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Una publicación semestral de la Asociación Civil Herpetológica Argentina (Paz Soldán 5100. Piso 1 Dpto 8. Ciudad Autónoma de Buenos Aires, Argentina). Incluye trabajos científicos relacionados con todos los aspectos de la investigación en Anfibios y Reptiles, abarcando tópicos como: sistemática, taxonomía, anatomía, fisiología, embriología, ecología, comportamiento, zoogeografía, etc. Comprende las siguientes secciones: Trabajos, Puntos de Vista, Notas, Novedades Zoogeográficas y Novedades Bibliográficas. Publica en formato digital online y en formato impreso artículos científicos originales asegurando a los autores un proceso de revisión por evaluadores externos sólido y trasparente más una alta visibilidad internacional de sus trabajos. Para los lectores, se garantiza el acceso libre a los artículos. Los idiomas aceptados son castellano, portugués e inglés.

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Trabajo

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Diversidad de herpetofauna en una reserva en recuperación en Comandante Andresito, Misiones, Argentina

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ABSTRACT
In this study, we report the herpetofauna of San Sebastian de la Selva Private Reserve, previously used as a fishing complex and cattle farm. We identified 4 sites based on plant communities, where species richness, abundance and other indexes were analyzed to determine alpha and beta diversity. Sampling was conducted actively by visual encounter surveys and acoustic surveys and passively by drift fence pitfall traps and artificial coverage, using a stratified random sampling design. We collected photographic records and calculated a rarefaction curve to assess sampling effort. As a result, we identified 38 species, including 21 species of anurans, 12 snakes, 3 lizards, 1 turtle and 1 amphisbaena. Alpha diversity was lowest on exotic grasslands and presented significant differences from the three other sites. There was low similarity among sites, with the exotic grassland showing the lowest values for both beta-diversity indices. We discussed the relationship between low alpha and beta diversity in the exotic grassland and the loss of biodiversity resulting from the destruction and replacement of native environments. We recommend a more thorough analysis of human impact on sites for a better correlation between habitat modification and biodiversity.

Key words: Community Ecology; Atlantic Forest; Pitfall Traps; San Sebastián de la Selva; Inventory.

RESUMEN
Estudiamos la herpetofauna de la Reserva Privada San Sebastián de la Selva (Misiones, Argentina), anteriormente utilizada como complejo de pesca y finca ganadera. Identificamos cuatro sitios en función de las comunidades vegetales presentes, donde se analizaron la riqueza de especies, la abundancia y distintos índices para determinar la diversidad alfa y beta. El muestreo se realizó de forma activa mediante búsqueda directa y transectas auditivas y de forma pasiva mediante trampas de caída y coberturas artificiales, utilizando un diseño de muestreo aleatorio estratificado. Se recopilaron registros fotográficos y se calculó una curva de rarefacción para evaluar el esfuerzo de muestreo. Como resultado, identificamos 38 taxones, incluidos 21 anuros, 12 serpientes, 3 lagartijas, 1 tortuga y 1 anfisbena. La diversidad alfa fue más baja en el pastizal exótico, con diferencias significativas respecto de los otros tres sitios. La similitud entre los sitios fue baja, siendo el pastizal exótico el que mostró los valores más bajos para ambos índices de diversidad beta. Discutimos la existencia de una relación entre la baja diversidad alfa y beta del pastizal exótico y la pérdida de biodiversidad derivada de la destrucción y el reemplazo de ambientes nativos. Recomendamos un análisis más detallado del impacto humano en los sitios para mejorar la correlación entre la modificación del hábitat y la biodiversidad.

Palabras claves: Ecología de comunidades; Selva Paranaense; Trampas de Caída; San Sebastián de la Selva; Relevamiento.

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Introducción

La Selva Paranaense es la eco-región más biodiversa de Argentina, presente únicamente en la provincia de Misiones donde ocupa 3 millones de hectáreas (Placi y Di Bitetti, 2006). En la región la temperatura media anual es de 20° C y la precipitación ronda los 2000 mm (Burkart *et al.*, 1999). Comprende selvas tropicales en su extremo norte y subtropicales en latitudes menores (Cuchietti *et al.*, 2021). La selva misionera ha sufrido una gran pérdida de biomasa debido a la actividad humana (Placi y Di Bitetti, 2006). La fragmentación de hábitat tiene efectos negativos sobre las poblaciones remanentes, especialmente para reptiles y anfibios (Cushman, 2006; Lopez-Bedoya *et al.,* 2022; Iglesias-Carrasco *et al.,* 2023), afectando disponibilidad de recursos, temperatura, flujos de agua y composición de suelo (Saunders *et al.*, 1991). La exclusión de prácticas dañinas como pesca y ganadería permiten la recuperación de ecosistemas y la renovación y sucesión de especies, aunque los efectos están poco estudiados (Fredericksen y Fredericksen, 2002; Leynaud y Bucher, 2005; Dobkin *et al.*, 2008).

Los relevamientos de fauna constituyen una gran fuente de información para conocer el estado de conservación y la densidad poblacional de especies, además de ser una herramienta útil en la mejora de estrategias de conservación para animales con riesgo de extinción (Heyer *et al.*, 1994; McCallum, 2007). La herpetofauna enfrenta un declive poblacional a nivel mundial, principalmente debido a la fragmentación y pérdida de hábitat, contaminación y otras causas tanto directas como indirectas relacionadas a actividades antrópicas (Alford y Richards, 1999; Gibbons *et al.*, 2000; Cano y Leynaud, 2009). Debido a esto, los estudios que abordan la riqueza, abundancia y diversidad de reptiles y anfibios adquieren un papel fundamental para su conservación. Se han realizado listados de herpetofauna en la provincia de Misiones (López y Kubisch, 2008; López y Nazer, 2009; Lescano *et al.*, 2013; Gangenova *et al.,* 2018; Anfuso *et al.*, 2020; López y Garey, 2021; Gangenova *et al.,* 2025) aunque pocos han contado con distintas metodologías de muestreo simultáneas. La utilización de diversas técnicas de muestreo permite un estudio más completo, logrando una mayor toma de datos y una mejor comprensión sobre la diversidad en una región amenazada y de alta diversidad como lo es la Selva Paranaense. Además, el muestreo estratificado permite conocer las diferencias en la diversidad entre los ambientes, arrojando información sobre la disposición de las comunidades de reptiles y anfibios frente a la fragmentación de hábitat en el Bosque Atlántico.

El objetivo de este trabajo es presentar un listado de la herpetofauna registrada en la reserva, analizar la diversidad alfa y beta en los sitios delimitados y comparar los resultados entre los sitios. Debido al impacto generado por la fragmentación de hábitats en comunidades de herpetofauna, se espera observar diferencias significativas entre los sitios.

Materiales y métodos

El estudio fue realizado en la Reserva Privada San Sebastián de la Selva (25°51'27.3"S; 53°58'32"W), ubicada en la localidad de Comandante Andresito, al noreste del Departamento General Belgrano, Misiones, Argentina (Fig. 1). La reserva forma parte del Corredor Biológico Urugua-í-Foerster, lo cual influye positivamente en el movimiento de fauna y la recolonización de ambientes por especies vegetales autóctonas (Bennett, 2003), transformándola en un excelente parche en recuperación rodeado de selva protegida y poco intervenida. Algunas zonas de la reserva, antiguamente explotadas para la pesca y la ganadería, han sido recuperadas gracias al cese de estas actividades y a los constantes esfuerzos de conservación y reforestación. Actualmente, la reserva comprende 92 hectáreas de bosque y abarca un amplio espectro de microambientes en su extensión: pastizales exóticos, cuerpos de agua estacionales y no estacionales artificiales (lagunas e interconexiones), selva primaria y selva secundaria.

Se llevaron a cabo 6 campañas desde 2019 hasta 2023, designando fechas de muestreo de acuerdo con los meses lluviosos. Cada campaña duró entre 8 y 10 días, independientemente de la cantidad de animales relevados. La reserva fue dividida en sitios utilizando la vegetación predominante (Matteucci y Colma, 1998) como parámetro. Se recopiló información histórica para aproximar la intervención humana sobre cada ambiente. Se delimitaron 4 sitios principales (Fig. 1):

Bosque primario (BP): considerado como la porción de territorio menos intervenida dentro de la reserva, cuenta con vegetación leñosa de gran tamaño e incluye especies emblemáticas tales como el Timbó Colorado (*Enterolobium contortisiliquum*), el Ibirá Pitá (*Peltophorum dubium*) o el Curupay (*Anadenanthera colubrina*). Posee cuerpos de agua lóticos y de bajo caudal, referidos como “arroyos selváticos”.

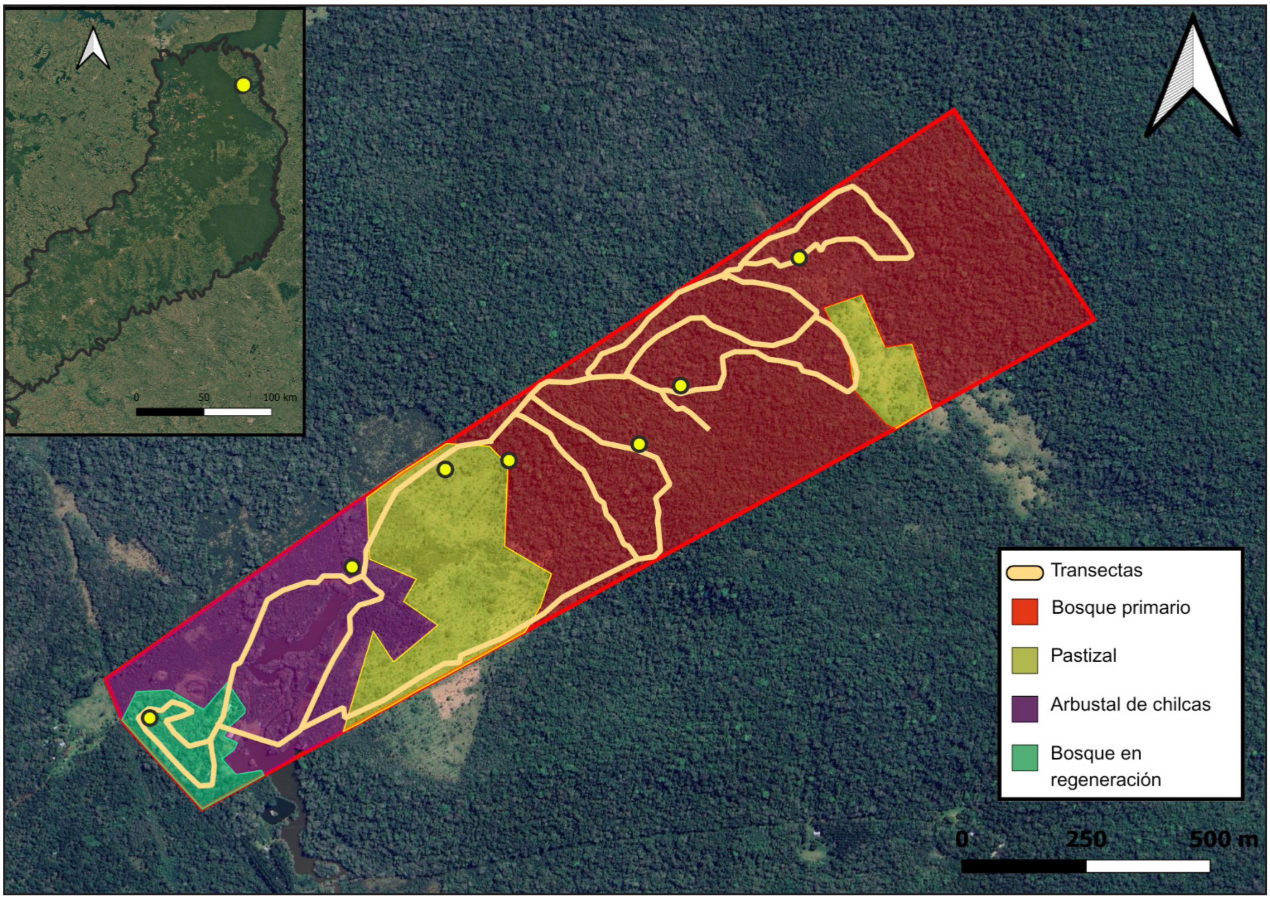

Figura 1. (Izq) Mapa satelital de Misiones, señalando la ubicación de la Reserva Privada San Sebastián de la Selva. (Der) Fotografía satelital de la Reserva Privada San Sebastián de la Selva, con polígonos delimitando la división de sitios propuesta.

Arbustal de chilcas (AC): territorio dentro de la reserva ocupado principalmente por arbustos como Chilca (*Baccharis salicifolia*) y Chichita (*Schinus terebinthifolia*), de origen natural con cierto grado de antropización. Este ambiente posee cuerpos de agua estacionarios de origen antrópico, denominados localmente como "tajamares". Cuenta con algunas edificaciones en uso.

Bosque en recuperación (BR): zona de bosque secundario, previamente explotada para extraer madera en pequeñas cantidades. Contiene especies vegetales de pocos años de antigüedad como Maria Preta (*Diatenopteryx sorbifolia*) y Guayubira (*Patagonula americana*), con pocas leñosas de gran tamaño como Laurel Amarillo (*Nectandra lanceolata*). En este ambiente se encuentran cuerpos de agua lénticos transitorios, los cuales se inundan durante periodos de lluvia.

Pastizal exótico (PE): Porción de pastura ubicada entre el arbustal de chilcas y el bosque primario, dominado por el Pasto Estrella Africano (*Cynodon nlemfuensis*), previamente utilizado con fines ganaderos. Cuenta con pequeñas regiones inundables en periodo de lluvias.

Se emplearon métodos de búsqueda activos y pasivos. El tiempo invertido por búsqueda activa fue aproximadamente de 8 horas/persona/día, realizándose transectas tanto de día como de noche, distribuidas uniformemente a través de los distintos sitios. Se implementaron trampas cerco-pozo (Bury y Corn, 1987; Gibbons y Semlitsch, 1981; Heyer *et al.*, 1994) compuestas por tres cercas dispuestas alrededor de un balde central y con baldes al final de cada cerca. Se utilizaron baldes de plástico con una capacidad de 10 litros y de 26 cm de diámetro y las cercas fueron confeccionadas con chapas de fibrocemento levemente enterradas. Las trampas se colocaron siguiendo la división de sitios previamente especificada, colocando 2 trampas por sitio. Las trampas fueron activadas al principio de cada campaña, siendo revisadas una vez por día, y desactivadas al final de esta. Además, se confeccionaron refugios/coberturas artificiales, debido a su alta eficacia en el muestreo de reptiles y anfibios

(Grant *et al.*, 1992; Engelstoft y Ovaska, 2000). Cada cobertura artificial contó con 6 láminas de chapa de fibrocemento, ocupando un área de 3 metros por 5 metros. Se dispusieron trampas en cada uno de los sitios delimitados. Con el fin de registrar la mayor cantidad posible de individuos, se llevó a cabo una colecta de registros audiovisuales de herpetofauna por parte del personal de la reserva y de visitantes casuales. Se tomaron en cuenta fotografías y registros para confirmar las coordenadas y la identificación del individuo por parte de los investigadores durante el periodo 2019-2023.

Todos los individuos avistados fueron colectados y posteriormente examinados para determinar el taxón. Se registró lugar y fecha de captura y método utilizado. Se realizó un registro fotográfico de los individuos y posteriormente fueron devueltos al punto de captura. No se efectuó la colecta de vouchers de estudio debido a las normas de manejo vigentes en la reserva. Se dimensionó el esfuerzo de muestreo a través de curvas de acumulación, estimando los valores de diversidad para cada grupo. Se determinó la diversidad alfa mediante el cálculo de la riqueza (S) para cada ambiente y el conjunto de la reserva. Se utilizó el índice de Shannon-Wiener (H) para cuantificar la diversidad de especies y la equitatividad de Shannon (E) para determinar la distribución de la abundancia de las especies en cada ambiente. Se realizó una prueba T de Hutcheson (Zar, 1996) para cuantificar diferencias entre los índices de Shannon-Wiener y se graficaron los resultados. Además, se graficaron curvas de rango-abundancia para la totalidad de los taxones en cada ambiente. Para la comparación entre ambientes se consideraron dos índices de similitud de diversidad beta, siendo el Índice de Jaccard (J) un parámetro cualitativo y el Índice de Czekanowski (C) uno cuantitativo. Todos los índices fueron calculados mediante el paquete Vegan de R Studio (Oksanen *et al.*, 2015).

Resultados

Se registraron 759 individuos correspondientes a 38 taxones: 21 especies de anuros (5 familias), 3 lacertilios (3 familias), 12 ofidios (4 familias), 1 anfisbénido (1 familia) y 1 tortuga (1 familia) (Tabla 1). El estado de conservación de los individuos fue mayoritariamente No Amenazado, presentando un taxón Amenazado, tres taxones Vulnerables y un taxón Insuficientemente Conocido a nivel nacional (Vaira *et al.*, 2012; Giraudo *et al.*, 2012; Abdala *et*

Tabla 1. Especies registradas durante el relevamiento de herpetofauna. Nomenclatura de sitios: Bosque Primario= BP, Bosque en recuperación= BR, arbustal de chilcas= AC, Pastizal exótico= PE, arbustal de chilcas, únicamente en edificaciones = AC*. Método de muestreo: BA= Búsqueda Activa, TA= Transecta auditiva, RF= Registro fotográfico, TC= Trampa de caída, TR= Trampa refugio.

