**	fw	LC							in			2132	2335
	Pseudoboa coronata	bo	LC		in	bo							262	314
	Pseudoeryx plicatilis	bl	LC						ou				175	175
	Rhinobothryum lentiginosum	bl	LC			in							212	212
	Siphlophis cervinus	bl	LC			ou							205	205
	Siphlophis compressus	bo	LC		bo	in				in			270	995
	Spilotes sulphureus	bo	LC		ou	in				in			269	1638
	Tachymenis peruviana	bo	LC							bo		in	2860	4181
	Tantilla melanocephala	bl	LC		bo				ou				182	1068
	Xenodon merremi	bl	LC		in	ou							267	302
	Xenodon severus	bl	LC		ou	in							205	454
	Xenopholis scalaris	bl	LC		in	ou				ou			205	1326

Tabla 2 (cont.). Lista de verificación de especies de reptiles registradas en el Parque Nacional y Área Natural de Manejo Integrado Madidi para este estudio. Las especies que son potencialmente nuevas para la ciencia pero que aún no han sido formalmente descritas se listan como "sp.". Rec = Tipo de registro, que puede ser fw = del trabajo de campo, bl = de la base de datos de línea base, o bo = ambos; CS = Estado de Conservación, categorías según la UICN; Ecorregiones que pueden estar in = dentro del parque, ou = fuera del parque, o bo = ambos: AFF = Bosque Inundable Amazónico, SAF = Bosques Amazónicos Subandinos, PAF = Bosques Amazónicos Preandinos, PNF = Bosques Amazónicos de Pando, CP = Cerrado Paceño, FSM = Sabana Inundable de los Llanos de Moxos, YU = Yungas, IDF = Bosques Secos Interandinos, HAV = Vegetación Altoandina; los valores en negritas representan la presencia estimada basada en la probabilidad del índice de Beals en el análisis de diversidad oscura.; * = nuevo registro para el parque, ** = nuevo registro para Bolivia.

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Fam	Species	Rec	CS	AFF	SAF	PAF	PNF	CP	FSM	YU	IDF	HAV	Min	Max
Elapidae	*Micrurus annellatus**	bo	LC			ou				in			205	1783
	Micrurus lemniscatus	bo	LC		in	bo							197	341
	*Micrurus obscurus**	fw	LC		in	in					in		264	770
	Micrurus spixii	bl	LC							in	in		1684	1791
	*Micrurus surinamensis**	fw	LC		in								292	292
Leptotyphlopidae	*Epictia albipuncta*	fw	LC							in			1170	2210
	Epictia striatula	bl	VU							ou			1326	1326
Typhlopidae	*Amerotyphlops brongersmianus*	bl	LC		in								322	327
	Amerotyphlops reticulatus	bl	LC		ou	ou							205	225
Viperidae	*Bothrocophias andianus**	fw	LC							in			2375	2375
	Bothrocophias microphthalmus	bl	LC		bo						in		452	1322
	Bothrops atrox	bo	LC		bo	bo				ou	in		206	1326
	Bothrops bilineatus	bl	LC			bo							205	264
	Bothrops oligolepis	bl	LC			ou							269	269
	Bothrops taeniatus	bl	LC		in								1068	1068
	*Crotalus durissus**	bo	LC							bo			1602	1679
	Lachesis muta	bo	LC		in	bo				ou			205	1068

Beta diversity

Beta diversity showed a high species turnover between ecoregions. The dissimilarity index (Fig. 3) shows that Sub-Andean Amazon Forests and Pre-Andean Amazon Forests are the most similar, in contrast, the Cerrado Paceño is entirely distinct from the other nearby ecoregions, sharing no species even though this ecoregion is almost exclusively surrounded by the Pre-Andean Amazonian Forests, which can mainly be attributed to its open grassland characteristics, quite unique in comparison to the other ecoregions sampled. The Inter-Andean Dry Forests are more similar to the Pre-Andean and Sub-Andean Amazon Forests. The Yungas shows greater similarity to High Andean Vegetation than Sub-Andean Amazon Forests.

The ternary diagram below (Fig. 4) illustrates that a third of the reptile diversity comparisons between the ecoregions in Madidi do not share any species (2, 6, 10, 12, 13), and consistently exhibit large differences in the number of unique species. The Sub-Andean Amazon Forests and Pre-Andean Amazon Forests (1) share eleven species, but the index value is only one-third of the shared species. Therefore, we can infer that all the ecoregions in Madidi are primarily composed of unique species assemblages.

Gamma diversity

The 50 km buffer outside the park included three new ecoregions not found inside Madidi, however, reptiles were recorded in only two of these ecoregions (Pando Amazon Forest and Llanos de

Moxos Flooded Savannahs). The total gamma diversity within the eight ecoregions found both inside and outside Madidi comprises 133 species, including both baseline and fieldwork records (Table 1). This study reports 25 new records for the park, including one new record for Bolivia, and six potentially new species to science (Table 2). These species, potentially new to science (*Kentropyx* sp., *Stenocercus* sp., *Tropidurus* sp., *Dipsas* sp., *Liolaemus* sp. 1 and 2), exhibit both pholidosis and body patterns that do not match their closest known relatives. In the case of the two possible new species of the genus *Liolaemus*, one was recorded on the eastern side of the Andes and the other on the western side, suggesting a significant barrier between the two populations. Currently, taxonomic and genetic studies are being conducted to confirm their taxonomy.

Dark diversity

The dark diversity index suggests that there is a high probability of recording a yellow-footed tortoise (*Chelonoidis denticulatus*) within additional ecoregions in the park, in Cerrado Paceño, Yungas, and Inter-Andean Dry Forests, as well as outside the park, in the Llanos de Moxos Flooded Savannahs (Table 2). Additionally, in the Pando Amazon Forests ecoregion, seven more species are expected to be present: two caimans *Caiman yacare*, *Paleosuchus palpebrosus*, three lizards *Alopoglossus andeanus*, *Polychrus liogaster*, *Gonatodes humeralis*, and two species of snakes: *Helicops polylepis* and *Leptodeira annulata*. In summary, eight species from the dark diversity list are predicted with a 95 % probability of future recording in the ecoregions (Table 2).