Especie	**N° de individuos**	**Sitios registrados**	**Categoría de conservación**	**Método de muestreo**
Lacertilios				
Familia Gekkonidae				
Hemidactylus mabouia	5	AC*	NA	BA
Familia Scincidae				
Notomabuya frenata	9	BP, AC	NA	BA, TC
Familia Teiidae				
Salvator merianae	27	BP, BR, AC, PE	NA	BA, TC, TR
Serpientes				
Familia Anomalepididae				
Liotyphlops ternetzii	25	BP, BR, AC, PE	NA	BA
Familia Colubridae				
Spilotes pullatus	4	BP, BR, AC*	VU	BA
Familia Dipsadidae				
Erythrolamprus macrosomus	2	BR	VU	BA
Erythrolamprus poecilogyrus schotti	1	AC	NA	BA
Dryophylax hypoconia	1	AC	NA	RF
Mesotes strigatus	1	PE	NA	RF

Philodryas olfersii	2	BR, AC*	NA	BA, RF, TR
Familia Elapidae				
Micrurus altirostris	3	BP, BR	VU	BA, RF
Micrurus corallinus	1	BR	VU	RF
Familia Viperidae				
Bothrops jararacussu	4	BP, BR, AC*, PE	AM	BA, RF
Bothrops aff. pubescens	7	BP, AC	NA	BA, RF
Crotalus durissus terrificus	4	BP, AC*	NA	BA, RF
Anfisbenas				
Amphisbaena prunicolor	1	AC	NA	BA
Tortugas				
Phrynops geoffroanus	1	BR	IC	BA
Anuros				
Familia Bufonidae				
Melanophryniscus devincenzii	1	BP	NA	BA
Rhinella diptycha	8	BR, AC	NA	BA, TA
Rhinella icterica	1	AC	NA	BA
Rhinella ornata	27	BP	NA	BA, TC
Familia Hylidae				
Boana stellae	8	BP	NA	BA, TA
Boana faber	19	BR, AC	NA	BA, TA
Boana raniceps	1	AC	NA	BA, TA
Dendropsophus minutus	88	BR, AC	NA	BA, TA
Dendropsophus nanus	59	BR, AC	NA	BA, TA
Dendropsophus sanborni	70	BR, AC	NA	BA, TA
Itapotihyla langsdorffii	10	BR	NA	BA, TA
Phyllomedusa tetraploidea	1	AC	NA	BA, TA
Scinax fuscovarius	105	BP, BR, AC, PE	NA	BA, TA
Trachycephalus typhonius	16	BR, AC	NA	BA, TA
Familia Leptodactylidae				
Leptodactylus elenae	7	BP, BR, AC	NA	BA
Leptodactylus fuscus	60	BR, AC	NA	BA, TA
Leptodactylus mystacinus	49	BR, AC	NA	BA, TA, TR
Leptodactylus luctator	38	BP, BR, AC	NA	BA
Physalaemus cuvieri	53	BP, BR, AC, PE	NA	BA, TA, TC
Familia Microhylidae				
Elachistocleis bicolor	37	BR, AC	NA	BA, TC, TR
Familia Odontophrynidae				
Odontophrynus sp.	3	BR, AC	NA	BA, TC

al., 2012; Prado *et al.*, 2012; Vaira *et al.*, 2017). Se graficó una curva de acumulación de riqueza observada y se estimó la riqueza esperada para el total de la herpetofauna, las serpientes, las lagartijas y los anfibios (Fig. 2). Se confeccionó una tabla indicando la abundancia total de individuos, riqueza, índice de Shannon-Wiener y equitatividad para cada uno de los ambientes delimitados (Tabla 2). Se realizó una comparación entre los índices de Shannon-Wiener mediante un Test T de Hutcheson y se graficaron los resultados, indicando diferencias significativas (Fig. 3). Se agregaron gráficos de rango-abundancia para

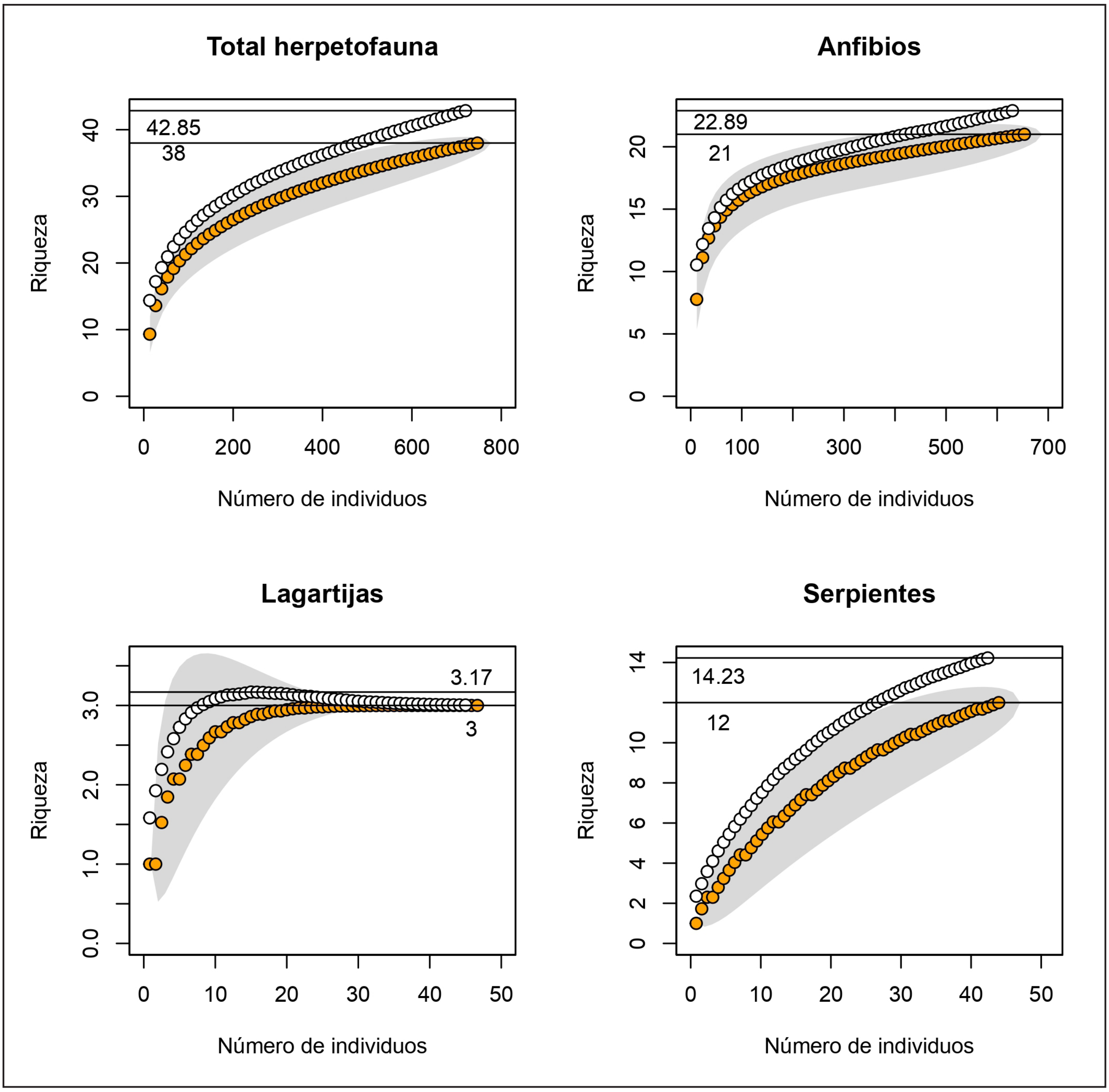

Figura 2. Curvas de rarefacción para a) herpetofauna total b) anfibios c) lagartijas d) serpientes. La curva blanca representa la riqueza esperada, la curva naranja representa la riqueza observada y la sombra gris representa el intervalo de confianza.

una mejor visualización de los resultados de equitatividad (Fig. 4). Además, se confeccionó una segunda tabla con los índices de Jaccard y Czekanowski para cada par de ambientes (Tabla 3). No se graficaron los datos para tortugas y anfisbenas debido al bajo número de taxones registrados. Por último, se tomaron fotografías a todos los individuos con el fin de crear material de referencia (Fig. 5 y Fig. 6)

Conclusión

Los resultados corroboran una riqueza de anfibios similar a la de otros inventarios de herpetofauna realizados en el área (López y Kubisch, 2008; López y Nazer, 2009; Lescano *et al.*, 2013; Anfuso *et al.*, 2020). En concordancia con estudios previos la familia más representativa fue Hylidae, con 10 taxones. Se registraron 3 individuos pertenecientes al género *Odontophrynus*, cuya identidad taxonómica a nivel de especie no pudo ser resuelta debido a la ausencia de estudios de cariotipo en este trabajo y la falta de caracteres morfológicos diagnósticos (Rosset *et al.*, 2022). Se confirmó la presencia de especies poco frecuentes, como *Boana stellae*, que puede diferenciarse

Tabla 2. Abundancia total, riqueza, índice de Shannon-Wiener y equitatividad registrada en los distintos sitios de la reserva.

	Bosque primario	Bosque en recuperación	Arbustal de chilcas	Pastizal	Total
Abundancia total	78	155	516	10	759
Riqueza	19	24	29	6	38
Shannon-Wiener	2,346	2,554	2,674	1,696	-
Equitatividad	0,797	0,815	0,794	0,946	-

de otras especies simpátricas mediante medidas de largo hocico-cloaca y análisis de canto (Kwet, 2008). Se registró un número de anuros menor al esperado según la curva de rarefacción, por lo cual se recomienda aplicar nuevas metodologías de muestreo para aumentar la riqueza registrada.

La riqueza de lagartijas (3 taxones) fue similar a la observada en zonas cercanas (López y Kubisch, 2008; López y Nazer, 2009) y próxima a la estimada por la curva de rarefacción, denotando un esfuerzo de muestreo acorde. Asociamos las bajas abundancias de anfisbenas a los hábitos fosoriales de este grupo y a la dificultad consecuente para registrar individuos (Measey, 2006).

Se registró una sola especie de tortuga, *Phrynops geoffroanus,* especie que suele habitar ríos y lagunas selváticas, incluyendo áreas alteradas por actividades humanas (Souza y Abe, 2006). Se obtuvieron múltiples registros de *P. geoffroanus* asoleándose en distintos cuerpos de agua lénticos permanentes. Debido a la cercanía y la repetición de las observaciones y fotografías obtenidas, asumimos que se trataba de un único individuo. Este registro representa la observación más al norte de Misiones y Argentina (Baldo *et al.,* 2007).

En lo que respecta a las serpientes, se registró una riqueza considerablemente menor que en otros listados de herpetofauna realizados (Montanelli y Acosta, 1991; Acosta *et al.*, 1994; López y Kubisch, 2008; López y Nazer, 2009). Se observa en la curva de rarefacción un valor menor al esperado según el esfuerzo de muestreo. El bajo número de ofidios capturados puede haber sido consecuencia de la poca profundidad de los baldes utilizados en las trampas de caída (Pesci *et al.*, 2018) y de la falta de trampas especializadas para ofidios como las trampas de embudo (Corn y Bury, 1990). Similar a estudios previos, la familia más representativa fue Dipsadidae, con 6 taxones (Montanelli y Acosta, 1991; Acosta *et al.*, 1994; Giraudo y Abranson, 1994; López y Kubisch, 2008; Anfuso *et al.*, 2020). Se observó un alto número de individuos de *Liotyphlops ternetzii* (25 individuos) en comparación a otros trabajos de la zona que, además, se calificó como "escasa" o "de difícil hallazgo" en trabajos previos sobre la selva de Misiones (López y Nazer, 2009; López y Prado, 2012). Los individuos fueron encontrados activos durante la noche en diversos ambientes, con la mayor cantidad de registros en el arbustal de chilcas. Se registraron 7 individuos del género *Bothrops* pertenecientes al grupo *neuwiedii*, determinados como *Bothrops aff. pubescens* según Carrasco *et al.* 2019. Entre los individuos registrados de *Micrurus altirostris*, uno de los ejemplares hallados presentaba una aberración en el patrón dorsal, tanto del cuerpo como de la cabeza. Se publicó una descripción de la aberración incluyendo fotografías (Sabaliauskas y Ortega, 2023).

La curva de acumulación para el total de la herpetofauna registrada se encuentra muy cercana al estimador, por lo cual consideramos que el esfuerzo de muestreo fue adecuado para caracterizar la comunidad a nivel global, a pesar de las variaciones observadas en grupos específicos. La búsqueda activa fue el método más eficaz de captura de individuos, logrando capturar el 92% de los taxones registrados. Los métodos pasivos, como las trampas de caída y los refugios artificiales, lograron menor resultado a comparación con los métodos activos. La utilización de trampas de caída en ambientes tropicales/subtropicales requiere de especial atención al material y al lugar de colocación para su mayor rendimiento (Cechin y Martins, 2000). Atribuimos el bajo rendimiento de estas trampas al uso de cercas de fibrocemento y baldes de baja profundidad, difiriendo de técnicas herpetológicas estándar (Todd *et al.,* 2007). Los refugios artificiales tuvieron resultados de manera inicial, aunque posteriormente quedaron obsoletos debido al crecimiento de la vegetación circundante, dificultando la captura de herpetofauna. Se recomienda repensar estrategias para colocar esta clase de trampas sin interferencia de las especies vegetales.

La diversidad alfa presentó diferencias entre los sitios, con variaciones según los índices evaluados. El arbustal de chilcas presentó los valores más altos de riqueza y de Shannon-Wiener, y el más bajo de equitatividad. Los altos valores de diversidad alfa pueden responder a una mayor superficie de agua y disponibilidad de otros recursos gracias a la generación de un ambiente estable debido a la acción antrópica (Gardner *et al.*, 2007). Entendemos que la alta abundancia de individuos registrados corresponde al uso de los tajamares como sitios de alimentación

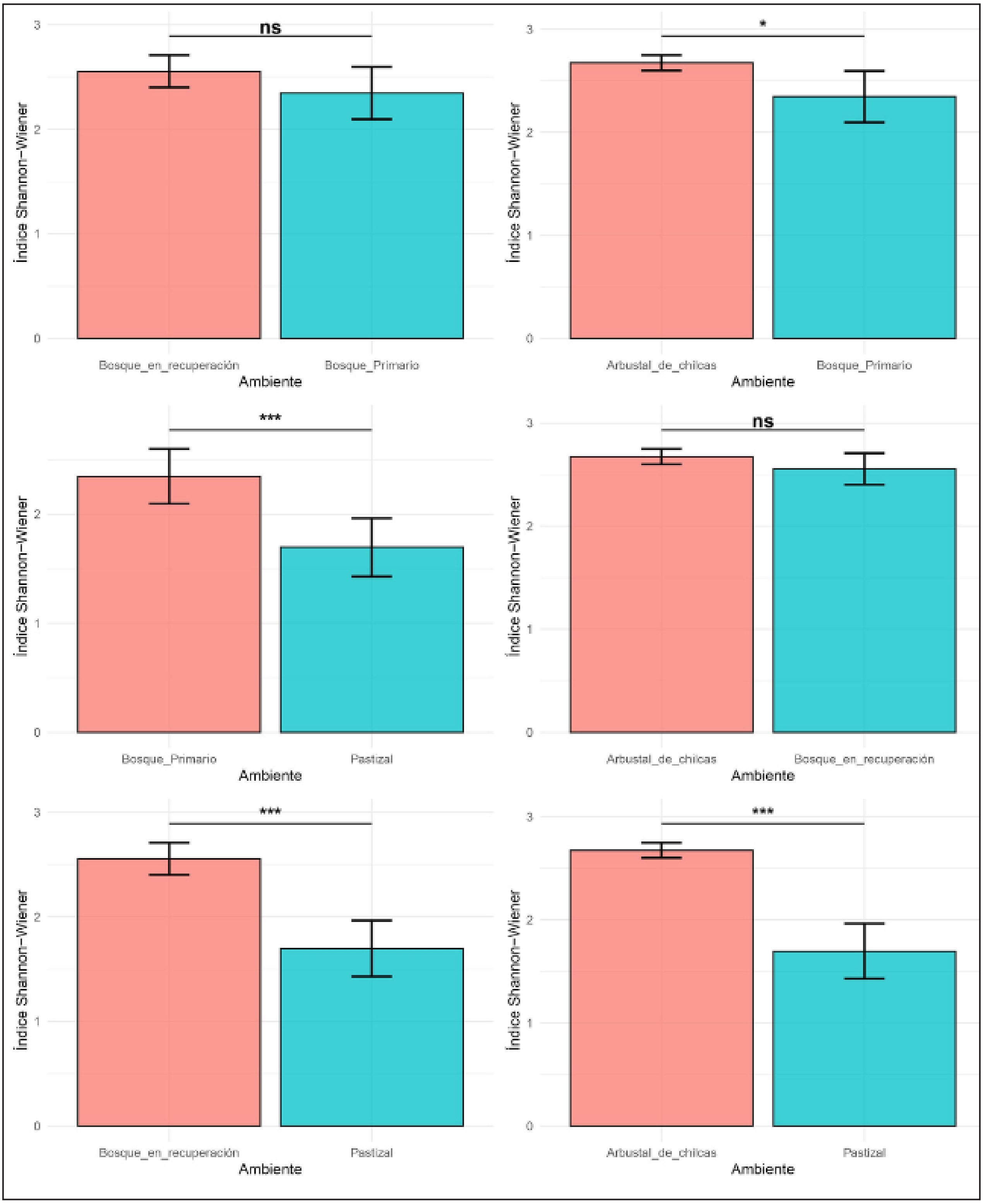

Figura 3. Comparación entre índices de Shannon-Wiener para cada ambiente mediante la prueba T de Hutcheson, con sus respectivos intervalos de confianza, para todos los taxa en conjunto. ns= no significativo, *= $p < 0.05$, ***=$p < 0.001$.

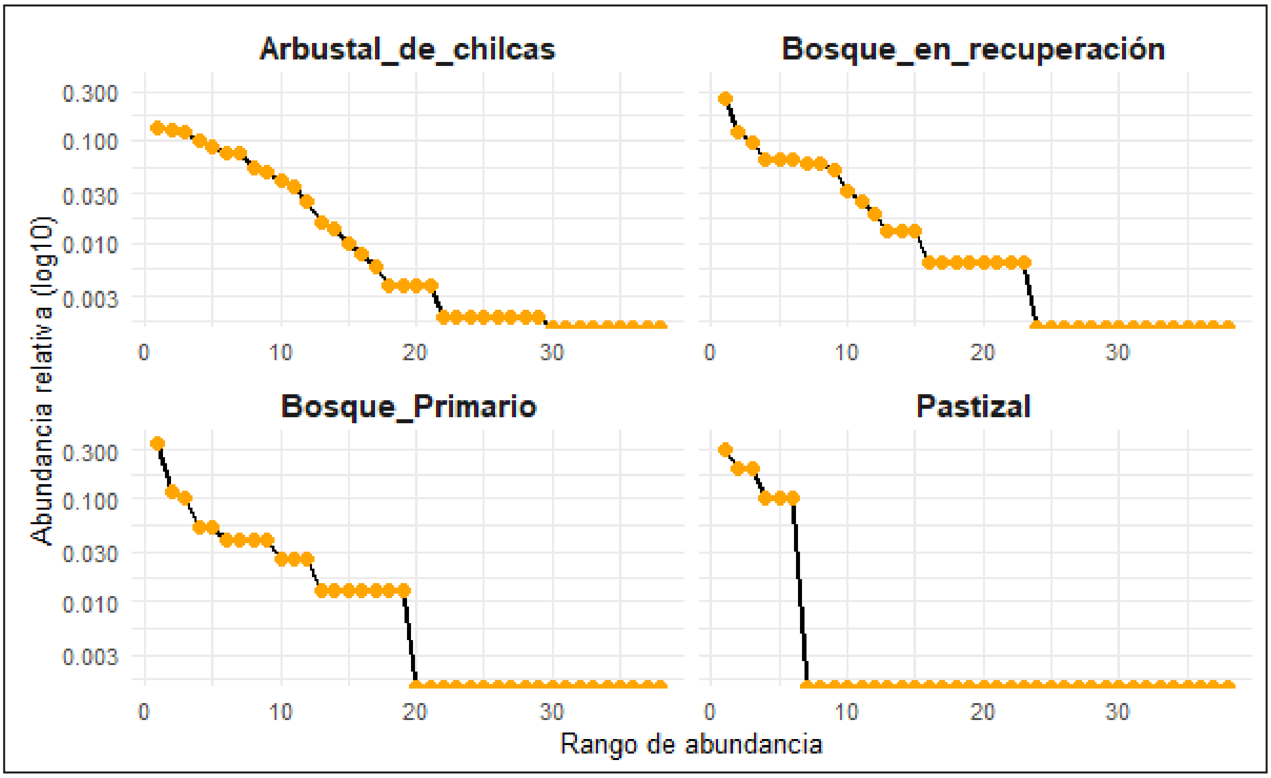

Figura 4. Curvas de rango-abundancia en cada ambiente para todos los taxones en conjunto.

y reproductivos para numerosos reptiles y anfibios (Jofré *et al.*, 2010). Sin embargo, la baja equitatividad puede estar respondiendo a una estructura de los ensambles con dominancia de especies. El siguiente sitio con una alta diversidad alfa fue el bosque en recuperación, con una riqueza e índice de Shannon-Wiener menor al arbustal de chilcas y una equitatividad similar al arbustal de chilcas y el bosque primario. Consideramos que, aunque el bosque en recuperación ha sido afectado por actividad humana, las condiciones naturales alcanzadas mantienen una comunidad de herpetofauna con una alta diversidad. En concordancia con otros estudios en áreas antropizadas, la pérdida de diversidad asociada a la actividad humana podría estar acompañada por el reemplazo de especies originales por especies colonizadoras. (Iglesias-Carrasco *et al.*, 2023). El bosque primario presentó una diversidad alfa menor, con valores de riqueza y de Shannon-Wiener inferiores a los de los sitios mencionados previamente, y una equitatividad similar. Se encontraron diferencias significativas entre el índice de Shannon-Wiener del bosque primario y el del arbustal de chilcas en la comparación entre índices. Esta menor diversidad alfa puede estar relacionada a la pérdida de especies en parches fragmentados de bosques tropicales o

Tabla 3. Diversidad beta entre sitios, reportando el índice de Jaccard (J) y el índice de Czekanowski (C) para cada par.