New record for the country

Euspondylus Tschudi, 1845. In this study, we report for the first time in Bolivia, a lizard of the genus *Euspondylus*, which belongs to the neotropical family Gymnophthalmidae. This group of lizards comprises 10 species distributed along the eastern side of the Andes, ranging from Venezuela to southern Peru (Fig. 5).

An individual was photographed at the community of Sarayoj on the 21st September 2017 at 12:25 h, camp coordinates 14.6134° S; 68.1924° W, elevation 1,158 m a.s.l. (Fig. 5). The individual was observed on a tree trunk in a vertical position, suggesting that it is an arboreal species which is characteristic of some species within this genus (Chávez et al., 2017). Unfortunately, the individual could not be caught, but with a high quality photograph we were able to diagnose the individual externally,

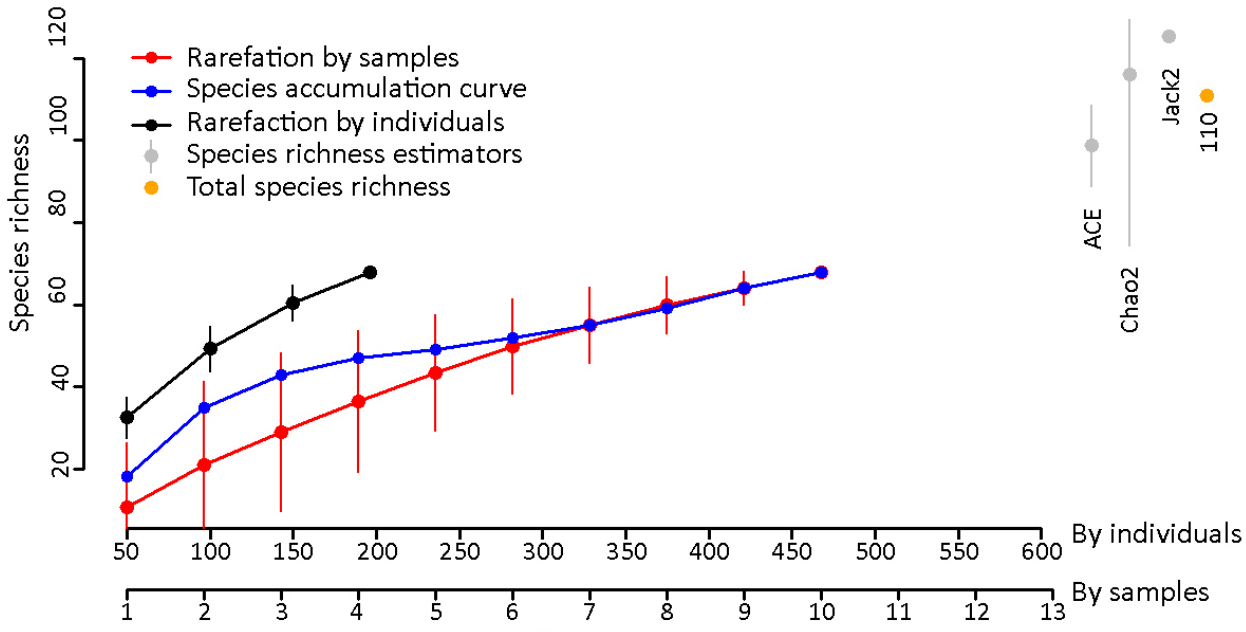

Figura 2. Curvas de acumulación y rarefacción de especies a partir de los datos del trabajo de campo. La curva de rarefacción por individuos estima que se registrarían 68 especies con una muestra de 200 individuos registrados. La riqueza total de especies es la suma de las especies registradas durante el trabajo de campo y aquellas provenientes de la línea base.

Figure 2. Species accumulation and rarefaction curves from fieldwork data. Rarefaction by individuals curve estimates that 68 species would be registered with a sample of 200 recorded individuals. Total species richness is the sum of species recorded during fieldwork and those from the baseline.

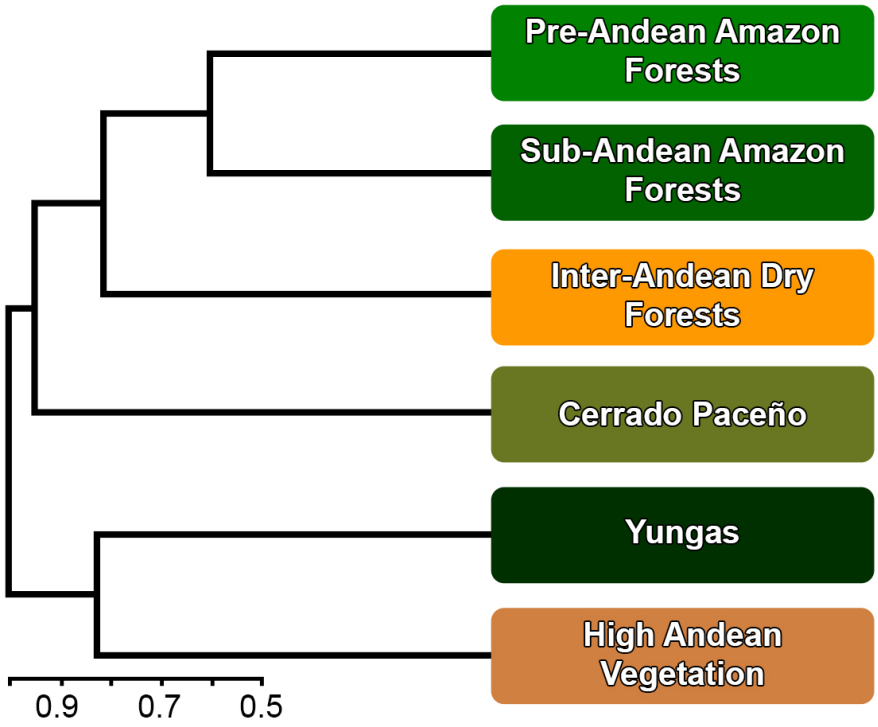

Figura 3. Dendrograma que muestra las disimilitudes en la composición de especies de reptiles entre las ecorregiones del Parque Nacional Madidi y el Área Natural de Manejo Integrado; los colores corresponden a los del mapa, y la escala indica el grado de diferencia entre las ecorregiones.

Figure 3. Dendrogram depicting dissimilarities in reptile species composition between ecoregions in Madidi National Park and Natural Integrated Management Area; colors correspond to those on the map, and the scale indicates the degree of difference between ecoregions.

distinguishing the arrangements and pattern of scales on the dorsal body surface (pholidosis) that characterizes the genus, with a rostral scale, nasals separated by an undivided frontonasal, the presence of two prefrontal scales, one frontal scale, striated and subimbricate dorsal scales, and lateral scales reduced when closer to ventral scales (Chávez et al., 2017). Unfortunately, we cannot observe the characteristics that would allow us to definitively identify the species, such as the palpebral disc, the number of femoral pores, the number of subdigital lamellae, anal scales and other features (Köhler & Lehr, 2004; Lehr et al., 2018). With this record, we extend its distribution by more than 250 km, making it the southernmost record known to date.

Other important records

During fieldwork along the Heath River, we photographed *Caiman crocodilus* (Linnaeus, 1758) on multiple occasions (Fig. 6), this species is widely distributed throughout northern South America, with its southern range extending to the center of the continent. It is characterized by bodies that range from olive-brown to light yellowish, almost whitish in color, with weak or absent markings on the jaws and lacking extensive dark bars on the lateral edges of the ventral scales (Brazaitis et al., 1998; Rueda-Almonacid et al., 2007).

Another significant record obtained during the fieldwork was the Sipo snake, *Chironius whipala* Quinteros-Muñoz et al. 2024 (Fig. 7). This specimen displayed the following morphological characteristics: SVL 79.5, total length 117.5, dorsal scale formula 10-10-8, 148 ventral scales, 115 subcaudals, 9 supralabials, with scales 4, 5, and 6 in contact with the orbit, and 9 infralabials. The hemipenis was unilobed, non-capitated, subcylindrical in shape, with an undivided sulcus spermaticus. The dorsal coloration was emerald green, while the rostral scale, nasal scales, and the lower portion of the supralabials were yellow. The ventral side of the head was immaculate white, transitioning to yellow-greenish along the first third of the body and turning green toward the posterior region (Quinteros-Muñoz et al., 2024).

DISCUSSION

In this study we explore the species diversity of reptiles in a protected area that has been proposed as the world's most diverse tropical protected area (Remsen & Parker, 1995; Salinas & Wallace, 2012; Ocampo et al., 2024). Throughout the study, we identified 110 reptile species, reporting one new taxon (genus) for the country, *Euspondylus*, as well as 24 new records for the park, and the potential discovery of six new species of reptiles for science. These findings underscore the remarkable