	Bosque primario	**Bosque en recuperación**	**Arbustal de chilcas**	**Pastizal**
Bosque primario	-	J = 0,448 C= 0,198	J = 0,455 C= 0,115	J =0,190 C= 0,160
Bosque en recuperación	J = 0,448 C= 0,198	-	J = 0,529 C= 0,417	J = 0,115 C= 0,060
Arbustal de chilcas	J = 0,455 C= 0,115	J = 0,529 C= 0,417	-	J = 0,167 C= 0,034
Pastizal	J = 0,190 C=0,160	J = 0,115 C= 0,060	J = 0,115 C= 0,034	-

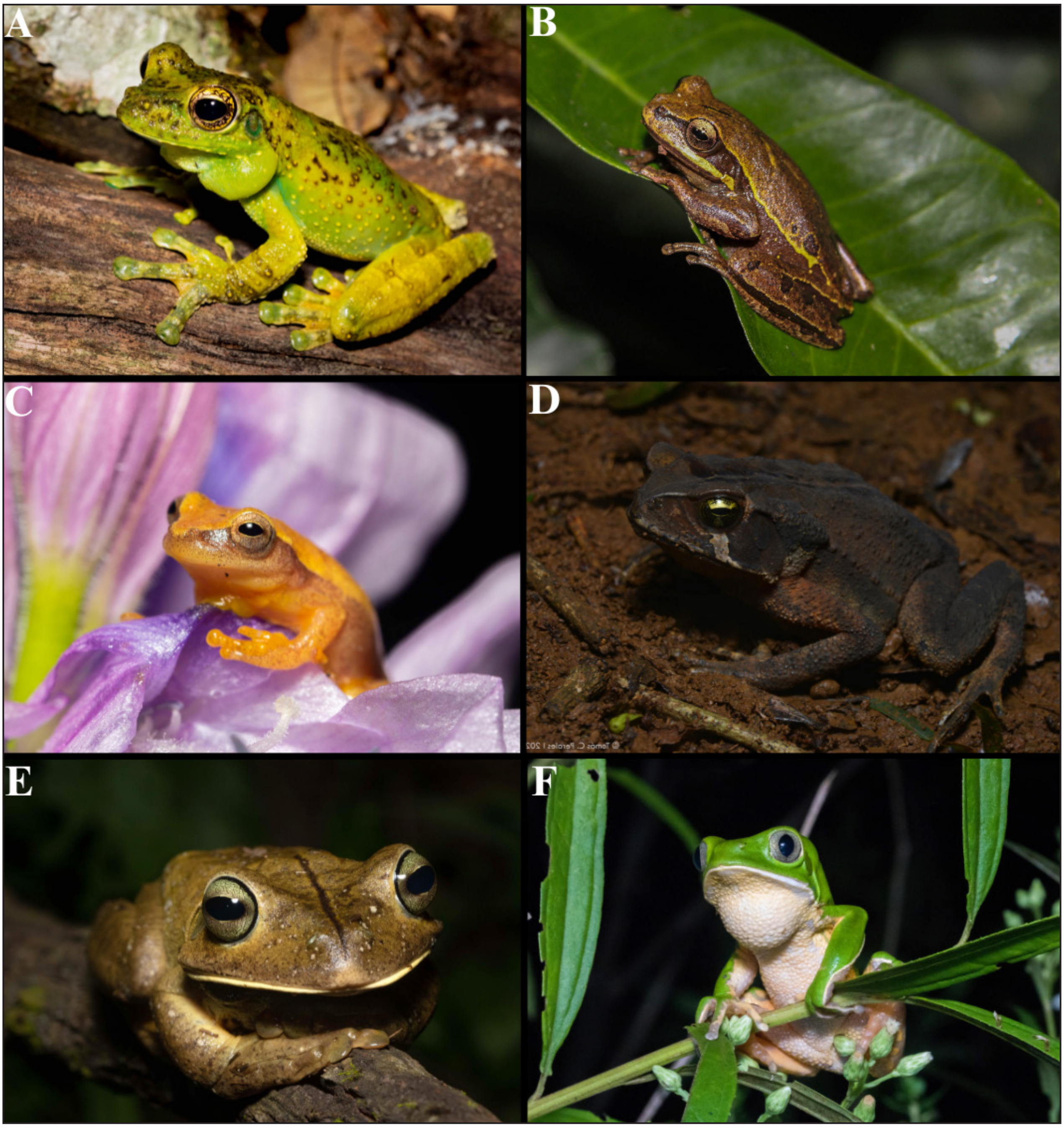

Figura 5. Anfibios de la Reserva Privada San Sebastián de la Selva: A) *Itapotihyla langsdorffi* B) *Boana stellae* C) *Dendropsophus minutus* D) *Rhinella ornata* E) *Boana faber* F) *Phyllomedusa tetraploidea*.

subtropicales (Turner, 1996) o un submuestreo del bosque primario, debido a la dificultad de observar ciertas especies, y el bajo rendimiento de las trampas de caída (Hsu *et al.*, 2005). Se sugiere, para futuros estudios, considerar un muestreo por cuadrantes para localizar taxones no registrados (Doan, 2009) y analizar cambios en la significancia de los datos. Por último, el pastizal exótico presentó los valores más bajos de riqueza y diversidad y una mayor equitatividad, distinta a los otros sitios. La comparación de los índices de Shannon-Wiener evidenció variaciones significativas entre los sitios, mostrando el pastizal valores significativamente menores respecto a los demás. Esta diferencia puede explicarse por la pérdida de especies al reemplazar un ambiente nativo por una plantación exótica casi homogénea. La baja diversidad alfa registrada responde a la alteración de las condiciones ambientales producto del uso

Figura 6. Reptiles de la Reserva Privada San Sebastián de la Selva: A) *Bothrops jararacussu* B) *Micrurus altirostris* C) *Amphisbaena prunicolor* D) *Philodryas olfersii* E) *Phrynops geoffroanus* F) *Notomabuya frenata.*

humano, siendo la destrucción de hábitats una de las causas principales en la pérdida de herpetofauna (Gibbons *et al.*, 2000) y el efecto negativo de pastizales exóticos sobre la herpetofauna (Lopez-Bedoya *et al.*, 2022). Aunque el pastizal exótico mostró la mayor equitatividad, creemos que estos resultados se asocian con la escasa cantidad de especies presentes y una abundancia relativamente uniforme entre ellas. Se recomienda optimizar las herramientas de muestreo pasivo para descartar sesgos de captura.

La diversidad beta evidenció diferencias en la composición de especies entre los ambientes, tanto para el índice de Jaccard como para el índice de Czekanowski. El índice de Jaccard reportó similitud media entre el bosque primario, el bosque en recuperación y el arbustal de chilcas, coincidente con la similitud en características ambientales y conectividad de ambientes distintos (Bell y Donnelly, 2006;

Kopp y Eterovick, 2006; Jofré *et al.,* 2010; López y Garey, 2021). Se observó una baja similitud entre cada uno de estos ambientes y el pastizal exótico, lo cual es esperable dada la pérdida de riqueza y diversidad alfa registrada en este sitio, consecuencia de la homogeneización y simplificación del paisaje. Por su parte, el índice de Czekanowski indicó una baja similitud en la abundancia de especies entre todos los sitios, aunque con una correspondencia ligeramente mayor entre el bosque primario y el bosque en recuperación. Debido a que el índice de Czekanowski pondera las abundancias de las especies, estos resultados refuerzan la idea de una comunidad herpetofaunística parcialmente compartida en ambientes con características estructurales similares, pero con diferencias en las abundancias de los taxones.

En este estudio se determinó una marcada pérdida de diversidad en el ambiente de pastizal exótico en comparación con otras zonas de la reserva. Los bajos valores de los índices alfa y beta evidencian que, independientemente del cese de las actividades antrópicas, los tiempos de recuperación son largos y los efectos negativos perduran en el tiempo (Meli *et al.,* 2017). Sin embargo, otros sitios de la reserva que sufrieron cambios antrópicos en menor medida han mostrado altos niveles de diversidad, incluso por encima de los ambientes protegidos y conservados. La creación de microhábitats que presentan condiciones bióticas y abióticas distintas a otros hábitats naturales puede favorecer a los reptiles y anfibios tanto en términos de termorregulación como de disponibilidad de presas y cuerpos de agua (Jofré *et al.,* 2010; Gardner *et al.*, 2007; Graitson *et al.,* 2020). Utilizando técnicas para estimar el grado de antropización de cada ambiente, se podrían obtener resultados más robustos sobre el papel de los cambios antrópicos en la distribución y la diversidad de las comunidades de herpetofauna. Sería ventajoso realizar estudios de variación temporal en la diversidad, tanto para corto como largo plazo.

La creación de reservas y áreas protegidas desempeña un papel central en la conservación de ambientes fragmentados, como la selva paranaense (Ervin, 2003; Avigliano *et al.*, 2019). Áreas previamente afectadas por actividades humanas pueden fomentar la conservación de comunidades de plantas y animales, incentivando la regeneración de ecosistemas y una recuperación de la biodiversidad. Investigar la composición de estas comunidades nos permite conocer de manera integral los desafíos de restaurar un ambiente y acercarnos al camino de la restauración ecológica.

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Trabajo

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Distribución geográfica y abundancia periférica de *Imantodes cenchoa* (Serpentes: Dispadidae) sugieren una inversión de los patrones biogeográficos clásicos

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ABSTRACT

The Rare Edge Hypothesis (REH) proposes that species are less abundant at the margins of their geographic ranges. This study assessed the geographical distribution and relative abundance patterns of *Imantodes cenchoa* in South America by integrating ecological niche modeling (MaxEnt) and generalized additive models (GAM). MaxEnt highlighted regions of high environmental suitability, particularly in Amazonian and Atlantic forest areas, while the GAM results indicated that suitability does not always correspond to higher relative abundance. Some regions with high predicted suitability, such as the southwestern Amazon moist forests, showed neutral or negative effects on abundance. Conversely, some marginal areas revealed unexpectedly positive abundance values. These findings suggest that unmodeled variables, such as canopy structure or anthropogenic disturbance, may influence local population densities. By combining both approaches, we identified ecoregions with overlooked conservation potential and emphasized the need to go beyond suitability alone when assessing species viability. The observed spatial patterns do not fully support either the Abundant-Center Hypothesis or the Rarity-at-the-Edges Hypothesis, pointing instead to a more complex distribution of abundance.

Key words: Abundant Centre Hypothesis, Common Blunt-headed Snake, Paraguay, Neotropics, Rare Edge Hypothesis.

RESUMEN

La Hipótesis de Rareza en los Bordes (REH) propone que las especies son menos abundantes en los márgenes de sus rangos geográficos. Este estudio evaluó la distribución geográfica y los patrones de abundancia relativa de *Imantodes cenchoa* en Sudamérica mediante un enfoque integrado que combina modelado de nicho ecológico (MaxEnt) y modelos aditivos generalizados (GAM). Los resultados del modelo MaxEnt identificaron áreas de alta idoneidad ambiental, principalmente en las regiones amazónicas y bosques atlánticos, mientras que el modelo GAM reveló que dicha idoneidad no se traduce necesariamente en mayor abundancia relativa. Algunas ecorregiones altamente adecuadas, como los bosques húmedos del suroeste de la Amazonía, presentaron efectos negativos o neutros sobre la abundancia. Por el contrario, ciertas regiones marginales exhibieron valores positivos inesperados. Estos hallazgos sugieren que variables no incluidas en los modelos, como la estructura del dosel o la presión antrópica, podrían estar modulando la abundancia observada. La integración de ambas metodologías permitió identificar regiones con potencial de conservación subestimado y refuerza la necesidad de incorporar métricas más allá de la idoneidad para evaluar la viabilidad poblacional de las especies. El patrón espacial observado no apoya plenamente la Hipótesis del Centro Abundante ni la Hipótesis de Rareza en los Bordes, lo que sugiere un patrón más complejo de distribución de la abundancia.

Palabras claves: Culebra cordelilla, Hipótesis del Centro Abundante, Hipótesis de Rareza en los Bordes, Paraguay, Noetrópico.

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Introducción

La distribución geográfica de las especies ha sido durante mucho tiempo un tema central en biogeografía, ecología y evolución. Un patrón de distribución bastante estudiado en este contexto ha sido la "Hipótesis del Centro Abundante" (*Abundant Centre Hypothesis*, ACH), que postula que las especies tienden a ser más abundantes en el centro de sus rangos corológicos reduciéndose la frecuencia hacia los bordes de la distribución (Wulff, 1950; Whittaker, 1975; Hengeveld y Haeck, 1982; Maurer, 1994). Sin embargo, esta hipótesis ha sido objeto de debate debido a la variabilidad empírica observada en diferentes grupos taxonómicos y ecosistemas (Sagarin y Gaines, 2002; Pironon *et al.*, 2017). Como respuesta a las limitaciones de la ACH, ha emergido recientemente un nuevo marco conceptual conocido como la "Hipótesis de Rareza en los Bordes" (*Rare Edge Hypothesis*, REH). Esta hipótesis propone que las especies presentan menores niveles de abundancia en las regiones periféricas de sus rangos geográficos, independientemente de si el centro de abundancia está estrictamente en el centro geográfico (Martin *et al.*, 2024). A diferencia de la ACH, que se enfoca en dónde se localiza el máximo de abundancia, la REH pone el énfasis en la escasez sistemática de individuos hacia los extremos espaciales del rango.

El reciente trabajo de Martin *et al.* (2024), basado en datos de ornitofauna obtenidos a través de ciencia ciudadana, ofrece una de las primeras validaciones empíricas sólidas de esta hipótesis aplicado a aves de Norteamérica. Sus resultados revelan que las zonas marginales presentan consistentemente menor abundancia relativa, sin importar la forma de cuantificación del borde o la metodología usada (Martin *et al.*, 2024). Esta interpretación ha sido también reforzada por Sexton (2024), quien argumenta que la REH ofrece un marco más robusto y generalizable que la clásica ACH para comprender los límites geográficos de las especies, dado que la REH no exige que el punto de máxima abundancia esté exactamente en el centro del rango, como lo hace la ACH. Solo predice que la abundancia será baja en los bordes, lo cual es más fácil de observar y comprobar en diferentes especies (Sexton, 2024).

La distribución de *Imantodes cenchoa*, una serpiente arborícola típicamente asociada a ambientes selváticos húmedos, se extiende ampliamente por América Central y del Sur (Nogueira *et al.*, 2019), pero sus registros en Paraguay son escasos y fragmentarios, especialmente en el este del país (Cacciali *et al.*, 2016; Cacciali, 2024). Esta rareza local podría interpretarse bajo el marco de la REH, dado que Paraguay se sitúa en el extremo sur del rango geográfico de la especie, lo que lo posiciona como una región limítrofe o de borde, por lo tanto es esperable que la abundancia —y en consecuencia la detectabilidad— disminuya significativamente. En este trabajo se pone a prueba la REH para intentar explicar la causa de la rareza de *I. cenchoa* en Paraguay.

Materiales y métodos

Imantodes cenchoa en Paraguay cuenta con escasos registros históricos, y su presencia ha sido documentada de forma esporádica. Recientemente se reportaron dos nuevos registros, uno de ellos en el presente trabajo (detalles en Apéndice 1), luego de un intervalo de 28 años sin nuevos datos confirmados. En la Figura 1 se presenta un resumen actualizado de todos los registros conocidos para *I. cenchoa* en Paraguay.

Con el objetivo de analizar el patrón espacial de distribución y abundancia de *Imantodes cenchoa* a lo largo de su rango geográfico, se recopiló una base de datos de ocurrencias confirmadas de la especie a partir del estudio de Nogueira *et al.* (2019). Estos datos fueron seleccionados por su amplia cobertura y validación taxonómica. Para Paraguay se emplearon los datos de Cacciali *et al.* (2016) sintetizados en la Figura 1, en donde se incorporan dos nuevos registros, referidos por Maciel-Méndez y Subeldía (2025) y el presente trabajo.

Para definir el área de distribución general de la especie, se construyó una envolvente convexa (*convex hull*) a partir de los puntos de ocurrencia registrados. Esta técnica permite generar un polígono continuo que engloba todos los registros, proporcionando una estimación espacial sencilla y reproducible del rango total. Se empleó una técnica de análisis radial mediante la construcción de anillos concéntricos equidistantes, siguiendo el enfoque propuesto por Sexton (2024) para estudios de abundancia geográfica. Se generaron anillos concéntricos equidistantes que subdividen el rango total en cuatro zonas clasificadas según cuartiles de distancia al centro: a) Centro, b) Medio interno, c) Medio externo y d) Borde. El ancho aproximado de cada anillo resultó ser de 300 km, producto de esta partición en cuartiles, y no de una decisión arbitraria o de una orientación geográfica predeterminada.

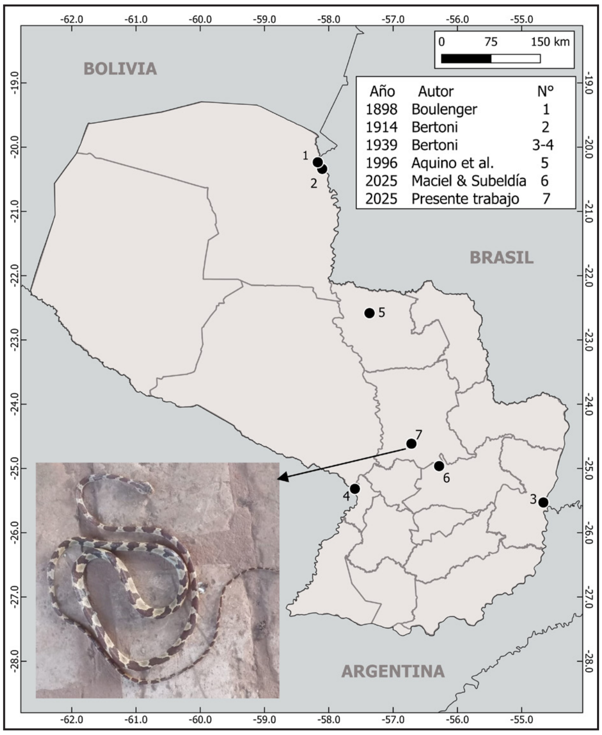

Figura 1. Registros de *Imantodes cenchoa* en Paraguay, indicando autor del registro y localidad.

Esta metodología permitió una segmentación equitativa del rango sin imponer un eje direccional (norte-sur o este-oeste), respetando la geometría del área de distribución. Todos los análisis espaciales y visualizaciones cartográficas fueron realizados utilizando QGIS 3.34.11, con soporte de complementos y herramientas de análisis vectorial integradas.

La abundancia relativa en cada zona fue estimada como el número de registros de presencia contenidos en cada anillo. Aunque los datos de ocurrencia no representan estimaciones directas de abundancia, son un robusto (y principal) indicador de este parámetro (He y Gaston, 2000). Se construyó un gráfico para representar el patrón de abundancia a lo largo de los cuatro cuartiles espaciales, visualizando posibles concentraciones o declives hacia los márgenes del rango. Además, se elaboró un mapa de calor (*heatmap*) de densidad de puntos de presencia con el fin de observar zonas de alta concentración de registros. Estas visualizaciones permiten explorar la posibilidad de ajustarse a la REH.