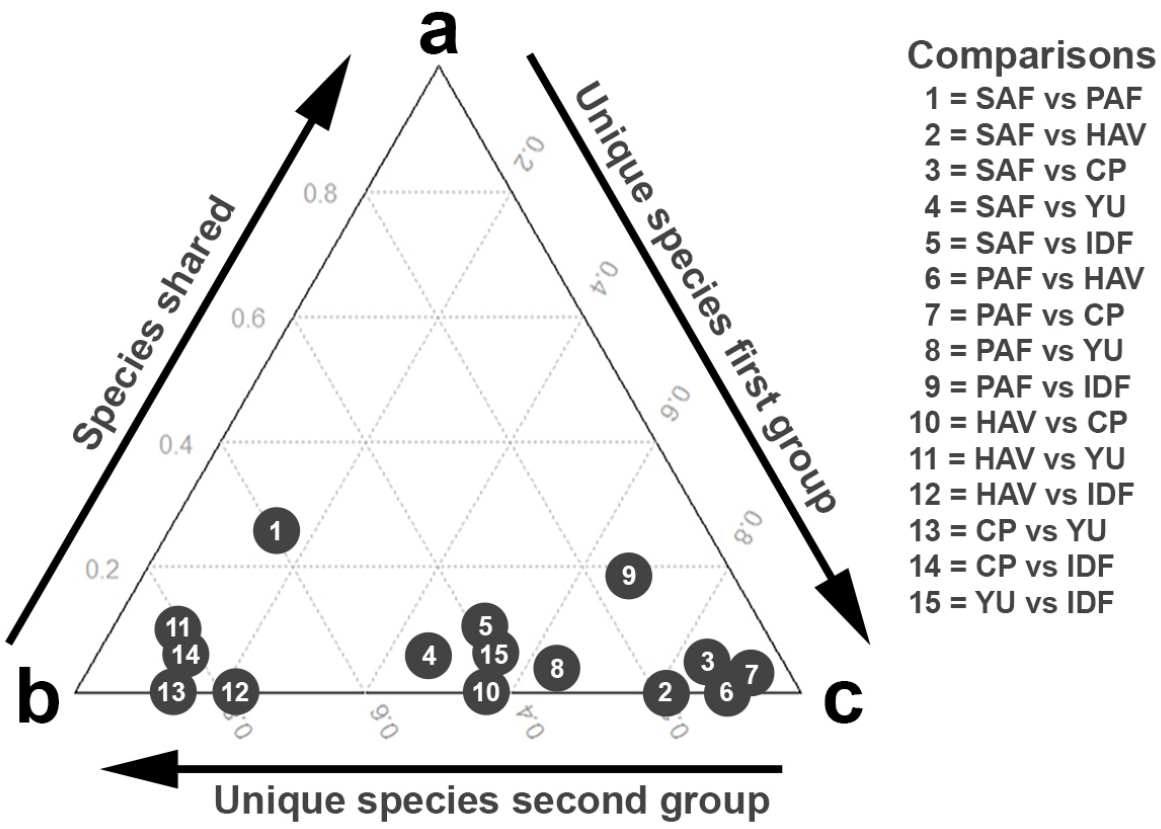

Figura 4. Diagrama ternario donde a representa el número de especies compartidas entre dos sitios, b y c representan el número de especies únicas (no compartidas). CP Cerrado Paceño, HAV Vegetación Altoandina, IDF Bosques Secos Interandinos, PAF Bosques Amazónicos Preandinos, SAF Bosques Amazónicos Subandinos, YU Yungas.

Figure 4. Ternary diagram where a is number of species shared between two sites, b and c the numbers of unique species (not shared). CP Cerrado Paceño, HAV High Andean Vegetation, IDF Inter-Andean Dry Forests, PAF Pre-Andean Amazon Forests, SAF Sub-Andean Amazon Forests, YU Yungas..

biodiversity richness of Madidi, reinforcing its conservation significance and our understanding of global reptile diversity. It is important to note that absolute estimates of species diversity are not plausible, even for long-term studies (Das, 2016).

The protected areas with the highest recorded reptile diversity in the world are Kinabalu (Borneo, 112 species), Yasuní (Ecuador, 121 species), and Manu (Peru, 132 species) (Malkmus et al., 2002; Bass et al., 2010; Catenazzi et al., 2013). However, it is important to note that in the case of Manu, probable species were included in their count without confirmed presence within the protected area. Our findings for Madidi National Park fall just below this range, and we are confident that with more extensive sampling efforts, in the coming years, new records will be added. Due to the challenging accessibility of the area, the 15 sites sampled were surveyed only once. Additionally, because of the extremely cryptic nature of reptiles, many of which are nocturnal and/or fossorial, their detectability is fleeting. Therefore, with more intense sampling, as well as visiting the sites in a different season of the year, Madidi National Park may emerge as the protected area harbouring the highest diversity of reptiles in the world.

The results of the dark diversity analysis based on Beals' index reveal that *Chelonoidis denticulatus* has a high probability of co-occurring with other species in the studied ecoregions. This is particularly evident in the Pando Amazon Forests, where only this species has currently been recorded. However, dark diversity estimates suggest that at least seven additional species should be present based on co-occurrence patterns: *Caiman yacare, Paleosuchus palpebrosus, Alopoglossus andeanus, Polychrus liogaster,*

Gonatodes humeralis, *Helicops polylepis*, and *Leptodeira annulata*. Furthermore, the projections indicate that *C. denticulatus* should also be present in four additional ecoregions where it has not yet been recorded: Cerrado Paceño, Llanos de Moxos Flooded Savannah, Yungas, and the Inter-Andean Dry Forests. This pattern can be explained by its broad distribution in South America, relatively generalist dietary and habitat requirements, and its high detectability in diverse ecological contexts (Rueda-Almonacid et al., 2007; Sobral-Souza et al.; 2017; Tavares et al., 2019). These characteristics facilitate its co-occurrence with species that share similar habitat needs.

On the other hand, the estimates indicate that no additional species should be added to the park's inventory based on co-occurrence. This suggests that the most common species have already been recorded and that those yet to be documented within the park are likely rarer or exhibit seasonal occurrence. This reasoning is supported by the decreasing slope of the