Dada la evidente existencia de vacíos geográficos en los registros de presencia, así como la concentración del esfuerzo de muestreo en regiones más accesibles y vacíos de conocimiento en el centro de Sudamérica (Nogueira *et al.*, 2019), se aplicó un modelo de distribución de especies (SDM) como herramienta para inferir el rango potencial de *I. cenchoa* a partir de sus requerimientos ecológicos. Este enfoque permite estimar áreas ambientalmente adecuadas que podrían estar submuestreadas o completamente ausentes en los registros actuales debido a limitaciones logísticas, institucionales o geopolíticas, como se ha reportado extensamente para la herpetofauna neotropical, e incorpora variables ambientales y climáticas. La modelación ecológica proporciona así una base más robusta para evaluar patrones de distribución y abundancia relativa, minimizando la dependencia exclusiva de los datos observados, los cuales están sujetos a sesgos de accesibilidad, infraestructura y actividad científica. Se utilizó el algoritmo MaxEnt versión 3.4.4 (Phillips *et al.*, 2017) para modelar la distribución potencial de *I. cenchoa*, empleando 545 registros de presencia y 20,000 puntos de fondo generados aleatoriamente dentro del área accesible definida por una envolvente convexa con buffer. Se utilizaron 14 variables ambientales continuas obtenidas de WorldClim (precipitación, temperatura, vapor de agua, nubosidad, altitud y ecorregiones) (Fick y Hijmans, 2017). El modelo se ajustó con las funciones lineal, cuadrática, producto y bisagra, utilizando regularización predeterminada y 1000 iteraciones. Se activaron las curvas de respuesta y el análisis jackknife.

Como aproximación adicional, se generó un modelo de distribución utilizando el algoritmo Bioclim (Hijmans *et al.*, 2005), implementado en Diva-GIS v7.5 (Hijmans *et al.*, 2001). Este enfoque permite estimar la idoneidad ambiental basada en el rango de condiciones observadas en los registros de presencia. Aunque se trata de un método más simple que MaxEnt, su inclusión permite evaluar la consistencia de los patrones espaciales obtenidos mediante distintos algoritmos.

Finalmente, a modo de evaluar la abundancia relativa de *I. cenchoa* en función de factores geográficos, ambientales y ecológicos, se emplearon Modelos Aditivos Generalizados (GAM) (Hastie y Tibshirani, 1990). Esta técnica es especialmente útil en estudios ecológicos, donde las relaciones entre la abundancia de una especie y las variables ambientales raramente son estrictamente lineales (Guisan *et al.*, 2002). Dada la estructura de los datos basada en registros de presencia y sin un esfuerzo de muestreo homogéneo, el uso de GAM ofrece una aproximación robusta que permite capturar patrones complejos y no lineales. Para generar una variable de abundancia relativa que pueda ser utilizada como variable respuesta, se agruparon los registros de *I. cenchoa* según su posición geográfica. Cada registro corresponde a la observación de un individuo, por lo que se asumió que múltiples registros en la misma coordenada indican una mayor abundancia relativa. Así, se calcularon los recuentos de observaciones únicos por combinación de latitud y longitud decimal (decimalLatitude y decimalLongitude en Apéndice 2), siguiendo una lógica similar a la empleada en estudios de distribución con datos de presencia únicamente (*presence-only*) (Elith *et al.*, 2011). A partir de esta agrupación, se generó una nueva tabla que incluye, para cada ubicación geográfica única, el número total de registros como una estimación de abundancia relativa (Apéndice 2). Esta tabla fue posteriormente complementada con variables ambientales obtenidas por extracción de valores raster a cada punto, incluyendo distancia al centroide del rango de distribución (HubDist), datos ecorregionales y variables ambientales empleadas para el MaxEnt. Para evitar sobreajuste y colinealidad se hizo un análisis de correlación de variables (excluyendo Ecorregiones) con el paquete *corrplot* (Wei y Simko, 2021). Los modelados de GAM se corrieron en R, con los paquetes *dplyr* (Wickham *et al.*, 2023), *ggplot2* (Wickham, 2016), *gratia* (Simpson, 2023), *mgcv* (Wood, 2017), *performance* (Lüdecke *et al.*, 2021) y *tidyverse* (Wickham *et al.*, 2019).

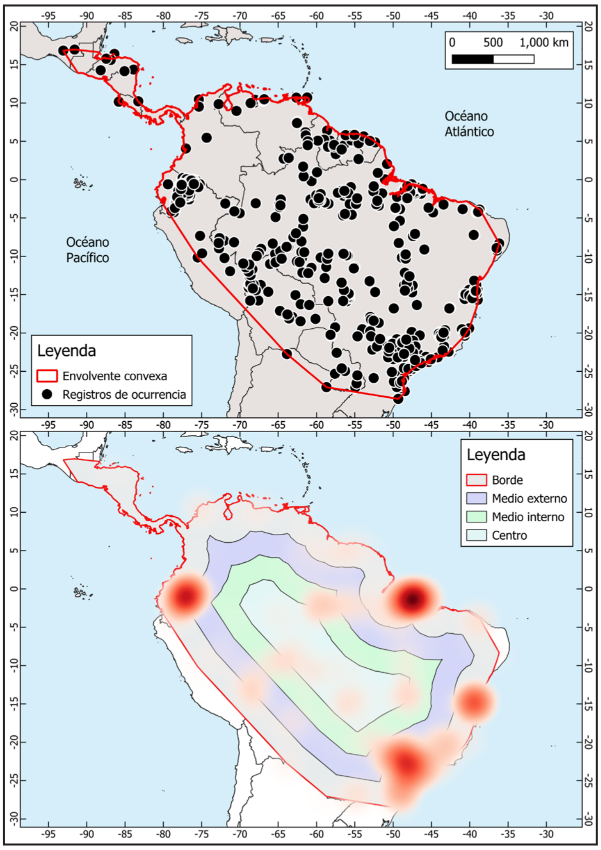

Figura 2. Arriba: Totalidad de los registros georreferenciados (puntos negros) utilizados en este estudio, y envolvente convexa (línea roja) delimitando el rango geográfico total de *Imantodes cenchoa*. Abajo: Clasificación del rango en cuartiles concéntricos de distancia al centro (Zonas: Centro, Medio interno, Medio externo y Borde) con un mapa de calor basado en la densidad de registros.

Resultados

La totalidad de los registros de ocurrencia de *I. cenchoa* se distribuyen principalmente a lo largo de la cuenca amazónica, el escudo guayanés, Centroamérica y porciones del Bosque Atlántico, y la envolvente convexa para la especie indica una vasta región de América Tropical, desde el sur de México hasta el noreste de Argentina (Fig. 2). El análisis de abundancia relativa en función de la distancia al centro de distribución reveló un patrón altamente asimétrico. La mayoría de los registros de *I. cenchoa* se concentran en el cuartil más externo (Borde), y las concentraciones de registros son comparativamente más dispersos o escasos hacia el centro (Fig. 2). Particularmente notables son las acumulaciones en el norte de Colombia, noreste de Brasil, sur de la Amazonía occidental y regiones atlánticas del este de Brasil, todas dentro del anillo más externo de la distribución (Fig. 2).

Con un total de 645 registros, lo que representa aproximadamente el 67.6% del total considerado, el Borde cuenta con más ocurrencias que todas las demás zonas juntas (Medio externo: 148 registros, Medio interno: 77 registros, Centro: 84 registros) (Fig. 3). Estos datos confirman espacialmente que las mayores densidades de observación se ubican en los márgenes del rango geográfico de la especie, contradiciendo no solo a la REH, sino que también a la ACH.

El modelo presentó un AUC de entrenamiento de 0.860 y una ganancia regularizada de 0.912, lo que indica un alto poder predictivo. Las variables que más contribuyeron al modelo fueron la precipitación del primer mes del año (23%), la precipitación anual (15.9%) y el vapor de agua (14.2%). El área predicha como adecuada para la especie representó entre el 24% y el 41% del área de calibración, dependiendo del umbral aplicado. El patrón de idoneidad ambiental sugiere una preferencia por regiones cálidas, húmedas y con alta nubosidad en el norte y centro de Sudamérica, específicamente en Surinam, Ecuador

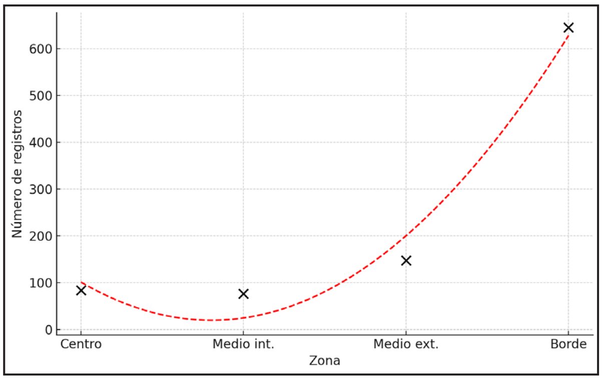

Figura 3. Relación entre la abundancia relativa de *Imantodes cenchoa* y la distancia al centro del rango geográfico. Las cruces indican el número de registros observados en cada zona, y la línea punteada representa una curva de ajuste polinomial para evidenciar la tendencia.

y el estado de San Pablo y parte de Minas Gerais en Brasil (Fig. 4). El modelo Bioclim mostró áreas de idoneidad elevada principalmente en la cuenca amazónica, la Mata Atlántica y el norte de Sudamérica, coincidiendo con los resultados obtenidos con MaxEnt. Las regiones clasificadas como "excelente" (percentil 20–38%) corresponden a zonas de alta humedad y temperaturas tropicales (Fig. 4). En definitiva, la menor probabilidad de presencia de la especie se encuentra en el Pantanal, y en la diagonal árida (Caatinga, Cerrado, Chaco) con mayor probabilidad en bosques húmedo asociados a áreas costeras y a zonas más continentales, también húmedas, en el suroeste amazónico (convergencia de Bolivia, Brasil y Perú), Napo (norte de Perú) y Caqueta (sur de Colombia), y una leve probabilidad en las zonas amazónicas de Madeira-Tapajós y Tapajós-Xindu (Fig. 4).

Los resultados de la correlación de variables ambientales para GAM se presentan en el Apéndice 3. El modelo aditivo generalizado (GAM) ajustado con familia binomial negativa y función de enlace logarítmica explicó un 31,8% de la desviación total en la abundancia relativa de *I. cenchoa*. Entre las variables continuas, la distancia al centroide presentó un efecto marginalmente significativo (p = 0.0550), no lineal, lo que sugiere que la especie no se distribuye homogéneamente respecto al centro de su área de ocurrencia, donde la abundancia relativa parece aumentar levemente en torno a 1500–2000 km del centro, sugiriendo mayor abundancia hacia zonas intermedias o periféricas, pero no en los bordes más extremos (Fig. 5). La precipitación anual mostró un efecto suavizado altamente significativo (Chi^2 = 16.36, p = 0.0112), indicando una relación no lineal con la abundancia, observando un aumento de abundancia en precipitaciones intermedias, pero disminuye con precipitaciones más altas (Fig. 5). En el caso de la elevación una relación negativa clara: a mayor elevación, menor abundancia. Por su parte la curva de temperatura es casi plana, y el intervalo de confianza es muy amplio, lo que indica que no hay una relación significativa clara entre temperatura media y abundancia en este modelo. Esto sugiere que la temperatura media por sí sola no explica bien la abundancia de la especie.

Respecto a las ecorregiones, el modelo detectó diferencias significativas en los niveles del factor categórico. Se observaron efectos positivos significativos sobre la abundancia en las ecorregiones Matorral xerófilo de Guajira-Barranquilla (p < 0.001), Bosque costero de Bahia (p = 0.006), Bosques húmedos de Tocantins/Pindaré (p = 0.009) y las Yungas Andinas del Sur (p = 0.003), entre otras (Fig. 6). Esto sugiere que la abundancia relativa de *I. cenchoa* varía según el tipo de ecosistema, favoreciendo especialmente ciertos bosques tropicales húmedos y regiones de sabana estacional.

Discusión

El análisis espacial de la abundancia en base al mapa de calor para *I. cenchoa* reveló un patrón contrario al predicho por la *Rare Edge Hypothesis* (REH). Esta hipótesis plantea que las especies tienden a ser menos abundantes en los márgenes de sus rangos geográficos debido a factores como la menor adecuación del hábitat, el aislamiento poblacional y la reducción del flujo génico (Eckert *et al*., 2008; Polechová, 2018). Sin embargo, los resultados obtenidos muestran una mayor concentración de registros en el borde externo del rango, lo que sugiere un patrón de abundancia periférica en lugar del gradiente clásico de decaimiento hacia los márgenes.

Los modelados de distribución muestran focos de hábitat más adecuado en zonas concordantes con los patrones mostrados por el mapa de calor, sugiriendo afinidad por bosques húmedos. Esto concuerda con estudios previos en donde si bien su presencia es confirmada en bosques secos, la mayor actividad de *I. cenchoa* se presenta en bosques húmedos (Rojas-Morales *et al*., 2014). Se destaca su ausencia de áreas abiertas (Nogueira *et al*., 2019) lo cual refuerza la asociación de la especie con ambientes forestales, en donde se desplaza en la

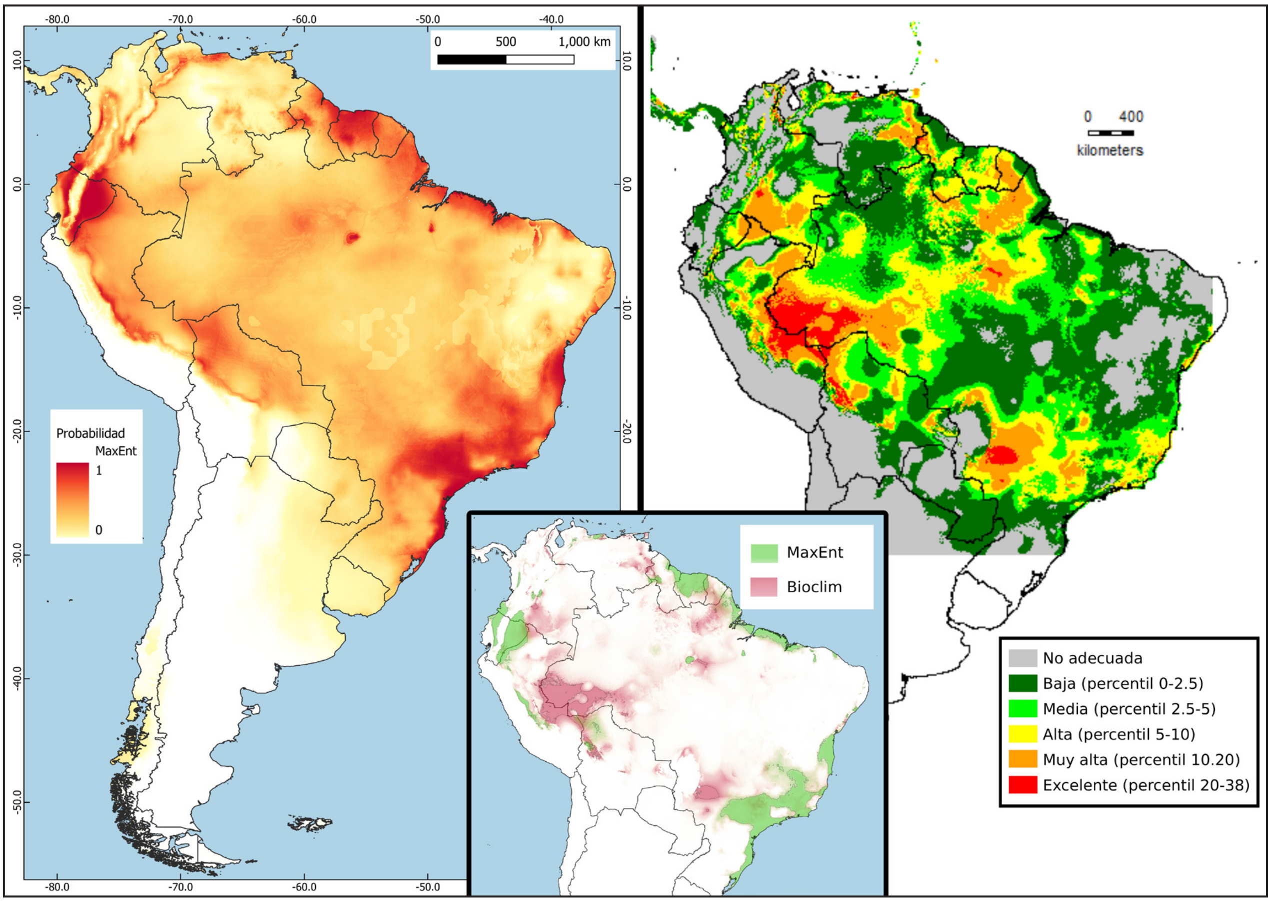

Figura 4. Modelados de distribución de *I. cenchoa* según algoritmos de MaxEnt (izquierda) y Bioclim (derecha). En el mapa inferior del centro se presenta una combinación de las condiciones muy altas y excelentes (estas últimas delimitadas con un contorno gris) para Bioclim y las condiciones de predicción de 0.7 en MaxEnt.

vegetación entre los 0.5 y 2.5 m de altura (Martins y Oliveira, 1998), por lo tanto es una especie cuyo registro se hace principalmente mediante búsqueda activa (Frota *et al.*, 2021).

Las altas frecuencias en la distribución periférica de *I. cenchoa* plantea interrogantes importantes sobre la universalidad de la REH, especialmente en especies tropicales ampliamente distribuidas y con alta tolerancia ecológica. En lugar de una estructura centrada, esta especie podría presentar una distribución no uniforme o multimodal, con múltiples centros periféricos de abundancia. Esta organización podría reflejar regiones ecológicamente estables o con condiciones históricas favorables, como ocurre en zonas del noreste de Brasil o Centroamérica.

Una alternativa adicional es que cada cúmulo de registros represente un linaje genético distinto, fenómeno observado en otras especies de distribución amplia (Carnaval *et al.*, 2009). En ese escenario, las poblaciones periféricas no estarían necesariamente en el "borde ecológico", sino en el centro de rangos históricos de linajes diferenciados, en cuyo caso la REH podría seguir siendo válida en un contexto filogeográfico.

Otra posible explicación involucra sesgos de muestreo, ya que áreas con mayor actividad científica y ciudadana, podrían estar sobre-muestreadas debido a su accesibilidad o concentración de proyectos. Esta asimetría en el esfuerzo de registro puede influir en la percepción del patrón espacial de abundancia y debe ser considerada al interpretar los resultados. Esto ya es remarcado para *I. cenchoa* por Costa *et al.* (2010) para el estado de Minas Gerais en Brasil. A pesar de estas consideraciones, el patrón observado representa un desafío conceptual para la REH y destaca la necesidad de incorporar enfoques más complejos, que consideren la heterogeneidad ambiental, la historia evolutiva de la especie y los vacíos de muestreo.