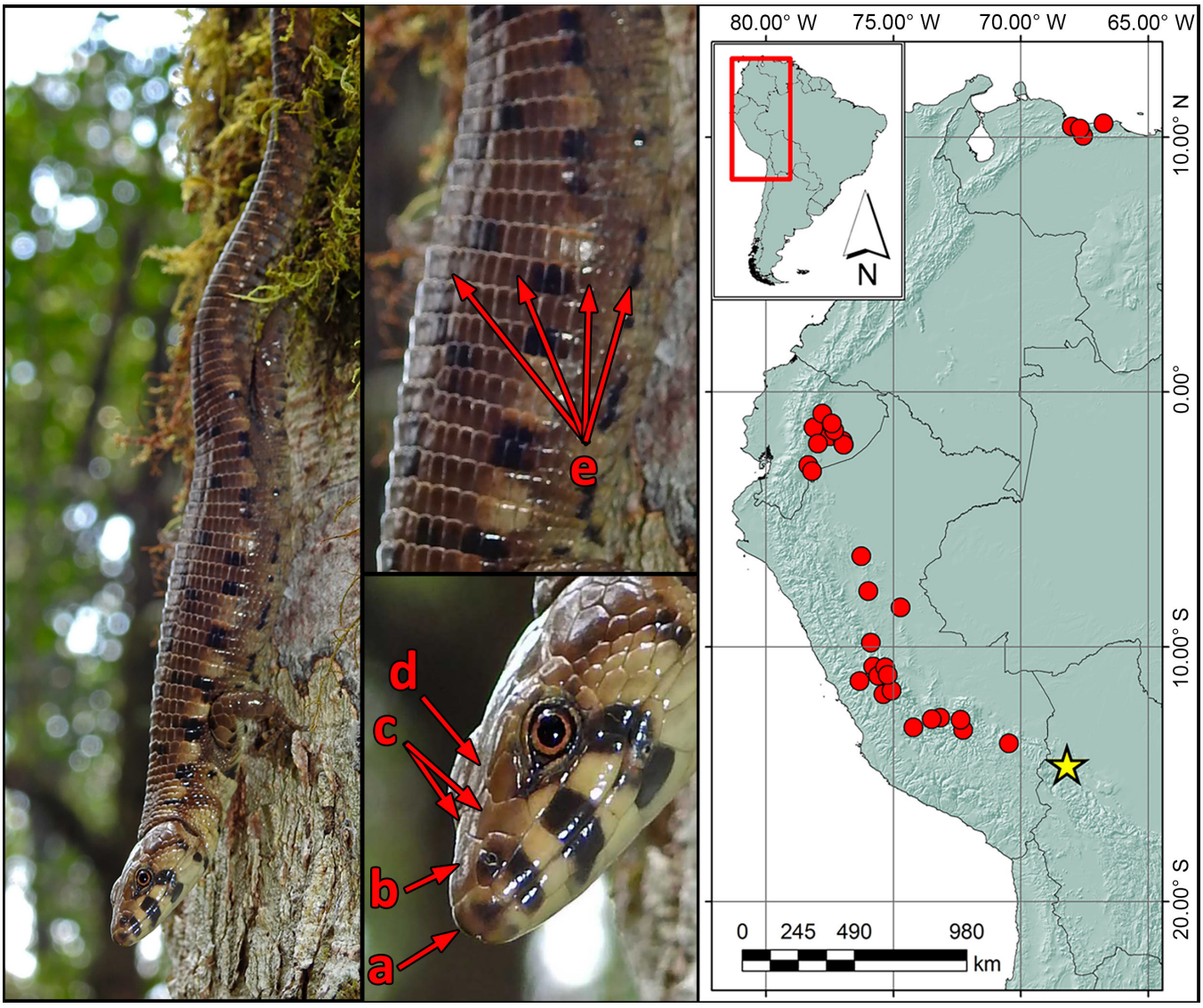

Figura 5. Nuevo género de lagartija para Bolivia, *Euspondylus* sp. de la localidad de Sarayoj; las flechas rojas indican la folidosis característica del género: a) rostral, b) frontonasal no dividida, c) dos prefrontales, d) una frontal, e) escamas dorsales estriadas y subimbricadas, y escamas laterales reducidas al acercarse a las ventrales. Foto: Guido Ayala/WCS. Puntos rojos representan registros de *Euspondylus* spp., estrella amarilla representa nuestro registro en el Parque Nacional Madidi.

Figure 5. New genus of lizard for Bolivia, *Euspondylus* sp. from the Sarayoj locality; the red arrows show the characteristic pholidosis of the genus, a rostral, b frontonasal undivided, c two prefrontals, d one frontal, e striated and subimbricate dorsal scales, and lateral scales reduced when closer to ventrals. Photo: Guido Ayala/WCS. Red dots represent records of *Euspondylus* spp., yellow star represents our record in Madidi National Park"

rarefaction curve, indicating that additional sampling efforts will yield a limited number of new records.

We found that the Sub-Andean Amazon Forest located at the eastern foothills of the Andean mountain range is the ecoregion with the highest diversity. One might speculate that this ecoregion constitutes an ecotone between the higher mountain forests (Yungas) and the lowlands (Pre-Andean Amazon Forest), with the confluence and coexistence of species from both ecoregions (Holland et al., 1991), however, the beta diversity analysis so far shows that Yungas and Sub-Andean Amazon Forest share very few species despite being adjacent to each other along the mountain range. Consequently, species turnover is high along the altitudinal gradient in Madidi, as the classification of ecoregions in mountainous chains is strongly correlated with this gradient (Ibisch et al., 2003).

The record of *Caiman crocodilus* represents the first documented occurrence of this species in Madidi National Park and the second for the La Paz Department and Bolivia. Until a few years ago, *C. crocodilus* had not been formally recorded in Bolivia, although distribution estimates suggested it might be near the Bolivian border (Rueda-Almonacid et al., 2007; Balaguera-Reina & Velasco, 2019). The closest records were from the Madre de