Aunque los modelos de distribución como MaxEnt identifican áreas con alta probabilidad de presencia, nuestros resultados sugieren que una

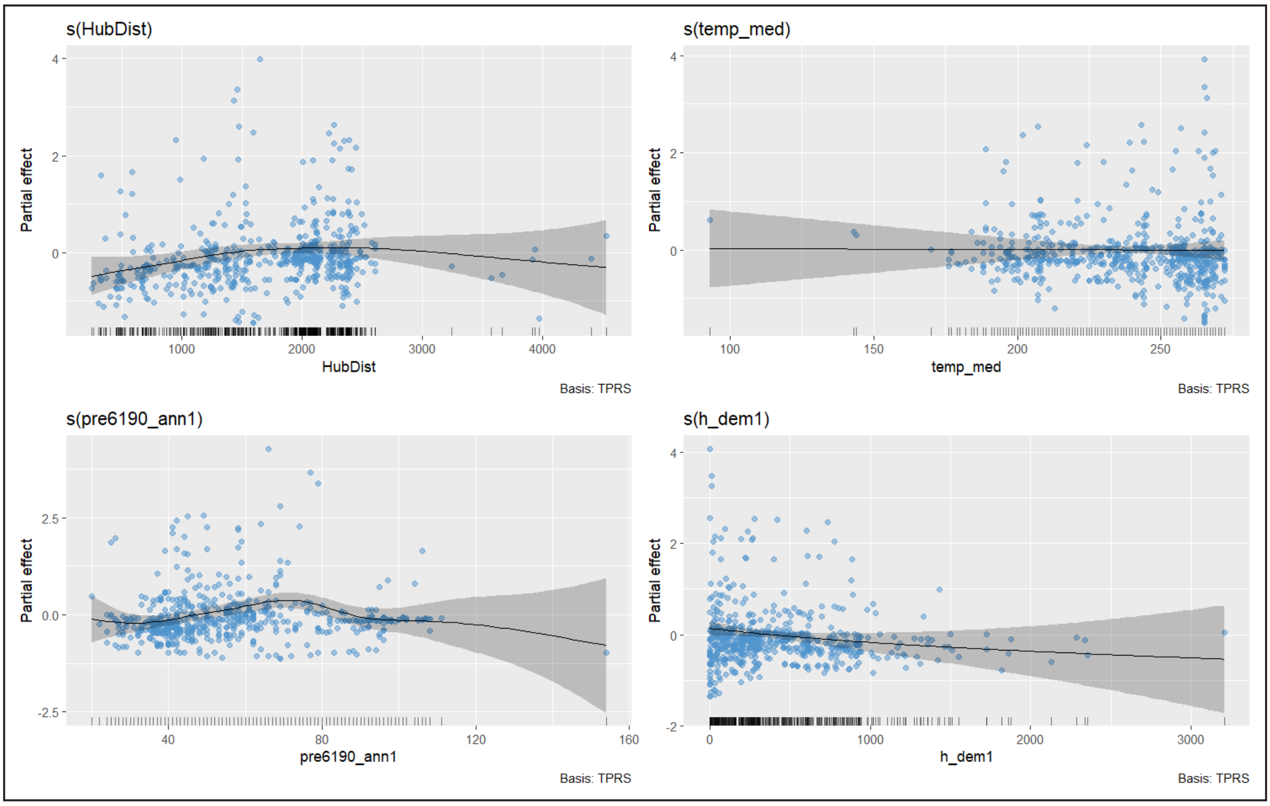

Figura 5. Efecto parcial de cada predictor sobre la abundancia relativa de *I. cenchoa*. El eje Y representa el efecto estimado (en una escala centrada en 0) y el eje X representa el valor del predictor. Se muestra el número de registros (puntos azules) con la representación de la función suavizada (línea negra) y el intervalo de confianza al 95% (sombra gris).

elevada idoneidad ambiental no necesariamente se traduce en mayores abundancias relativas. Si bien el modelo GAM sugiere una tendencia a la disminución de la abundancia relativa de *I. cenchoa* con el aumento de la distancia al centro del rango de distribución, este patrón no fue estadísticamente robusto. Ecorregiones como los bosques húmedos del suroeste de la Amazonía, con alta adecuación predicha, mostraron efectos neutros o negativos en los modelos GAM. Además, se observaron altos niveles de abundancia en ecorregiones periféricas, como Yungas Andinas del Sur y Matorrales xerófilos de Guajira-Barranquilla, lo cual contradice las predicciones tanto de la ACH como de la REH. Este patrón ya ha sido documentado en otros estudios, donde la validez universal de la ACH ha sido cuestionada en varios grupos taxonómicos (Sagarin y Gaines, 2002; Pironon *et al*., 2017). En resumen, si bien no es concluyente que la distribución de *I. cenchoa* se ajusta por completo a una distribución del tipo REH, definitivamente no se enmarca de lo esperado para un rango corológico del tipo ACH.

Desde una perspectiva de conservación, este hallazgo tiene importantes implicancias. En Paraguay *I. cenchoa* estaba considerada como amenazada de extinción en una categorización del estado de conservación hecha por Motte *et al.* (2009), sin embargo, en la última categorización esta especie está considerada como con Datos insuficientes (Martínez *et al*., 2020). Esto se debe a su baja frecuencia, más que a un declive poblacional. Sin embargo, está documentado que la mayor abundancia de esta serpiente se da en áreas de bosques naturales y bien conservados (Martins y Oliveira, 1998; Frota *et al*., 2021). Por otro lado, las poblaciones marginales son importantes para la conservación, ya que podrían representar reservorios de diversidad genética o tener un rol clave en la resiliencia adaptativa ante el cambio climático (Hampe y Petit, 2005). En este sentido, cabe señalar que en Paraguay esta especie está protegida en unidades de conservación (Cacciali *et al*., 2015).

La biología, como ciencia del cambio y la diversidad, rara vez se ajusta a reglas fijas. Si bien las hipótesis estructuradas como la REH o la ACH proporcionan marcos valiosos para interpretar patrones espaciales, su aplicabilidad debe evaluarse caso por caso, con apertura al dinamismo inherente de los

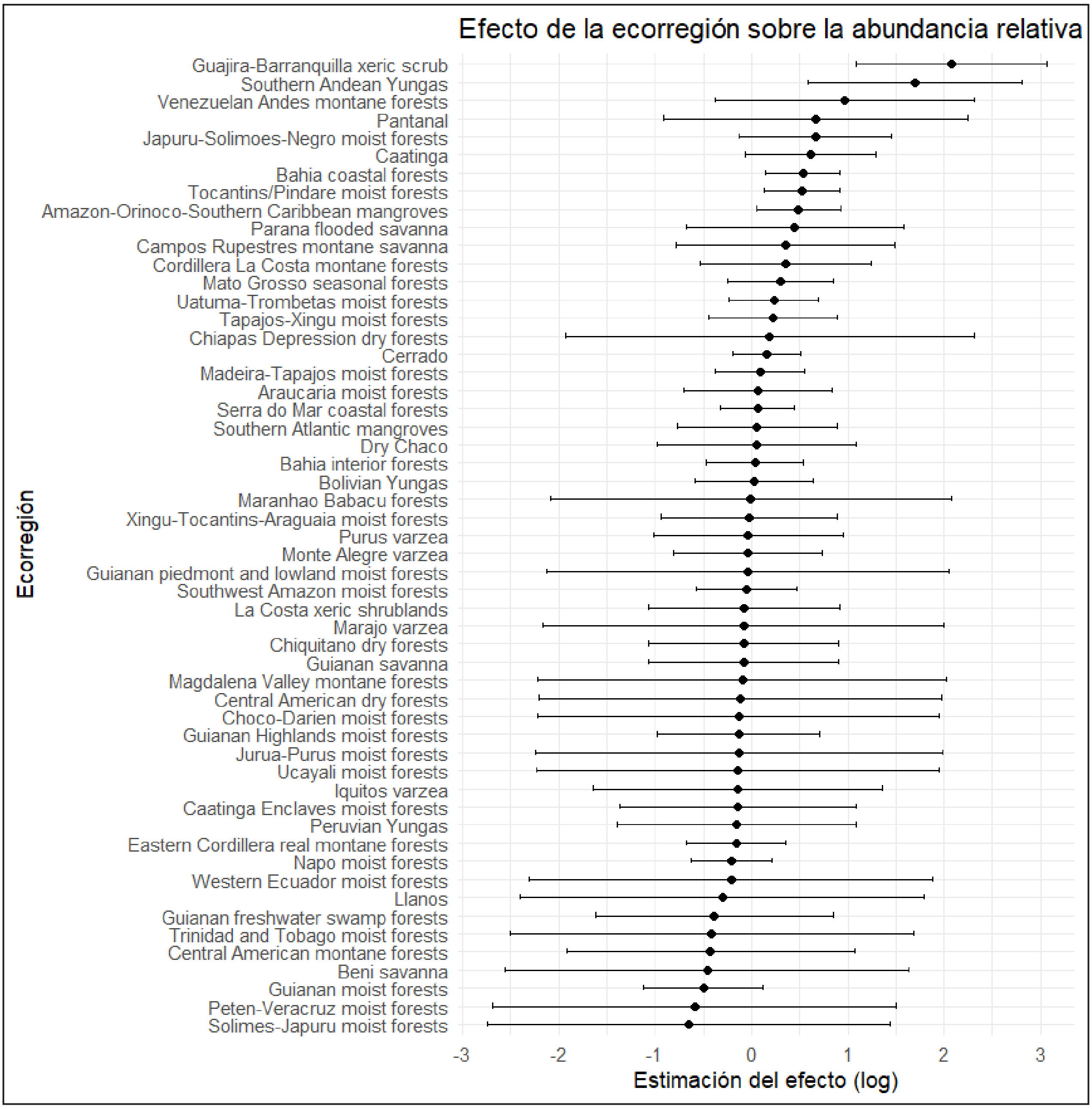

Figura 6. Efecto estimado de la ecorregión sobre la abundancia relativa de *I. cenchoa*, modelado GAM con distribución binomial negativa. Los puntos indican la estimación del coeficiente en escala logarítmica para cada ecorregión, mientras que las barras representan el intervalo de confianza al 95%. Un valor positivo indica mayor abundancia relativa en comparación con la categoría base, mientras que un valor negativo indica menor abundancia relativa.

sistemas naturales. La diversidad de historias evolutivas, condiciones ecológicas y factores históricos que influyen en la distribución de las especies exige una aproximación flexible, crítica y actualizada. Por ello, es fundamental que los estudios de distribución geográfica mantengan un enfoque dinámico, en el que los modelos no se impongan como reglas universales, sino que sirvan como herramientas interpretativas en constante revisión.

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Apendice 1

Registro de *Imantodes cenchoa* en la localidad de Friesland (Lat -24.6149, Long -56.7141, en fecha 2-III-2025. Fotografía: Christof Siebert.

Apendice 2

Tabla de variables y abundancia calculada por número de registros por localidad

N°	abundancia	decimal Latitude	decimal Longitude	HubDist	ECO_NAME	cld6190_ ann1	dtr6190_ ann	frs6190_ ann1	h_ dem1	pre6190	pre|1-3	pre|4-6	pre|7-9	pre|10-12	temp_	t_ min	t_ max	vap
1	1	-1.0411	-77.714	2106.63	Napo moist forests	82	129	10	572	101	87	134	96	97	218	144	290	213
2	1	-0.424	-76.893	2045.196	Napo moist forests	82	115	0	292	97	81	128	97	93	254	186	318	253
3	1	-1.049	-77.6	2094.375	Napo moist forests	82	127	7	508	102	87	135	98	98	228	155	298	224
4	1	-0.97	-77.889	2127.614	Eastern Cordillera real montane forests	81	134	26	608	82	71	111	75	81	191	115	265	182
5	1	-4.6667	-56.5333	454.5393	Madeira-TapajÃƒÂ³s moist forests	79	96	0	46	57	81	87	21	32	269	210	331	309
6	1	-21.6833	-51.0667	1853.433	Alto ParanÃƒÂ¡ Atlantic forests	64	117	0	479	37	68	28	11	43	229	127	312	197
7	1	4.9833	-54.9933	1448.788	Guianan moist forests	69	90	1	39	65	74	85	78	23	262	212	326	224
8	1	-22.4692	-48.9875	2045.184	Cerrado	69	115	0	610	37	68	23	12	42	215	114	302	182
9	3	-14.6694	-39.1908	2392.333	Bahia coastal forests	67	71	0	18	49	43	60	53	43	244	186	297	252
12	1	-1.457	-77.534	2072.777	Napo moist forests	82	128	1	406	108	91	142	105	102	241	167	313	238
13	1	-1.47	-77.535	2072.428	Napo moist forests	82	128	1	406	108	91	142	105	102	241	167	313	238
14	1	-1.47	-77.486	2067.254	Napo moist forests	82	127	1	372	107	90	141	104	101	243	169	314	240
15	1	-1.471	-77.486	2067.219	Napo moist forests	82	127	1	372	107	90	141	104	101	243	169	314	240
16	1	-1.469	-77.487	2067.395	Napo moist forests	82	127	1	372	107	90	141	104	101	243	169	314	240

17	1	-1.453	-77.443	2063.311	Napo moist forests	82	127	1	351	106	89	140	104	100	245	171	315	242
18	1	-1.45	-77.443	2063.416	Napo moist forests	82	127	1	351	106	89	140	104	100	245	171	315	242
19	1	-1.454	-77.441	2063.065	Napo moist forests	82	127	1	351	106	89	140	104	100	245	171	315	242
20	1	-1.505	-77.509	2068.464	Napo moist forests	81	128	1	451	107	91	142	104	101	241	167	313	238
21	1	-9.9	-55.9	518.038	Madeira-TapajÃƒÂ³s moist forests	77	124	1	313	62	101	68	2	61	256	167	340	276
22	1	-15.1106	-40.12	2313.662	Bahia interior forests	69	85	1	306	32	41	36	26	30	234	169	295	225
23	1	-21.0256	-47.3739	2027.822	Cerrado	71	104	0	928	42	88	27	8	47	211	117	279	181
24	1	-3.77	-78.551	2116.911	Eastern Cordillera real montane forests	74	152	26	1275	42	41	55	36	38	198	113	288	179
25	1	-3.899	-78.478	2106.228	Eastern Cordillera real montane forests	74	150	23	1384	44	43	57	39	41	204	121	293	184
26	1	-4.251	-78.617	2114.443	Eastern Cordillera real montane forests	73	155	24	1723	35	36	46	27	34	194	107	287	170
27	1	-1.028	-77.728	2108.581	Napo moist forests	82	129	10	572	101	87	134	96	97	218	144	290	213
28	1	-2.5666	-76.6333	1940.755	Napo moist forests	80	123	2	240	86	72	113	87	78	256	183	325	252
29	3	-1.5898	-77.7541	2091.484	Napo moist forests	81	131	4	685	106	92	141	101	101	230	153	304	226
30	1	-14.8717	-55.7856	951.5257	Cerrado	67	126	3	267	42	79	42	1	44	257	155	337	247
31	1	-0.1963	-60.6485	782.3157	Uatuma-Trombetas moist forests	75	93	1	100	56	51	79	64	33	264	213	324	281
32	2	-22.65	-50.4	1980.641	Cerrado	66	120	1	561	38	64	27	15	44	218	112	311	184
33	1	-22.6667	-50.4167	1981.308	Cerrado	66	120	1	561	38	64	27	15	44	218	112	311	184

35	2	-1.7911	-77.808	2090.492	Eastern Cordillera real montane forests	81	135	10	890	97	85	130	91	93	221	143	297	216
37	1	-23.0972	-48.9047	2106.686	Cerrado	71	114	1	850	36	62	23	14	41	204	104	294	174
38	1	-0.633	-77.432	2092.654	Eastern Cordillera real montane forests	82	123	9	745	93	80	124	90	90	227	157	294	224
39	1	-15.5833	-56.0833	1008.679	Cerrado	67	122	1	198	37	73	40	3	37	262	161	337	254
40	1	-27.6	-48.4806	2550.777	Serra do Mar coastal forests			1										
41	1	-1.247	-76.668	1989.328	Napo moist forests	81	122	0	264	97	77	127	99	94	257	185	325	255
42	2	-13.7494	-67.2858	1096.069	Southwest Amazon moist forests	63	99	0	206	52	88	51	20	42	262	181	328	255
44	1	-11	-66.0667	810.2345	Southwest Amazon moist forests	73	105	0	145	46	83	51	5	41	268	193	341	275
45	1	-14.6333	-66.3	1088.385	Southwest Amazon moist forests	61	102	0	199	49	93	45	18	42	262	176	331	251
46	1	5.085	-58.2372	1370.414	Guianan moist forests	62	85	0	46	77	78	83	109	34	261	213	319	235
47	1	-15.5642	-40.6461	2278.779	Bahia coastal forests	70	92	0	677	26	40	26	13	25	227	157	292	211
48	6	-15.1917	-39.4917	2380.243	Bahia coastal forests	68	77	0	219	44	46	51	45	42	240	179	296	242
54	1	-22.4167	-42.6167	2491.49	Serra do Mar coastal forests	69	93	3	325	33	62	27	9	30	206	124	285	201
55	1	5.3833	-55.1575	1483.665	Guianan moist forests	68	88	0	35	61	67	80	75	26	267	217	329	229
56	1	-0.6245	-76.494	1995.718	Napo moist forests	82	116	0	270	93	73	122	96	92	258	189	324	257

57	2	4.5	-61.15	1304.54	Guianan Highlands moist forests	65	109	0	1019	55	23	60	90	47	232	173	296	219
59	1	-1.832	-46.365	1600.21	Tocantins/ Pindare moist forests	75	87	0	30	63	77	126	49	11	265	216	322	289
60	1	-9.75	-61.9167	367.8334	Madeira-TapajÃƒÂ³s moist forests	77	109	2	200	56	95	67	4	55	259	180	333	280
61	1	-8.78	-63.7	468.0814	Monte Alegre varzeÃƒÂ¡	79	101	0	77	58	97	74	8	57	264	189	331	290
62	1	-13.7703	-39.2006	2362.449	Bahia coastal f forests	71	77	0	138	40	35	54	43	32	244	185	300	249
63	2	-19.5167	-54.0333	1495.057	Cerrado	62	117	0	392	41	81	34	10	41	244	145	319	224
65	1	-0.177	-75.676	1931.181	Napo moist forests	81	111	0	234	86	59	112	91	87	260	195	325	261
66	1	-20.4333	-54.6333	1563.432	Cerrado	61	111	0	592	40	76	34	14	44	238	142	311	217
67	2	-14.7978	-39.1708	2398.794	Bahia coastal forests	67	71	0	72	50	44	60	54	44	244	186	297	252
70	1	-26.8333	-49	2451.487	Serra do Mar coastal forests	73	87	3	151	45	59	35	32	48	200	114	287	192
71	1	-1.28	-47.92	1468.109	Tocantins/ Pindare moist forests	75	90	0	25	77	106	140	52	20	265	217	323	294
72	1	-1.7922	-51.4336	1100.778	Xingu-Tocantins-Araguaia moist forests	78	95	0	1	64	88	114	49	19	268	217	331	303
73	1	4.8667	-52.3464	1569.062	Amazon-Orinoco-Southern Caribbean mangroves	58	76	1	2	94	127	136	72	20	256	214	313	295
74	1	-0.993	-77.4132	2076.877	Napo moist forests	82	125	4	325	102	86	135	100	97	237	165	305	234
75	1	-10.0645	-75.5459	1766.035	Peruvian Yungas	74	131	37	856	38	57	35	16	46	188	103	263	169

76	9	-14.7675	-39.2281	2391.885	Bahia coastal forests	67	71	0	95	50	44	60	54	44	244	186	297	252
85	1	-15.866	-56.077	1037.643	Cerrado	67	121	0	154	37	72	39	4	35	264	163	337	257
86	1	-15.4333	-55.75	1008.715	Cerrado	67	124	4	747	38	74	40	2	39	257	156	333	247
87	1	-15.3	-55.85	990.7512	Cerrado	67	124	4	301	38	74	40	2	39	257	156	334	247
88	2	-14.6667	-52.35	1154.916	Cerrado	67	124	1	345	48	97	38	1	50	256	155	338	243
89	1	-17.3895	-64.4053	1233.809	Bolivian Yungas	57	118	5	609	41	83	33	17	35	223	122	301	192
90	1	-17.2849	-64.7567	1239.557	Bolivian Yungas	57	123	5	478	42	86	35	18	34	219	113	299	186
91	1	-17.1168	-64.7703	1223.609	Southwest Amazon moist forests	57	119	2	248	48	97	41	22	40	228	124	307	199
92	1	3.3667	-57.3486	1200.153	Guianan moist forests	66	94	1	153	58	50	74	80	17	258	206	323	219
93	1	3.3333	-57.485	1193.258	Guianan moist forests	65	94	1	191	57	48	72	80	17	258	207	323	220
94	1	5.8667	-54.9889	1540.284	Guianan freshwater swamp forests	66	80	1	1	62	69	79	75	25	266	222	323	239
95	1	-0.3	-77.133	2075.102	Napo moist forests	82	116	0	302	98	84	130	96	93	247	179	310	246
96	1	-1.372	-76.947	2013.971	Napo moist forests	81	123	0	288	100	81	131	101	96	255	182	323	252
97	1	-1.371	-76.946	2013.902	Napo moist forests	81	123	0	288	100	81	131	101	96	255	182	323	252
98	1	-2.187	-76.845	1975.223	Napo moist forests	80	125	1	255	92	76	121	94	86	254	181	324	251
99	1	-2.1048	-56.489	671.1587	Monte Alegre varzeÃƒÂ¡	76	85	0	19	58	69	96	38	23	272	226	334	301
100	1	-23.4333	-47.2	2241.393	Serra do Mar coastal forests	75	97	1	792	41	75	28	16	42	198	110	278	178
101	1	-20.5	-43.8667	2257.05	Bahia interior forests	65	117	4	915	40	89	21	6	41	197	97	278	181

102	1	-23.295	-50.077	2058.804	Alto ParanÃƒÂ¡ Atlantic forests	68	122	1	617	38	60	27	17	43	210	103	309	179
103	1	-0.3374	-77.1777	2078.172	Napo moist forests	82	116	0	302	98	85	130	96	94	245	178	308	244
104	1	4.7	-56.2136	1374.925	Guianan moist forests	67	87	1	68	66	77	88	88	21	259	212	320	215
105	1	4.4167	-56.4836	1336.473	Guianan moist forests	68	89	1	111	69	78	90	92	21	256	208	318	212
106	1	-22.7333	-63.8167	1771.583	Dry Chaco	53	128	3	422	27	62	32	3	16	225	91	337	181
107	6	-22.75	-63.8667	1774.693	Southern Andean Yungas	53	128	3	427	27	62	32	4	17	225	91	336	181
113	1	-19.937	-43.472	2251.947	Bahia interior forests	65	115	2	887	39	87	22	5	41	207	109	289	189
114	5	-14.8108	-39.6494	2350.395	Bahia interior forests	69	78	0	235	41	42	47	40	37	239	177	295	239
116	1	-0.715	-77.812	2129.104	Eastern Cordillera real montane forests	81	132	32	1288	76	65	103	67	76	182	108	254	173
117	1	-0.6913	-75.9196	1933.689	Napo moist forests	81	116	0	229	87	63	114	91	87	260	191	327	259
118	1	-14.9169	-40.6744	2250.305	Bahia coastal forests	70	92	4	914	24	36	25	12	22	221	153	284	201
119	1	-0.73	-47.85	1503.401	Amazon-Orinoco-Southern Caribbean mangroves	72	84	0	2	79	108	154	55	12	266	219	322	295
120	1	-2.5398	-77.7295	2058.985	Eastern Cordillera real montane forests	79	133	9	452	88	79	118	87	79	238	162	315	232
121	1	-24.3667	-47.2833	2317.722	Serra do Mar coastal forests	72	86	0	1017	52	81	46	29	46	214	131	293	202
122	1	-2.0381	-76.5122	1944.77	Napo moist forests	80	123	1	213	91	73	119	93	85	257	185	326	254

123	1	-14.38	-40.0742	2291.881	Bahia coastal forests	71	86	2	532	29	35	33	23	25	231	166	291	221
124	2	-23.1833	-44.1917	2428.189	Serra do Mar coastal forests	62	100	5	241	45	78	46	17	40	212	122	292	206
125	1	-21.794	-48.176	2037.212	Cerrado	70	111	0	691	39	77	25	9	44	217	121	294	183
126	1	-22.284	-48.127	2082.579	Cerrado	72	107	0	670	39	76	24	11	45	208	116	287	176
127	5	-27.057	-49.518	2448.384	Serra do Mar coastal forests	73	95	6	270	44	53	33	34	49	189	98	280	180
132	4	-21.603	-48.366	2008.393	Cerrado	69	113	0	607	39	78	25	9	43	221	124	298	188
133	1	-0.046	-77.527	2126.313	Eastern Cordillera real montane forests	81	120	20	1105	67	58	90	61	66	196	129	260	188
134	1	-2.5833	-60.7833	524.5964	JapurÃƒÂ¡-Solimoes-Negro moist forests	82	86	0	36	62	77	95	37	42	271	223	326	301
135	2	-19.883	-43.35	2258.711	Bahia interior forests	65	116	2	699	39	85	22	5	41	209	110	292	192
137	1	-21.0547	-48.4761	1954.357	Cerrado	66	116	0	609	39	81	26	8	42	227	128	301	196
138	1	-23.025	-48.8083	2105.879	Cerrado	71	113	1	836	36	63	23	14	41	204	105	292	173
139	1	-22.1625	-49.3833	1993.791	Cerrado	67	119	0	492	36	68	23	11	41	221	118	309	187
140	1	-20.9667	-48.5625	1941.12	Alto ParanÃƒÂ¡ Atlantic forests	65	117	0	610	39	81	26	7	42	229	129	303	198
141	1	-21.6692	-48.2461	2021.93	Cerrado	70	111	0	667	39	78	25	9	44	219	122	295	185
142	1	-21.6661	-48.4472	2008.518	Cerrado	69	113	0	610	39	77	25	9	43	221	124	299	187
143	1	-22.2444	-47.9583	2090.063	Cerrado	73	106	0	858	40	77	25	11	46	206	115	284	174
144	1	-23.4167	-49.9833	2075.307	Alto ParanÃƒÂ¡ Atlantic forests	69	121	1	610	38	59	27	17	43	207	100	305	177
145	1	-23.4267	-47.2433	2238.053	Serra do Mar coastal forests	75	97	1	792	41	75	28	16	42	198	110	278	178
146	2	-24.4	-47.0667	2333.972	Serra do Mar coastal forests	70	86	0	153	56	86	52	31	53	212	128	289	203

148	1	-21.4167	-50.1639	1879.81	Alto ParanÃƒÂ¡ Atlantic forests	63	122	0	452	37	73	26	10	40	232	127	316	200
149	1	-19.8583	-47.5833	1919.517	Cerrado	64	111	0	696	43	88	32	6	50	220	124	289	195
150	1	-19.5333	-40.8	2460.186	Bahia coastal forests	66	107	5	97	32	58	23	10	39	235	147	317	234
151	1	-23	-48.6833	2111.112	Cerrado	71	111	1	841	37	64	23	14	42	204	106	291	174
152	1	-21.6397	-48.2967	2016.082	Cerrado	69	112	0	637	39	78	25	9	44	220	123	296	186
153	2	-22.74	-48.4561	2101.779	Cerrado	72	110	0	553	38	68	24	13	43	210	114	294	179
155	1	-1.0495	-77.7166	2106.595	Napo moist forests	82	129	10	572	101	87	134	96	97	218	144	290	213
156	1	-0.0527	-77.083	2080.368	Napo moist forests	82	114	0	433	96	84	127	93	91	245	179	307	244
157	1	-3.1167	-71.9167	1422.124	SolimÃƒÂµes-JapurÃƒÂ¡ moist forests	80	98	0	100	76	86	105	54	73	262	207	318	292
158	3	-19.3833	-40.0667	2518.239	Bahia coastal forests	66	92	1	21	33	51	28	18	42	244	167	319	252
159	1	-27.5997	-48.4831	2550.625	Serra do Mar coastal forests			1										
160	1	-1.4083	-77.99	2122.651	Eastern Cordillera real montane forests	80	139	21	1132	80	68	107	73	78	194	115	273	185
161	1	-1.07	-46.8	1590.174	Tocantins/ Pindare moist forests	70	87	0	1	69	82	132	57	11	265	218	325	290
162	1	-20.55	-43.75	2270.031	Bahia interior forests	66	115	3	933	39	88	21	6	40	196	97	278	181
163	3	-11.5	-60.6667	484.5113	Madeira-TapajÃƒÂ³s moist forests	73	119	4	400	50	89	53	2	48	254	167	334	266
164	2	-11.5833	-55.1333	700.8149	Mato Grosso seasonal forests	73	130	3	396	59	100	54	0	58	253	156	341	262
165	1	-15.6667	-38.9333	2454.429	Cerrado	67	73	0		51	54	64	58	53	244	186	298	252
166	2	-19.7822	-52.991	1570.79	Cerrado	61	119	1	488	40	80	31	9	44	242	140	317	219

168	1	-4.5756	-55.4037	563.284	Bahia coastal forests	79	99	1	119	55	72	84	20	30	266	205	331	307
171	1	-1.766	-55.866	741.0156	Napo moist forests	76	89	0	15	55	70	97	30	22	269	221	332	296
172	1	-0.892	-75.446	1876.495	Bahia coastal forests	80	116	0	196	83	57	109	90	84	265	195	332	264
173	4	-14.4333	-39.1836	2385.143	Bahia coastal forests	68	72	0	112	47	41	59	51	40	245	186	299	251
177	1	-15.2031	-39.5294	2376.848	Serra do Mar coastal forests	69	78	0	306	43	47	50	43	41	239	178	296	241
178	1	-27.2139	-49.1	2483.435	Eastern Cordillera real montane forests	72	86	7	482	44	55	33	33	47	191	106	278	184
179	1	-2.921	-78.407	2121.46	Cerrado	77	153	40	1424	52	49	71	45	48	179	92	267	165
180	2	-19.8667	-47.5667	1921.403	Cerrado	64	111	0	696	43	88	32	6	50	220	124	289	195
182	1	-0.7	-77.729	2121.01	Napo moist forests	81	129	22	1183	85	73	115	79	83	198	126	269	191
183	1	-0.497	-76.373	1988.537	Southwest Amazon moist forests	82	115	0	254	92	71	120	94	91	259	191	324	258
184	1	-10.2333	-72.0167	1389.733	Monte Alegre varzeÃƒÂ¡	74	107	0	358	65	96	68	28	72	253	177	316	262
185	1	-2.1	-56.4833	671.9473	Serra do Mar coastal forests	76	85	0	19	58	69	96	38	23	272	226	334	301
186	1	-25.0833	-47.9333	2343.693	Bahia interior forests	71	83	1	2	53	83	49	31	46	206	127	285	197
187	1	-19.519	-41.016	2439.977	Bahia interior forests	66	110	4	112	32	60	23	8	39	236	145	319	233
188	1	-14.9969	-39.9314	2328.487	Bahia interior forests	69	83	1	283	35	41	39	31	32	234	171	293	229
189	1	-21.75	-43.35	2386.081	Serra do Mar coastal forests	69	107	0	758	41	92	25	6	37	207	111	292	199
190	1	-26.027	-48.855	2381.623	TapajÃƒÂ³s-Xingu moist forests	76	89	4	164	46	68	37	30	46	193	109	278	184

191	2	-3.4	-51.8833	969.0111	TapajÃƒÂ³s-Xingu moist forests	81	97	0	26	57	88	106	28	19	265	206	326	295
193	1	6.4	-58.6197	1510.691	Napo moist forests	64	79	0	1	71	76	66	94	40	261	216	316	272
194	1	-0.653	-76.453	1990.31	Napo moist forests	82	117	0	270	94	73	122	96	92	258	189	324	257
195	1	-0.7166	-77.3666	2082.575	Guianan Highlands moist forests	82	122	6	478	98	83	130	96	94	235	165	302	233
196	1	5.2164	-59	1377.087	Napo moist forests	62	90	0	348	93	96	100	124	42	257	206	316	240
197	1	-2.057	-76.796	1974.25	Guianan moist forests	80	125	1	266	93	76	122	95	87	255	182	325	252
198	1	4.285	-58.5094	1279.045	Guianan Highlands moist forests	61	91	1	46	70	61	77	106	27	260	211	322	225
199	1	6.1833	-61.4333	1493.128	Llanos	60	100	0	638	55	31	49	79	53	241	184	302	235
200	1	7.4833	-62.5333	1654.221	Guianan piedmont and lowland moist forests	56	98	0	526	35	16	22	62	33	255	198	317	251
201	1	7.3833	-62.55	1643.708	Bolivian Yungas	57	98	0	507	36	16	23	65	34	254	198	316	249
202	1	-15.7667	-67.6	1275.179	Bolivian Yungas	57	112	7	985	38	68	30	8	36	216	130	285	164
203	1	-14.4246	-67.9207	1196.77	Bolivian Yungas	60	96	5	577	50	83	48	19	41	237	162	300	214
204	2	-14.0654	-68.847	1250.041	Bolivian Yungas	60	102	26	1036	56	97	53	22	55	207	134	272	173
206	2	-13.6324	-68.741	1212.801	Bolivian Yungas	62	99	3	471	66	109	62	30	61	239	165	302	219
208	1	-13.6323	-68.7409	1212.786	Beni savanna	62	99	3	471	66	109	62	30	61	239	165	302	219
209	1	-12.6801	-68.7118	1152.948	Bolivian Yungas	64	107	0	195	58	98	60	21	49	254	175	324	241
210	1	-13.7667	-68.4167	1193	Bolivian Yungas	62	98	2	1005	60	100	58	27	54	239	165	303	220
211	1	-13.7167	-68.2167	1172.361	Bolivian Yungas	62	98	0	370	58	96	56	25	50	245	171	309	230
212	2	-13.5878	-68.6424	1201.23	Bolivian Yungas	62	99	2	501	64	107	61	29	58	242	168	306	224
214	1	-15.7833	-68.6667	1357.123	Napo moist forests	57	136	138	3207	20	44	16	1	15	93	-10	178	66

215	1	-2.975	-77.802	2054.711	PetÃƒÂ©n-Veracruz moist forests	78	134	11	505	77	70	102	78	66	238	162	316	229
216	1	16.9716	-91.5857	4407.72	Napo moist forests	60	126	1	900	61	29	27	93	92	238	150	329	235
217	1	0.052	-76.882	2064.297	Madeira-TapajÃƒÂ³s moist forests	82	111	0	401	96	82	125	93	91	250	186	312	251
218	1	-1.8167	-56.1167	720.517	ParanÃƒÂ¡ flooded savanna	76	88	0	28	56	69	96	33	22	271	222	333	298
219	3	-27.065	-58.704	2199.93	ParanÃƒÂ¡ flooded savanna	44	116	1	66	37	52	55	16	38	215	104	332	191
222	1	-0.3998	-76.616	2017.642	Napo moist forests	82	114	0	271	95	76	124	95	92	258	190	322	257
223	2	-0.399	-76.6166	2017.737	Napo moist forests	82	114	0	271	95	76	124	95	92	258	190	322	257
225	1	-12.1281	-61.8506	590.1519	Guianan moist forests	71	117	5	400	44	82	46	2	42	256	167	334	261
226	1	2.6833	-54.5181	1239.469	Guianan moist forests	74	90	2	406	63	71	99	66	17	250	202	315	254
227	1	5.1333	-55.4658	1446.103	Napo moist forests	68	89	0	47	62	69	83	78	23	265	215	327	223
228	1	-0.25	-76.425	2004.398	Xingu-Tocantins-Araguaia moist forests	81	113	0	267	92	72	121	93	91	258	192	323	258
229	1	-5.3667	-49.1167	1194.729	Amazon-Orinoco-Southern Caribbean mangroves	79	102	0	53	56	94	97	6	37	268	204	336	291
230	1	-0.78	-47.45	1539.98	Guianan moist forests	75	85	0	1	76	95	152	57	9	265	218	323	292
231	1	4.75	-54.5039	1445.876	Bahia coastal forests	68	90	1	57	68	77	89	78	24	258	209	322	226

232	4	-14.5125	-39.2003	2386.059	Bahia coastal forests	68	72	0	223	48	42	59	52	41	245	186	298	251
233	1	-15.3722	-39.59	2377.071	Uatuma-Trombetas moist forests	69	80	0	213	41	47	48	41	40	239	177	297	240
234	1	0.4337	-61.6882	872.4793	Guianan freshwater swamp forests	73	96	0	52	59	45	77	76	38	267	215	326	285
235	1	5.8167	-55.4656	1517.648	Napo moist forests	66	78	0	8	59	64	69	75	27	268	224	325	237
236	1	-2.0667	-76.95	1990.291	Uatuma-Trombetas moist forests	80	126	2	281	95	78	125	96	88	252	179	323	249
237	1	-1.4667	-56.7833	715.9944	Napo moist forests	77	86	1	65	56	66	94	42	20	271	224	333	296
238	1	-0.031	-76.32	2003.261	Alto ParanÃƒÂ¡ Atlantic forests	81	111	0	261	91	71	118	91	90	258	193	322	259
239	3	-26.5667	-54.7833	2205.674	Alto ParanÃƒÂ¡ Atlantic forests	55	121	2	149	46	52	53	32	55	208	97	319	197
242	2	-19.2748	-57.5719	1355.106	Pantanal	61	107	0	306	29	56	27	10	28	258	165	337	245
244	1	-1.166	-48.4635	1420.37	Pantepui	74	87	0		81	119	143	50	23	267	219	322	299
245	1	5.0821	-59.8327	1359.704	Napo moist forests	63	98	2	1512	75	65	82	105	43	234	179	298	219
246	1	-2.059	-76.96	1991.606	Cerrado	80	126	2	281	95	78	125	96	88	252	179	323	249
247	1	-14.8705	-55.7887	951.2538	Madeira-TapajÃƒÂ³s moist forests	67	126	3	267	42	79	42	1	44	257	155	337	247
248	1	-3.1667	-55.6703	636.656	Serra do Mar coastal forests	77	91	0	80	56	67	92	30	23	268	214	330	302
249	1	-23.3625	-44.825	2396.442	Eastern Cordillera real montane forests	74	90	12	130	52	92	51	23	48	199	111	272	197

250	1	-1.663	-78.0702	2122.56	Southwest Amazon moist forests	79	145	33	2128	65	55	88	57	65	176	94	258	165
251	1	-10.2263	-65.3767	702.5255	Southwest Amazon moist forests	76	104	2	122	46	85	55	3	42	265	192	336	280
252	1	-10.2262	-65.3762	702.4719	Southwest Amazon moist forests	76	104	2	122	46	85	55	3	42	265	192	336	280
253	1	-9.7	-65.3833	677.9375	Madeira-TapajÃƒÂ³s moist forests	77	103	1	121	50	89	60	5	46	266	193	335	285
254	1	-9.6852	-65.4012	679.0904	Southwest Amazon moist forests	77	103	1	139	50	89	61	5	47	266	193	335	286
255	1	-10.1792	-65.3562	698.114	Madeira-TapajÃƒÂ³s moist forests	76	104	2	121	47	86	56	4	42	265	192	336	281
256	1	-9.6862	-65.4021	679.2248	Southwest Amazon moist forests	77	103	1	139	50	89	61	5	47	266	193	335	286
257	1	-12.3132	-68.6689	1128.631	Southwest Amazon moist forests	66	109	0	200	54	92	58	16	46	254	172	326	242
258	1	-12.1966	-68.6345	1119.117	Southwest Amazon moist forests	66	109	0	200	53	90	58	14	46	254	172	327	243
259	1	-12.4667	-68.6	1130.513	Southwest Amazon moist forests	65	107	0	185	55	93	58	17	47	254	174	325	243
260	1	-11.68	-68.37	1067.004	Southwest Amazon moist forests	68	110	0	183	50	85	59	11	47	257	173	329	250