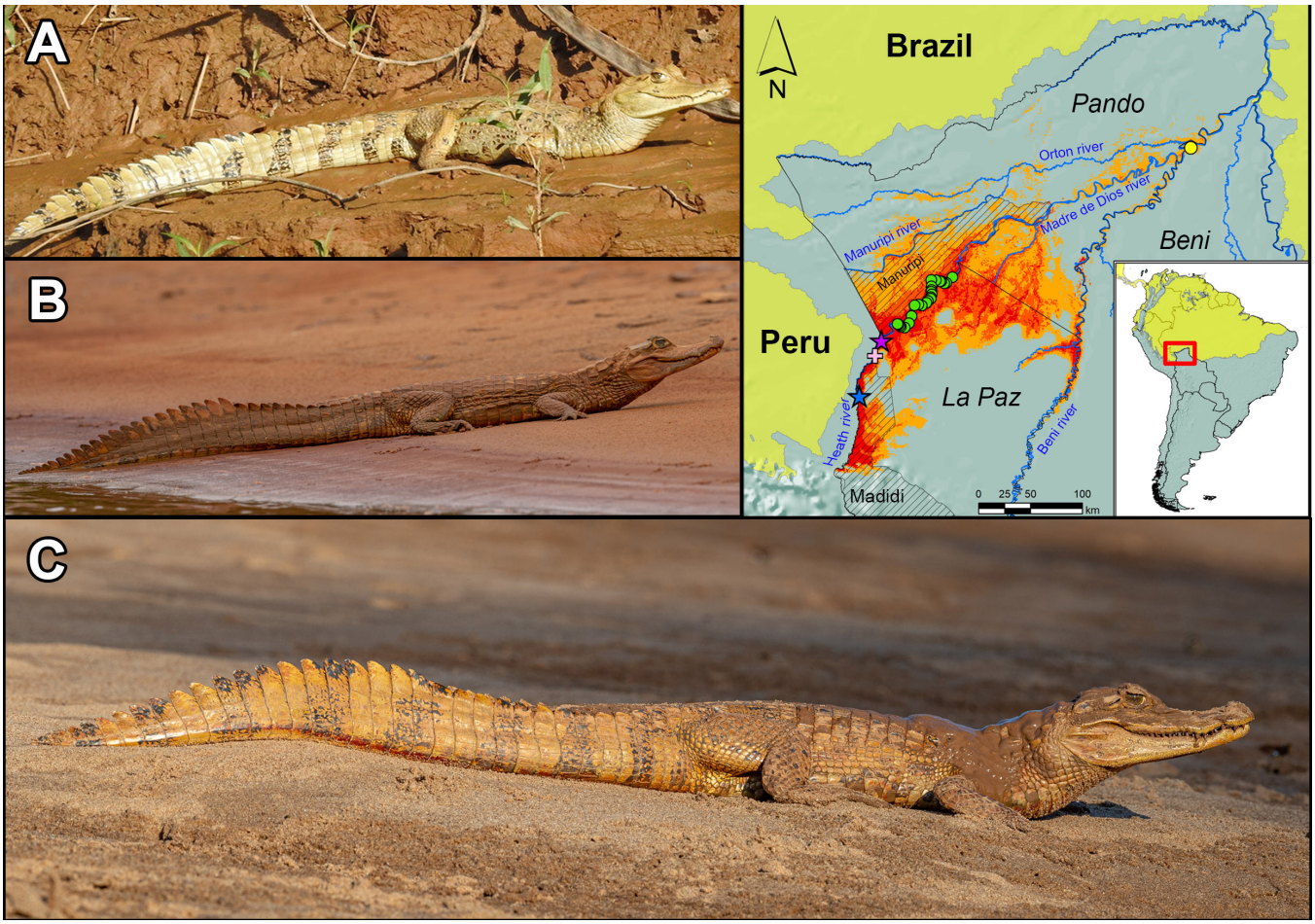

Figura 6. Registros fotográficos de *Caiman crocodilus*: A) Foto de Mauricio Ocampo, B) y C) Fotos de Robert Wallace. El mapa muestra la distribución de *C. crocodilus* según la IUCN resaltada en amarillo mostaza; la estrella púrpura indica el primer registro para Bolivia en 2014 por Declan Troy, la estrella azul indica nuestros registros en 2017, la cruz rosa y el círculo amarillo indican los registros de Ken Oeser y Vincent A. Vos, respectivamente, en 2018, y los círculos verdes indican los registros de Roque et al. en 2021. El degradado de rojo a naranja representa la distribución potencial de *C. crocodilus* en Bolivia.

Figure 6. Photographic records of *Caiman crocodilus*: A) Photograph by Mauricio Ocampo, B) and C) Photos by Robert Wallace. The map shows the IUCN distribution of *C. crocodilus* highlighted in mustard yellow, purple star indicating the first record for Bolivia in 2014 by Declan Troy, the blue star indicating our records in 2017, the pink cross and yellow circle indicating records by Ken Oeser and Vincent A. Vos respectively in 2018, and the green circles indicating records by Roque et al. in 2021. The gradient from red to orange represents the potential distribution of *C. crocodilus* in Bolivia.

Dios River in Peru, and even though this river enters and crosses northern Bolivia through the departments of Pando, La Paz, and Beni, the species had not been documented there.

In 2014, Declan Troy photographed *C. crocodilus* along the lower Heath River (12.53615° S, 68.660015° W), and this image was uploaded to the iNaturalist platform in 2018, becoming the first formal record of *C. crocodilus* at the Bolivia-Peru border. Later, in 2017, we photographed this species in the upper Heath River (13.0163° S, 68.8520° W) (Identidad Madidi, 2020). In 2018, Ken Oeser photographed a juvenile in the same river (12.66873° S, 68.7141° W), and Vincent A. Vos photographed an individual resting on a log northeast of Riberalta, Beni, Bolivia (10.86299°

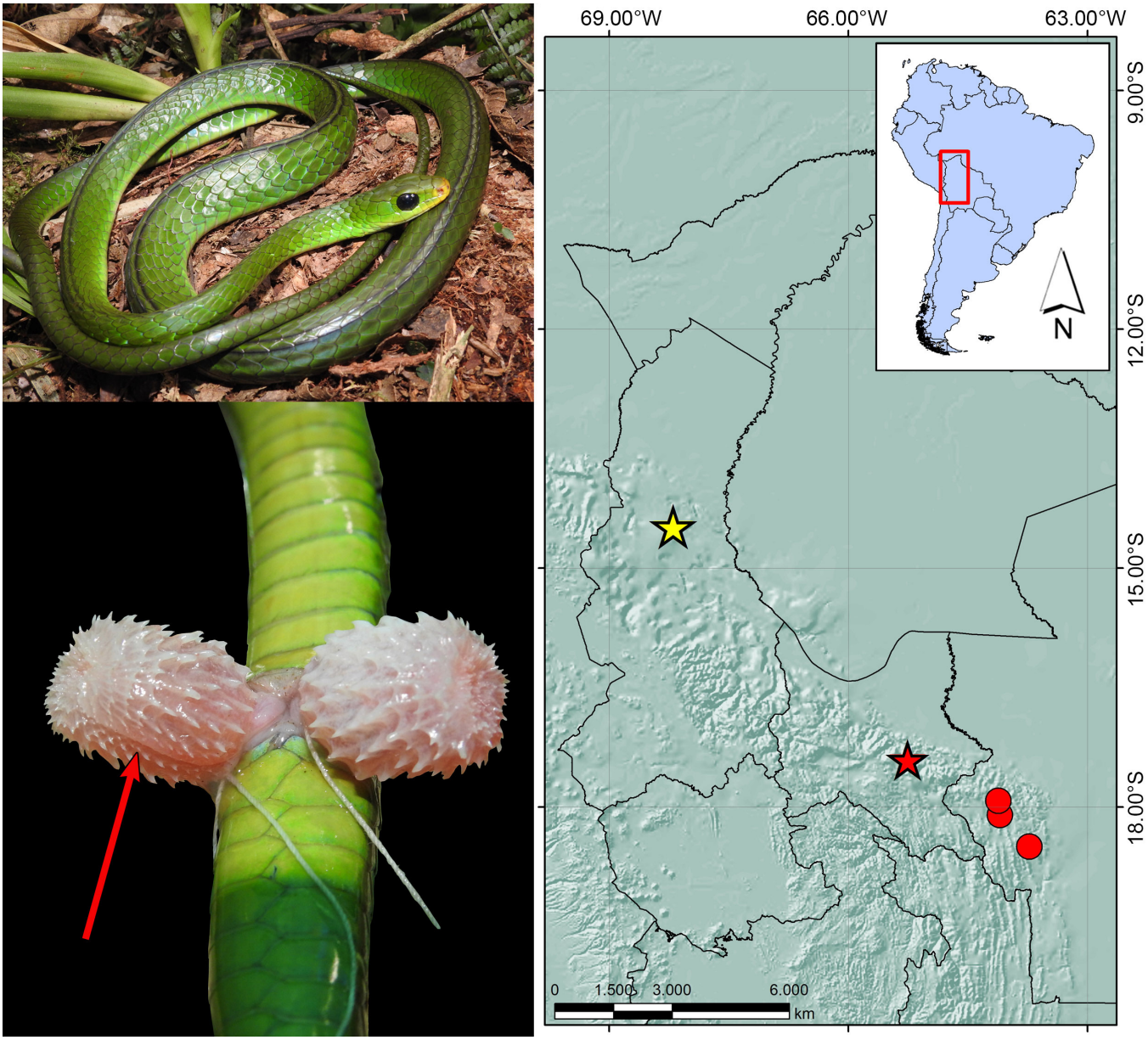

Figura 7. Registro y ampliación de la distribución de *Chironius whipala* Quinteros-Muñoz et al. 2024 en el Parque Nacional Madidi. La flecha roja indica el surco espermático no dividido en los hemipenes. La estrella roja representa la localidad tipo de la especie, los puntos rojos indican las localidades de los paratipos y la estrella amarilla marca nuestro registro en el Parque Nacional Madidi.

Figure 7. Record and distribution extension of *Chironius whipala* Quinteros-Muñoz et al. 2024 in Madidi National Park. The red arrow indicates the undivided sulcus spermaticus in the hemipenis. The red star represents the type locality of the species, red dots indicate the localities of the paratypes, and the yellow star marks our record in Madidi National Park.

S, 65.97538° W), which became the first confirmed record within Bolivian territory. These records were uploaded to iNaturalist platform in 2021 and 2022, respectively.

In 2020, Bolivia's Ministry (Ministerio de Medio Ambiente y Agua) published a book mentioning the species' distribution within the Manuripi National Park, but without citing confirmed records (Aliaga-Rossel et al., 2020). However, in 2021, Roque et al. provided numerous photographic records of *C. crocodilus* in the Bolivian section of the Madre de Dios River, which forms the southern boundary of the Manuripi National Park (Roque et al., 2024). These records collectively confirm that *C. crocodilus* is present in northern Bolivia, primarily along the Madre de Dios River, extending at least 100 km into Bolivia from the border areas with Brazil and Peru.

On the other hand, with our record of *Chironius whipala* in Madidi National Park, we have extended the previously known distribution of the species by more than 450 km to the northwest, covering the humid forests of the Yungas ecoregion in Bolivia. This finding offers valuable insights into the species' distribution and ecological range.

Currently, Bolivia is known to be home to around 325 reptile species (Uetz et al., 2024), meaning that, to the best of our knowledge, Madidi National Park protects about one-third of Bolivia's reptile diversity, and we are confident that this number will increase in the future. This research highlights the importance of conserving and protecting highly diverse places, whilst also emphasizing that protected areas established around these zones should receive support for conducting scientific research to monitor biodiversity consistently.

CONCLUSIONS

The geological formation during the uplift of the tropical Andes has created a mosaic of ecosystems that host an exceptional diversity of plants and animals. Few places in the world offer the opportunity to conserve such high-diversity areas under a protected designation. In the case of Madidi National Park and Natural Integrated Management Area in Bolivia, this protection encompasses six distinct ecoregions across an altitudinal range of 5,864 meters. Through extensive research over three years, combining literature reviews and fieldwork, we have compiled the most comprehensive list of confirmed reptile records for Madidi National Park to date. Our study confirms the presence of 110 reptile species within the park, and our analyses suggest that the full extent of the park's reptile diversity remains to be discovered. Our findings also indicate that the reptile composition across the different ecoregions is unique, with very few species shared among them, highlighting the singular value of each ecoregion. We report 25 new records for the park, one new record for Bolivia, and the discovery of six potential new species to science. This study underscores the incredible reptile diversity harbored by Madidi National Park and the ongoing need for further inventories to fully appreciate the natural value of this area.

Acknowledgements.– We dedicate this study to the memory of our dear friend and colleague, the Bolivian herpetologist James Aparicio Effen (1967—2023), the first author of this paper, acknowledging the important contributions he made to biological research and conservation in Bolivia. We are grateful for the support of the National Protected Area Service (SERNAP) in facilitating our visits to Madidi National Park and Natural Integrated Management Area, as well as to the park rangers for their valuable contribution to the conservation of protected areas in Bolivia. We also acknowledge the Wildlife Conservation Society (WCS) and the Gordon and Betty Moore Foundation for their support to the Identidad Madidi project, and to the Institute of Ecology at the Universidad Mayor de San Andrés (UMSA) and the Bolivian Ministry of Environment and Water for facilitating this project through the research permit: MMAYA/ VMABCCGDF/DGBAP/UVSAP No. 354/2014.