261	1	-12.0002	-68.8756	1132.166	Southwest Amazon moist forests	66	111	0	201	54	90	60	14	49	252	169	325	240
262	1	-11.4384	-69.2332	1140.987	Southwest Amazon moist forests	68	113	0	200	51	82	62	10	52	249	162	322	236
263	1	-11.0232	-68.7602	1075.562	Southwest Amazon moist forests	70	111	0	257	51	84	64	8	54	256	169	327	253
264	1	-11.08	-68.78	1079.958	Tocantins/ Pindare moist forests	70	111	0	289	51	84	64	8	54	255	169	327	252
265	1	-1.07	-46.79	1591.177	Bahia coastal forests	70	87	0	1	69	82	132	57	11	265	218	325	290
266	1	-15.4164	-39.6625	2371.451	Cerrado	69	81	0	185	39	47	45	38	39	238	175	297	237
267	1	-10.176	-48.867	1242.05	Amazon-Orinoco-Southern Caribbean mangroves	68	121	1	304	47	81	53	1	58	265	175	350	262
268	1	5.8	-56.2044	1492.137	Serra do Mar coastal forests	64	73	0	3	49	58	58	71	20	268	227	321	235
269	1	-23.7667	-46.3333	2326.163	Bahia interior forests	75	88	2	682	49	86	42	22	48	201	116	276	191
270	2	-19.95	-43.9083	2216.266	Madeira-TapajÃƒÂ³s moist forests	64	117	4	979	40	92	21	5	41	205	104	284	184
271	1	-10.783	-65.339	729.826	Cerrado	74	105	1	130	43	82	50	1	36	266	192	339	277
272	1	-20.317	-46.521	2034.47	Cerrado	67	115	2	947	42	91	30	7	45	208	103	280	188
273	1	-17.9122	-52.9839	1393.004	Cerrado	63	123	10	823	42	86	33	5	43	236	133	315	216
274	1	-22.5833	-57.3667	1719.852	Napo moist forests	53	109	1	327	37	49	41	13	44	243	144	335	218
275	1	-0.676	-76.355	1979.238	Napo moist forests	82	117	0	263	92	71	120	95	91	259	190	325	258
276	1	-0.654	-76.451	1990.063	Napo moist forests	82	117	0	270	94	73	122	96	92	258	189	324	257

277	1	-0.674	-76.398	1983.764	Napo moist forests	82	117	0	263	92	71	120	95	91	259	190	325	258
278	1	-0.675	-76.338	1977.523	Napo moist forests	82	117	0	262	92	70	119	94	91	259	190	325	258
279	1	-0.457	-76.591	2012.671	Napo moist forests	82	115	0	268	94	75	123	95	92	258	190	323	257
280	1	-0.6605	-75.9604	1939.184	Alto ParanÃƒÂ¡ Atlantic forests	81	116	0	232	88	64	114	92	88	260	191	327	259
281	6	-27.1667	-55	2264.848	Alto ParanÃƒÂ¡ Atlantic forests	53	119	1	418	49	51	54	35	60	207	97	317	188
287	1	-0.7211	-77.423	2088.277	Napo moist forests	82	123	8	550	96	82	128	93	92	230	159	297	227
288	1	-0.2786	-77.348	2098.188	Napo moist forests	82	118	5	569	92	80	122	88	88	232	164	296	229
289	1	-0.7944	-77.4308	2086.258	Peruvian Yungas	82	124	7	532	98	83	130	95	94	231	160	299	228
290	1	-10.0694	-75.5283	1764.215	Serra do Mar coastal forests	74	131	37	856	38	57	35	16	46	188	103	263	169
291	1	-23.45	-46.6417	2279.058	Cerrado	75	94	3	773	43	80	31	16	43	196	108	273	181
292	1	-22.8833	-48.4333	2115.884	Uatuma-Trombetas moist forests	72	109	0	630	38	67	24	14	42	208	112	293	178
293	2	-1.4833	-56.3833	735.9056	Uatuma-Trombetas moist forests	76	87	1	27	56	66	95	38	21	271	223	333	296
295	1	-7.195	-47.2353	1382.755	Cerrado	71	111	1	311	45	83	61	2	40	264	186	347	255
296	1	-18.25	-52.8833	1430.265	Eastern Cordillera real montane forests	63	123	9	769	42	86	32	6	43	235	132	314	214
297	1	-1.628	-77.909	2106.616	JuruÃƒÂ¡-Purus moist forests	80	138	18	1462	85	73	115	79	83	203	124	281	195
298	1	-4.8443	-65.3436	671.8254	Monte Alegre varzeÃƒÂ¡	82	92	0	80	66	90	95	29	59	267	210	323	306
299	2	-8.75	-63.9	487.4823	Monte Alegre varzeÃƒÂ¡	79	101	0	81	58	96	73	8	56	264	190	331	290

301	1	-0.432	-77.049	2060.985	Napo moist forests	82	116	0	300	98	83	129	97	94	250	182	314	249
302	1	-1.8142	-76.7247	1974.878	Napo moist forests	81	124	0	256	95	76	125	97	90	256	183	326	254
303	1	-0.6479	-76.4604	1991.285	Napo moist forests	82	116	0	270	93	73	122	96	92	258	189	324	257
304	1	-1.0779	-76.181	1945.016	Napo moist forests	81	119	0	232	90	68	118	95	89	260	189	328	258
305	1	-0.7406	-76.166	1957.053	Peruvian Yungas	82	117	0	243	90	67	117	93	89	259	190	326	258
306	1	-10.1489	-75.5153	1764.213	Eastern Cordillera real montane forests	74	131	38	925	39	57	35	16	46	186	100	260	167
307	1	-0.1133	-77.441	2114.636	Napo moist forests	81	119	13	857	79	70	107	74	77	214	147	278	209
308	1	-0.465	-76.979	2052.396	Eastern Cordillera real montane forests	82	116	0	298	98	82	129	97	94	252	184	316	251
309	1	0.2	-77.482	2132.151	Napo moist forests	81	116	16	789	67	60	91	61	66	198	132	260	190
310	2	-1.05	-77.633	2097.801	Napo moist forests	82	128	6	464	104	88	137	100	99	228	154	298	224
312	1	-2.926	-77.726	2047.821	Madeira-TapajÃƒÂ³s moist forests	78	132	8	305	80	73	107	82	68	243	168	320	235
313	1	-10.1934	-61.8779	403.9025	Bahia coastal forests	76	110	4	200	53	93	64	3	52	257	176	331	275
314	6	-14.9589	-40.5492	2264.551	Bahia coastal forests	70	90	3	778	26	37	27	15	24	224	157	287	208
320	10	10.45	-75.3667	2609.477	Guajira-Barranquilla xeric scrub	55	93	1	38	34	4	22	40	69	272	213	330	291
330	2	-25.8809	-52.5366	2203.417	Araucaria moist forests	68	115	5	625	49	53	44	40	58	192	88	293	174
332	1	-9.24	-36.423	2580.032	Napo moist forests	66	91	1	457	30	15	51	55	11	241	180	311	231

333	1	-0.259	-75.89	1949.3	Napo moist forests	81	112	0	236	87	62	113	91	88	260	193	325	260
334	1	-0.0017	-76.175	1989.807	Napo moist forests	81	111	0	255	89	68	116	90	90	259	193	322	259
335	1	-0.0022	-76.14	1986.225	Napo moist forests	81	110	0	259	89	67	116	91	89	259	193	322	260
336	1	-0.087	-76.1414	1982.569	Caatinga	81	111	0	254	89	67	116	91	89	259	193	323	260
337	2	-3.948	-38.624	2368.502	Caatinga	65	77	0	126	34	33	89	18	4	267	214	318	266
339	1	-22.45	-42.65	2491.226	Serra do Mar coastal forests	69	90	2	383	33	61	27	9	30	209	129	287	205
340	1	-22.45	-42.7667	2482.032	Iquitos varzeÃƒÂ¡	69	91	2	120	33	63	28	9	30	209	128	287	204
341	1	-8.9633	-72.7342	1443.425	Southwest Amazon moist forests	78	106	0	200	61	84	69	25	68	261	190	325	277
342	1	-7.9552	-72.0765	1362.075	Napo moist forests	81	105	0	200	60	85	75	21	66	263	193	325	288
343	1	-0.5861	-75.2413	1868.653	Napo moist forests	80	113	0	197	82	55	108	90	83	266	198	332	266
344	1	-0.207	-76.236	1986.921	Bahia interior forests	81	113	0	257	90	69	118	92	90	259	192	324	259
345	1	-20.086	-43.79	2235.238	Bahia coastal forests	65	115	5	872	40	91	20	5	41	200	103	279	180
346	1	-14.7322	-39.2039	2393.143	Eastern Cordillera real montane forests	67	71	0	156	50	44	60	54	44	244	186	297	252
347	1	-4.1082	-78.9634	2155.047	Chiapas Depression dry forests	73	164	36	1727	29	31	43	17	26	170	75	267	148
348	1	16.8336	-93.0671	4529.949	Eastern Cordillera real montane forests	63	134	3	1330	34	7	10	65	40	221	127	314	202
349	1	-0.695	-77.73	2121.306	Cerrado	81	129	23	1312	82	70	111	75	80	196	123	266	189
350	1	-16.7333	-42.5667	2145.546	Cerrado	66	115	1	482	24	52	14	1	33	234	140	312	206
351	1	-16.8	-42.6667	2139.498	Napo moist forests	66	116	1	812	25	54	14	1	33	232	137	310	205

352	1	-0.509	-76.387	1989.475	Napo moist forests	82	115	0	258	92	71	120	94	91	259	190	324	258
353	1	-0.493	-76.078	1958.371	Napo moist forests	81	115	0	237	89	66	116	92	89	260	192	325	259
354	1	-0.679	-75.65	1906.483	Napo moist forests	81	116	0	209	85	59	111	90	86	262	192	328	261
355	1	-0.43	-76.784	2033.697	Western Ecuador moist forests	82	115	0	284	97	79	126	96	93	256	189	320	256
356	1	-0.6036	-79.3961	2299.355	Napo moist forests	81	121	12	153	68	120	128	24	27	228	158	295	218
357	1	-0.7102	-76.344	1976.697	Guianan moist forests	82	117	0	256	92	70	119	95	91	259	190	325	258
358	1	5.6333	-53.8375	1565.338	Guianan moist forests	63	79	1	9	65	77	94	61	18	264	222	321	261
359	1	4.3333	-57.7103	1296.929	Guianan moist forests	63	89	1	107	66	63	77	95	24	260	211	321	219
360	1	4.5333	-57.7025	1318.858	Araucaria moist forests	63	88	1	191	68	65	78	96	26	260	212	320	220
361	1	-25.35	-48.8833	2316.108	Serra do Mar coastal forests	76	94	5	160	43	67	35	28	44	184	97	268	172
362	1	-23.4222	-47.1686	2242.448	Campos Rupestres montane savanna	75	97	2	794	41	75	28	16	42	198	110	278	178
363	1	-20.1333	-43.5	2262.576	Napo moist forests	65	115	3	1499	39	86	21	5	40	203	104	285	186
364	1	-1.0489	-77.532	2087.245	Eastern Cordillera real montane forests	82	126	6	494	102	87	135	99	98	232	159	301	228
365	1	-2.1541	-77.7272	2070.307	Alto ParanÃƒÂ¡ Atlantic forests	80	133	9	725	96	84	129	93	90	235	157	310	230
366	3	-27.091	-54.977	2257.242	Alto ParanÃƒÂ¡ Atlantic forests	54	119	1	205	48	51	53	34	59	208	97	317	190
369	1	-0.0266	-77.1066	2083.908	Napo moist forests	82	113	1	526	96	85	127	92	91	243	177	304	242

370	1	-2.7612	-78.2747	2111.43	Napo moist forests	78	149	34	874	62	57	84	56	58	195	112	281	183
371	1	-0.254	-76.425	2004.225	Napo moist forests	81	113	0	267	92	72	121	93	91	258	192	323	258
372	1	-0.2499	-76.4166	2003.541	Napo moist forests	81	113	0	272	92	73	120	93	91	258	192	322	258
373	1	-0.249	-76.416	2003.519	Tocantins/ Pindare moist forests	81	113	0	272	92	73	120	93	91	258	192	322	258
374	16	-1.36	-48.24	1432.368	Bahia coastal forests	75	90	0	11	79	114	137	50	25	266	217	323	297
375	1	-15.4553	-39.6206	2377.16	Bahia interior forests	69	81	0	152	40	48	47	39	40	239	176	297	239
376	2	-19.95	-43.4	2258.869	Bahia interior forests	65	116	2	777	39	84	22	5	40	208	109	291	191
378	1	0.082	-76.99	2076.653	Napo moist forests	82	112	1	456	96	84	125	92	91	247	182	308	246
379	1	0.05	-76.982	2074.441	Madeira-TapajÃƒÂ³s moist forests	82	112	0	375	96	83	126	93	91	247	182	309	247
380	1	-10.6667	-62.5667	491.3218	Chiquitano dry forests	75	111	5	200	50	89	57	2	47	257	176	332	271
381	1	-17.9404	-63.1571	1242.729	Chiquitano dry forests	57	113	0	494	31	58	28	13	28	244	150	326	214
382	1	-17.9103	-63.1591	1239.62	Dry Chaco	57	113	0	494	31	58	28	13	28	244	150	326	214
383	1	-18.1667	-60.1333	1212.413	Dry Chaco	61	130	6	612	30	56	27	5	28	248	142	336	216
384	1	-18.4753	-62.0841	1271.17	Dry Chaco	57	127	0	332	22	39	20	5	19	250	145	340	214
385	1	-18.1136	-63.6082	1276.172	Dry Chaco	57	120	6	1360	24	45	21	7	19	211	113	292	178
386	1	-18.1038	-63.5977	1274.777	Madeira-TapajÃƒÂ³s moist forests	57	119	6	1318	25	47	22	7	20	215	118	296	182
387	1	-15.0867	-62.7738	931.0919	Madeira-TapajÃƒÂ³s moist forests	62	119	0	248	35	67	27	7	30	255	161	337	242
388	1	-15.06	-62.75	927.4166	Bolivian Yungas	62	119	0	248	35	67	27	7	30	255	161	337	242

389	1	-17.5833	-63.8	1228.325	Chiquitano dry forests	57	116	5	419	32	64	25	11	28	219	124	297	190
390	1	-16.25	-62.0667	1030.789	Tocantins/ Pindare moist forests	59	127	0	402	30	58	22	8	27	245	144	331	222
391	1	-1.75	-47.65	1472.6	Bahia coastal forests	75	94	0	31	72	98	127	48	22	265	213	326	294
392	4	-14.7086	-39.1828	2394.492	Bahia coastal forests	67	71	0	156	50	44	60	54	44	244	186	297	252
396	2	-22.0167	-47.8833	2075.481	Bahia coastal forests	73	108	0	837	40	78	25	10	46	209	115	286	177
397	1	-15.2064	-39.4078	2389.284	Uatuma-Trombetas moist forests	68	77	0	137	45	47	53	46	43	240	179	297	244
398	1	0.95	-59.9833	903.1129	Cerrado	68	94	1	208	51	35	67	74	24	266	214	327	272
399	1	-14.7	-47.5167	1572.313	Napo moist forests	64	109	2	1062	43	90	38	2	46	233	147	309	198
400	1	-1.7307	-77.484	2058.108	Napo moist forests	81	129	1	409	105	89	139	102	99	243	168	315	240
401	1	-1.746	-77.491	2058.337	Eastern Cordillera real montane forests	81	129	1	409	105	89	139	102	99	243	168	315	240
402	1	-2.078	-78.2039	2123.578	Eastern Cordillera real montane forests	78	155	56	2340	43	37	60	33	46	144	60	233	131
403	1	-3.696	-78.4914	2112.022	Bahia coastal forests	75	150	25	1020	46	44	60	41	42	201	118	290	183
405	1	1.7	-61.75	1010.284	Caatinga	65	101	1	712	56	28	68	92	38	256	201	317	265
406	7	-4.25	-39.0833	2312.731	Caatinga	68	86	0	261	25	26	65	11	2	263	206	322	252
413	1	-4.2333	-38.9167	2331.285	Caatinga	67	83	0	789	28	28	71	13	3	263	207	320	255
414	2	-3.9	-38.7167	2359.259	Caatinga	67	76	0	480	34	34	90	19	4	265	213	316	266
416	1	-8.3284	-36.1483	2606.482	Eastern Cordillera real montane forests	67	93	2	577	26	14	48	42	12	235	171	304	224

417	1	-1.481	-78.036	2125.032	Napo moist forests	80	141	26	1550	72	62	98	65	72	185	106	265	175
418	1	-1.018	-76.891	2021.329	Eastern Cordillera real montane forests	82	121	0	291	99	80	131	101	96	255	184	322	254
419	1	-1.493	-78.0511	2126.224	Napo moist forests	80	143	30	2355	65	56	89	58	66	177	96	258	165
420	1	-0.1999	-76.6333	2027.913	Guianan moist forests	82	112	0	274	94	77	123	94	91	257	191	320	257
421	1	5.05	-53.0458	1547.46	Serra do Mar coastal forests	60	79	1	56	81	104	121	67	19	260	216	318	279
422	1	-23.6083	-47.1167	2261.833	Caatinga Enclaves moist forests	75	95	3	914	42	75	29	17	42	194	107	273	176
423	1	-4.2456	-38.9617	2326.138	Serra do Mar coastal forests	67	84	0	933	27	28	70	13	3	263	207	321	255
424	1	-26.05	-48.7417	2389.658	Eastern Cordillera real montane forests	75	84	2	60	47	72	40	30	46	200	119	284	192
425	1	-2.459	-78.169	2108.501	Southern Atlantic mangroves	78	151	44	1049	56	50	77	49	55	176	93	263	164
426	2	-25.2222	-48.4583	2327.091	Southern Atlantic mangroves	76	86	3	75	48	77	40	29	43	194	115	277	183
428	1	-0.977	-75.427	1870.99	Napo moist forests	80	117	0	194	84	58	109	90	84	265	195	332	264
429	1	-0.49	-76.772	2029.976	Napo moist forests	82	115	0	287	97	79	127	97	93	256	189	321	256
430	1	-0.118	-76.355	2002.985	Napo moist forests	81	112	0	267	91	72	119	92	90	258	192	322	258
431	1	-1.2083	-76.7167	1995.88	Napo moist forests	81	122	0	271	98	78	128	100	95	257	184	325	255
432	1	-1.399	-76.616	1978.224	Mato Grosso seasonal forests	81	122	0	257	96	76	126	99	93	258	185	326	256
433	1	-11.4462	-55.0494	697.3253	Madeira-TapajÃƒÂ³s moist forests	74	129	2	300	59	100	55	0	59	253	157	340	263