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SUPPLEMENTARY DATA

Apéndice S1. Ubicación de los sitios de estudio del trabajo de campo en el Parque Nacional Madidi. ** = sitios donde se utilizaron trampas de caída de 60 l, * = sitios donde se utilizaron trampas de caída de 10 l, Letras en superíndice representan las fechas del trabajo de campo, donde "a" es del 3/jun/15 al 5/jul/15, "b" del 18/ago/15 al 12/sep/15, "c" del 4/oct/15 al 22/nov/15, "d" del 22/abr/16 al 16/may/16, "e" del 16/jun/16 al 7/jul/16, "f" del 25/sep/16 al 19/oct/16, "g" del 20/jun/17 al 17/jul/17, "h" del 15/sep/17 al 28/sep/17, "i" del 10/nov/17 al 26/nov/17.

Appendix S1. Location of fieldwork study sites in Madidi National Park. ** = sites where 60 l pitfall traps were used, * = sites where 10 l pitfall traps were used. Superscript letters represent the fieldwork dates, where "a" corresponds from June 3, 2015 to July 5, 2015; "b" from August 18, 2015 to September 12, 2015; "c" from October 4, 2015 to November 22, 2015; "d" from April 22, 2016 to May 16, 2016; "e" from June 16, 2016 to July 7, 2016; "f"' from September 25, 2016 to October 19, 2016; "g" from June 20, 2017 to July 17, 2017; "h" from September 15, 2017 to September 28, 2017; and "i" from November 10, 2017 to November 26, 2017..

Site	Latitude S	Longitude W	Elevation (m a.s.l)	Ecoregions
[i]Chokollo	14.7369	69.2156	4814	High Andean Vegetation
[b]Puina Alto	14.6107	69.1372	4750	High Andean Vegetation
[b]Puina Medio	14.6107	69.1372	4250	High Andean Vegetation
[b]Puina Bajo	14.6107	69.1372	3837	High Andean Vegetation
[f]Isañuyoj*	14.6288	69.0464	3460	Yungas
[i]Chullina	14.6896	69.0514	2851	Yungas
[f]Cargadero	14.5772	68.9778	2155	Yungas
[a]Machariapo*	14.6921	68.2853	1763	Yungas
[e]Mamacona	14.4697	68.1921	1566	Yungas
[h]Sarayoj	14.6134	68.1924	1158	Yungas
[a]Sipia*	14.4081	68.5475	740	Inter-Andean Dry Forests
[d]Hondo Alto**	14.6335	67.8509	301	Sub-Andean Amazon Forests
[c]Alto Madidi**	13.6332	68.7417	252	Sub and Pre-Andean Amazon Forests
[g]Heath Bosque**	13.0163	68.852	198	Pre-Andean Amazon Forests
[g]Heath Pampa**	12.9683	68.7383	198	Cerrado Paceño

Appendix S2. List of species collected and deposited in the Colección Boliviana de Fauna (CBF).

Appendix S2. Lista de especies colectadas y depositadas en la Colección Boliviana de Fauna (CBF)

Alopoglossus brevifrontalis CBF 4541-42; *Ameiva ameiva* CBF 4278-79, 4472, 4558-61; *Anolis fuscoauratus* CBF 4348-50, 4474, 4569; *Anolis punctatus* CBF 4489, 4494; *Bachia dorbignyi* CBF 4283,4337-38; *Boa constrictor* CBF 4293; *Bothrocophias andianus* CBF 4270; *Bothrops atrox* CBF 4346; *Caiman yacare* CBF 4354; *Cercosaura argulus* CBF 4328-29; *Cercosaura bassleri* CBF 4557; *Cercosaura eigenmanni* CBF 4248, 4508; *Cercosaura schreibersii* CBF 4244-45, 4250, 4274; *Chironius fuscus* CBF 4325, 4490, 4493, 4545; *Chironius whipala* CBF 4491; *Clelia Clelia* CBF 4295, 4553; *Copeoglossum nigropunctatum* CBF 429,4473, 4565; *Corallus hortulana* CBF 4339,4487, 4544; *Dipsas bucephala* CBF 4509; *Dipsas catesbyi* CBF 4294, 4546; *Dipsas* sp. CBF 4574; *Drepanoides anomalus* CBF 4562; *Drymarchon corais* CBF 4277, 4543; *Drymoluber dichrous* CBF 4342, 4344, 4466; *Epicrates cenchria* CBF 4471; *Epictia albipuncta* CBF 4507, 4575; *Erythrolamprus aesculapii* CBF 4289; *Erythrolamprus miliaris* CBF 4488; *Erythrolamprus typhlus* CBF 4326; *Gonatodes humeralis* CBF 4332, 4548; *Helicops polylepis* CBF 4463, 4476; *Imantodes cenchoa* CBF 4333, 4464, 4568; *Imantodes lentiferus* CBF 4330; *Kentropyx pelviceps* CBF 4327, 4566-67; *Kentropyx* sp. CBF 4549-52; *Leptodeira annulata* CBF 4334-35, 4547; *Mastigodryas boddaerti* CBF 4280; *Micrurus bolivianus* CBF 4251; *Micrurus lemniscatus* CBF 4470, 4563; *Micrurus obscurus* CBF 4279, 4331, 4468; *Micrurus surinamensis* CBF 4475; *Oxybelis inkaterra* CBF 4275; *Oxyrhopus melanogenys* CBF 4341; *Oxyrhopus petolarius* CBF 4492; *Paleosuchus trigonatus* CBF 4469; *Phrynops geoffroanus* CBF 4467; *Plica umbra* CBF 4324, 4343, 4539-40; *Pseudablabes patagoniensis* CBF 4271-72; *Pseudoboa coronata* CBF 4345; *Siphlophis compressus* CBF 4347; *Spilotes sulphureus* CBF 4340; *Stenocercus caducus* CBF 4273,4281-82, 4291, 4554-56; *Stenocercus roseiventris* CBF 4243, 4249-47, 4249, 4576; *Stenocercus* sp. CBF 4577; *Thecadactylus solimoensis* CBF 4336, 4564; *Tropidurus melanopleurus* CBF 4465.