434	1	-4.4667	-56.3003	488.5425	Uatuma-Trombetas moist forests	79	95	0	48	57	77	86	22	30	269	211	331	309
435	4	-1.8992	-59.4783	588.5121	Uatuma-Trombetas moist forests	80	86	1	67	58	76	91	42	28	268	221	327	293
438	1	-9.3311	-64.7344	596.3888	Mato Grosso seasonal forests	78	102	2	97	53	92	65	6	50	264	191	333	286
439	1	-10.2128	-48.3603	1296.881	Cerrado	67	120	2	202	46	79	51	1	56	264	174	350	256
440	1	-12.2296	-48.3884	1364.675	Cerrado	64	121	0	255	44	90	40	1	46	262	167	350	245
441	1	-18.6739	-51.8806	1527.986	Mato Grosso seasonal forests	61	123	1	577	42	89	33	7	45	241	141	319	218
442	1	-10.3	-48.35	1300.324	Mato Grosso seasonal forests	67	120	2	215	46	79	50	1	57	264	173	350	255
443	2	-9.75	-48.4	1281.265	Mato Grosso seasonal forests	68	121	0	157	46	80	54	1	56	266	176	352	262
445	1	-14.9833	-55.7333	965.0768	Cerrado	67	126	4	299	41	78	42	1	43	256	154	335	246
446	5	-14.8667	-55.8	950.3196	Cerrado	67	126	3	277	42	79	42	1	44	257	156	338	248
451	1	-12.1432	-48.466	1353.183	Alto ParanÃƒÂ¡ Atlantic forests	65	121	0	250	45	91	41	1	47	262	168	349	246
452	1	-22.1833	-52.7167	1820.518	Cerrado	65	108	0	307	39	60	32	11	57	225	131	305	199
453	1	-20.75	-51.6667	1732.778	Cerrado	61	119	0	302	36	71	28	9	42	244	139	323	216
454	1	-16.35	-46.9	1726.118	Tocantins/ Pindare moist forests	64	113	0	608	40	84	29	4	46	231	136	305	198
455	1	-1.44	-48.67	1385.832	Alto ParanÃƒÂ¡ Atlantic forests	75	89	0	1	79	119	135	48	27	267	218	323	300
456	1	-27.0833	-54.9333	2257.452	Serra do Mar coastal forests	54	119	1	243	48	51	54	34	58	207	97	317	190
457	1	-26.9222	-49.1	2455.186	Guianan Highlands moist forests	73	89	4	159	45	57	34	33	48	197	110	285	189
458	1	2.7333	-64.2839	1209.542	Guianan savanna	70	110	6	805	81	36	89	125	67	229	170	295	239

459	1	5.7667	-61.4069	1447.057	Guianan savanna	63	101	1	1169	65	27	64	93	68	204	144	265	192
460	1	5	-61.1333	1359.245	La Costa xeric shrublands	66	107	1	892	60	28	67	89	55	211	151	275	197
461	1	10.05	-68.1392	2123.34	Cordillera La Costa montane forests	65	117	1	594	35	3	26	66	45	240	167	318	232
462	1	10.4167	-68.0028	2153.32	La Costa xeric shrublands	66	109	1	117	31	7	22	52	40	246	175	312	240
463	1	10.4167	-66.8703	2103.107	La Costa xeric shrublands	65	98	3	1147	28	8	16	45	39	220	153	278	209
464	1	10.3333	-66.9508	2097.951	La Costa xeric shrublands	65	100	1	940	29	7	16	49	40	220	151	280	209
465	1	10.3333	-66.9528	2098.035	La Costa xeric shrublands	65	100	1	940	29	7	16	49	40	220	151	280	209
466	1	10.4167	-66.9667	2107.136	Cordillera La Costa montane forests	65	98	2	1218	28	8	16	46	40	220	152	278	209
467	1	10.4833	-66.8306	2108.283	Cordillera La Costa montane forests	64	97	4	882	28	9	16	43	39	218	152	275	207
468	3	9.9833	-68.6067	2139.995	Cordillera La Costa montane forests	66	111	0	1430	37	4	29	74	43	247	179	321	242
471	1	9.85	-72.7833	2376.412	Bahia interior forests	59	110	2	157	45	11	52	38	86	248	179	315	239
475	1	-0.568	-77.594	2112.064	Cordillera La Costa montane forests	81	125	17	1821	84	72	112	78	81	208	138	277	203
476	1	10.69427	-62.6325	2005.861	Eastern Cordillera real montane forests	55	92	1	604	36	21	14	55	50	253	193	307	263
477	1	-2.248	-78.205	2118.548	Napo moist forests	78	157	60	2284	42	36	60	32	44	143	58	233	130

478	1	-1.23	-77.689	2097.15	Napo moist forests	82	128	2	478	111	95	146	107	105	234	160	305	230
479	1	-2.975	-77.795	2053.956	Serra do Mar coastal forests	78	133	9	468	79	72	104	80	67	242	166	319	233
481	1	-1.202	-46.143	1650.365	Araucaria moist forests	75	82	0		66	74	133	56	7	265	217	320	289
482	2	-25.3583	-48.8833	2316.889	Araucaria moist forests	76	94	5	160	43	67	35	28	44	184	97	268	172
484	1	3.9333	-56.7192	1277.962	Eastern Cordillera real montane forests	68	93	2	346	69	74	91	92	21	245	195	310	203
485	1	-0.687	-77.601	2108.155	Magdalena Valley montane forests	81	127	18	1489	86	74	116	81	84	207	135	276	201
486	1	5.4665	-74.3384	2142.463	Napo moist forests	66	95	0	1204	65	34	91	44	99	217	166	270	215
487	1	-0.564	-76.014	1948.774	Tocantins/ Pindare moist forests	81	115	0	234	88	65	115	92	88	260	191	326	259
488	1	-1.9607	-48.1898	1408.299	Alto ParanÃƒÂ¡ Atlantic forests	76	95	0	57	73	107	123	44	29	266	213	326	298
489	1	-21.685	-51.073	1853.253	Alto ParanÃƒÂ¡ Atlantic forests	64	117	0	479	37	68	28	11	43	229	127	312	197
490	1	-21.4333	-51.0139	1832.803	Cerrado	63	119	0	303	37	70	27	10	42	233	130	315	201
491	1	-20.4333	-52.8833	1639.622	Cerrado	62	117	1	309	39	75	31	9	47	240	139	314	216
492	1	-22.469	-48.988	2045.135	Cerrado	69	115	0	610	37	68	23	12	42	215	114	302	182
493	1	-22.4667	-48.9833	2045.214	MarajÃƒÂ³ varzeÃƒÂ¡	69	115	0	610	37	68	23	12	42	215	114	302	182
494	1	-1.523	-52.582	1014.633	Madeira-TapajÃƒÂ³s moist forests	77	90	0	4	63	72	117	53	15	269	220	330	299
495	1	-9.876	-56.086	499.845	TapajÃƒÂ³s-Xingu moist forests	77	124	1	292	62	101	68	2	61	255	168	340	276
496	1	-3.2033	-52.2064	946.9955	Cerrado	81	96	0	41	57	82	107	32	19	265	207	326	295

497	1	-21.026	-47.374	2027.847	Cerrado	71	104	0	928	42	88	27	8	47	211	117	279	181
498	1	-21.025	-47.3833	2027.108	Guianan Highlands moist forests	71	104	0	928	42	88	27	8	47	211	117	279	181
499	1	2.8333	-63.6333	1191.613	Purus varzeÃƒÂ¡	69	109	6	902	78	32	83	126	64	226	167	293	235
500	2	-3.1667	-64.85	720.5489	Purus varzeÃƒÂ¡	82	90	0	44	68	83	95	44	55	268	216	322	306
502	1	2.053	-50.793	1428.727	Serra do Mar coastal forests	69	73	0	1	82	113	142	68	10	263	222	319	296
503	1	-22.7167	-46.7667	2209.033	Serra do Mar coastal forests	74	103	3	866	42	82	28	13	44	199	103	277	176
504	1	-22.701	-46.764	2207.905	Tocantins/ Pindare moist forests	74	103	3	866	42	82	28	13	44	199	103	277	176
505	1	-1.3667	-48.3833	1417.86	Serra do Mar coastal forests	75	89	0	12	79	116	137	49	26	266	218	323	298
506	1	-23.439	-47.061	2250.815	Serra do Mar coastal forests	75	97	2	816	41	76	28	16	42	197	110	277	178
507	1	-23.4333	-47.0667	2249.957	Alto ParanÃƒÂ¡ Atlantic forests	75	97	2	816	41	76	28	16	42	197	110	277	178
508	1	-21.2167	-50.45	1844.756	Alto ParanÃƒÂ¡ Atlantic forests	63	122	0	422	37	73	26	9	40	235	130	317	203
509	1	-21.209	-50.433	1845.045	Madeira-TapajÃƒÂ³s moist forests	63	122	0	415	37	74	26	9	40	235	130	317	203
510	4	-10.167	-59.459	328.238	Madeira-TapajÃƒÂ³s moist forests	76	117	3	197	58	97	67	2	56	255	171	333	275
514	1	-10.9414	-69.5669	1154.508	Amazon-Orinoco-Southern Caribbean mangroves	70	113	0	297	53	81	63	11	56	249	163	321	246

515	2	-1.0217	-46.635	1609.043	Amazon-Orinoco-Southern Caribbean mangroves	70	87	0	1	68	81	131	56	11	265	218	324	290
517	1	-14.3667	-39.3603	2364.756	Bahia coastal forests	69	75	0	140	43	39	54	45	37	243	184	298	247
518	1	-14.3167	-39.325	2366.745	Cerrado	69	74	0	44	44	39	55	46	38	244	185	298	248
519	1	-22.1583	-49.3333	1996.413	Cerrado	67	119	0	456	36	69	23	11	41	221	118	309	188
520	2	-22.147	-49.333	1995.415	Cerrado	67	119	0	469	36	69	23	11	41	222	119	310	188
522	1	-23.1	-48.9167	2106.232	Cerrado	71	114	1	765	36	62	23	15	41	203	103	293	173
523	1	-23.099	-48.926	2105.593	MaranhÃƒÂ£o BabaÃƒÂ§u forests	71	114	1	850	36	62	23	14	41	204	104	294	174
524	1	-4.2833	-44.7833	1689.498	Uatuma-Trombetas moist forests	71	101	0	31	46	77	97	13	12	272	208	339	278
526	5	-2.7606	-52.0694	984.2195	TapajÃƒÂ³s-Xingu moist forests	80	94	0	17	59	82	110	39	17	267	211	329	298
531	1	-14.8083	-39.475	2368.091	Bahia coastal forests	68	75	0	158	44	43	52	46	40	241	181	296	244
532	2	-14.7606	-39.4361	2370.387	Bahia coastal forests	68	74	0	131	46	43	54	48	41	241	182	296	246
534	1	-20.949	-48.479	1945.217	Tocantins/ Pindare moist forests	66	116	0	596	40	82	26	7	43	229	129	301	198
535	10	-1.456	-48.504	1401.391	Tocantins/ Pindare moist forests	75	90	0		79	117	134	48	27	267	218	323	299
561	1	-4.383	-70.031	1180.207	Alto ParanÃƒÂ¡ Atlantic forests	82	96	0	83	74	98	96	39	80	260	206	317	303
562	1	-23.0167	-49.4833	2065.775	Alto ParanÃƒÂ¡ Atlantic forests	69	119	1	674	36	61	24	14	41	209	104	304	177
563	1	-23.013	-49.474	2065.964	Alto ParanÃƒÂ¡ Atlantic forests	69	119	1	674	36	61	24	14	41	209	104	304	177

564	1	-21.3	-50.3333	1859.202	Serra do Mar coastal forests	63	122	0	455	37	73	26	9	40	234	129	316	202
565	2	-26.919	-49.066	2456.529	Serra do Mar coastal forests	73	87	4	121	45	58	34	32	48	198	112	285	190
567	3	-26.9167	-49.0667	2456.273	Serra do Mar coastal forests	73	87	4	121	45	58	34	32	48	198	112	285	190
570	1	-9.0261	-67.2367	848.4868	Bolivian Yungas	79	102	0	213	57	97	67	10	58	265	191	331	292
571	1	-14.184	-68.3127	1212.249	Cerrado	60	98	11	935	52	87	50	19	47	223	151	286	195
572	1	-22.569	-48.971	2055.126	Cerrado	69	115	1	609	37	67	23	12	42	212	112	300	180
573	2	-22.886	-48.445	2115.406	Cerrado	72	109	0	630	38	67	24	14	42	208	112	293	178
575	13	-1.0536	-46.7656	1594.41	Tocantins/ Pindare moist forests	70	87	0	1	69	82	132	57	11	265	218	325	290
588	1	-20.1	-44.0417	2215.33	Bahia coastal forests	64	120	4	1220	40	92	21	5	41	203	99	283	183
589	1	-15.0636	-39.2936	2395.667	Serra do Mar coastal forests	68	74	0	129	48	47	57	52	45	242	183	297	249
590	1	-23.308	-47.133	2234.916	Serra do Mar coastal forests	75	98	1	620	41	76	27	15	42	200	111	279	179
591	1	-23.3	-47.1333	2234.21	Serra do Mar coastal forests	75	98	1	620	41	76	27	15	42	200	111	279	179
592	1	-23.101	-45.707	2313.329	Serra do Mar coastal forests	74	98	12	585	49	92	40	19	47	188	90	260	177
593	1	-23.1	-45.7	2313.735	Serra do Mar coastal forests	74	98	12	585	49	92	40	19	47	188	90	260	177
594	1	-28.6041	-49.3379	2608.714	Alto ParanÃƒÂ¡ Atlantic forests	68	74	3	111	42	47	34	34	43	188	109	268	182
595	1	-21.803	-49.61	1947.789	Alto ParanÃƒÂ¡ Atlantic forests	65	121	0	457	37	71	24	10	40	226	122	313	193
596	1	-21.8	-49.6	1948.12	Xingu-Tocantins-Araguaia moist forests	65	121	0	457	37	71	24	10	40	226	122	313	193
597	3	-2.244	-49.496	1263.608	Xingu-Tocantins-Araguaia moist forests	77	98	0	1	69	110	120	37	28	268	214	328	304

600	3	-13.79	-48.571	1423.411	Cerrado	65	116	1	601	45	94	40	1	46	249	158	333	224
603	1	-20.4667	-54.6167	1567.507	Cerrado	61	111	0	541	40	75	34	14	44	237	142	310	217
604	1	-20.443	-54.646	1563.949	Southern Atlantic mangroves	61	111	0	592	40	76	34	14	44	238	142	311	217
605	1	-25.0167	-47.9333	2337.614	Southern Atlantic mangroves	72	83	1	12	53	82	48	31	46	206	127	286	197
606	3	-25.015	-47.927	2337.819	Southern Atlantic mangroves	72	83	1	12	53	82	48	31	46	206	127	286	197
609	1	-15.6833	-38.95	2453.377	Tocantins/ Pindare moist forests	67	73	0	1	50	54	63	56	52	244	185	298	252
610	5	-1.75	-47.07	1531.505	Tocantins/ Pindare moist forests	76	92	0	50	68	85	126	50	16	264	213	326	290
615	1	-23.625	-45.4167	2376.136	Serra do Mar coastal forests	70	91	11	44	55	94	51	25	54	191	100	264	185
616	2	-23.62	-45.413	2375.983	Serra do Mar coastal forests	70	91	11	44	55	94	51	25	54	191	100	264	185
618	1	-7.3636	-47.4053	1363.825	Cerrado	71	112	1	162	46	85	61	2	43	265	188	347	257
619	1	-7.0774	-47.1409	1393.44	Cerrado	72	112	2	277	43	81	61	2	38	263	184	345	254
620	2	-21.774	-47.086	2109.095	Cerrado	72	112	1	616	42	83	27	10	45	208	104	283	179
622	1	-21.7667	-47.0833	2108.682	Tocantins/ Pindare moist forests	72	112	1	616	42	83	27	10	45	208	104	283	179
623	19	-1.3601	-47.9855	1457.609	Tocantins/ Pindare moist forests	75	90	0	12	77	107	137	51	22	265	216	324	295
642	3	-13.798	-47.458	1529.726	Cerrado	64	111	3	882	42	90	39	1	43	238	153	319	207
645	1	-18.408	-52.549	1464.078	Mato Grosso seasonal forests	62	123	8	687	42	87	32	6	44	236	134	314	213
647	1	-4.8854	-65.35	670.6997	Serra do Mar coastal forests	82	92	0	82	66	90	95	29	60	267	210	323	306
648	1	-28.6	-49.3333	2608.511	Cerrado	68	74	3	111	42	47	34	34	43	188	109	268	182
649	2	-14.151	-48.078	1489.47	Cerrado	64	113	1	585	44	92	40	2	45	245	156	325	214

651	2	-8.258	-49.265	1162.926	Mato Grosso seasonal forests	73	125	0	116	49	81	65	3	54	264	180	352	286
653	1	-20.5	-43.85	2258.416	Bahia interior forests	65	117	4	915	40	89	21	6	41	197	97	278	181
654	1	-20.5	-43.858	2257.761	Alto ParanÃƒÂ¡ Atlantic forests	65	117	4	915	40	89	21	6	41	197	97	278	181
655	1	-23.1833	-50.65	2017.982	Alto ParanÃƒÂ¡ Atlantic forests	68	118	0	611	40	64	31	18	46	213	107	307	180
656	1	-23.181	-50.647	2017.918	Araucaria moist forests	68	119	0	610	40	64	31	18	45	213	107	308	180
657	2	-26.4333	-49.2333	2401.476	Araucaria moist forests	76	97	6	431	44	58	33	30	48	189	98	278	180
659	1	-7.234	-39.409	2246.9	Caatinga	61	108	3	732	27	46	58	6	5	255	181	334	204
660	1	-7.213	-39.4802	2239.089	Southwest Amazon moist forests	61	108	3	783	26	45	57	5	5	254	181	334	204
661	1	-7.6311	-72.67	1426.376	TapajÃƒÂ³s-Xingu moist forests	81	105	0	200	59	81	77	20	65	265	197	327	289
662	1	-3.15	-54.8333	706.8364	Amazon-Orinoco-Southern Caribbean mangroves	77	95	0	85	55	64	98	30	19	264	207	327	297
663	2	-0.7289	-47.8481	1503.645	Amazon-Orinoco-Southern Caribbean mangroves	73	84	0	3	79	106	155	55	11	266	219	322	294
665	1	-14.4031	-56.427	874.4626	Bahia coastal forests	68	128	1	283	45	85	44	2	47	259	155	343	251
666	1	-20.363	-40.659	2521.141	Cerrado	66	97	10	644	33	52	27	17	39	222	144	300	220
667	1	-22.4333	-50.2	1971.362	Madeira-TapajÃƒÂ³s moist forests	65	121	1	610	37	65	26	13	42	219	113	311	185
670	1	9.5124	-75.3575	2532.811	Bahia interior forests	58	102	0	284	35	6	28	42	59	270	209	338	284

671	1	-14.9917	-39.925	2328.944	Uatuma-Trombetas moist forests	69	83	1	283	35	41	39	31	32	234	171	293	229
672	1	-1.7139	-57.2133	670.4033	Uatuma-Trombetas moist forests	77	84	1	55	57	70	93	43	21	272	226	333	298
673	2	-0.9628	-55.5222	835.7915	Uatuma-Trombetas moist forests	76	89	1	247	54	64	98	36	17	265	218	329	288
675	1	-8.9276	-36.4992	2569.937	Mato Grosso seasonal forests	66	94	2	756	27	15	46	47	11	233	170	306	221
676	2	-13.242	-53.08	989.4059	Mato Grosso seasonal forests	69	126	0	318	52	97	46	1	54	261	163	346	257
678	1	-21.384	-50.211	1874.054	Tocantins/ Pindare moist forests	63	122	0	466	37	73	26	9	40	233	128	316	201
679	1	-3.84277	-49.0969	1238.269	Madeira-TapajÃƒÂ³s moist forests	78	102	1	99	63	104	119	18	27	269	209	331	305
680	1	-10.3167	-64.55	629.2796	Serra do Mar coastal forests	76	106	4	155	47	86	55	2	42	261	186	333	276
681	1	-25.8833	-48.5833	2382.198	Serra do Mar coastal forests	73	84	3		49	77	43	30	47	196	116	279	188
682	1	-25.883	-48.575	2382.609	Monte Alegre varzeÃƒÂ¡	73	84	3		49	77	43	30	47	196	116	279	188
683	2	-7.506	-63.021	361.9962	Monte Alegre varzeÃƒÂ¡	80	99	0	62	61	93	85	9	58	264	195	330	296
685	2	-27.05	-49.5167	2447.761	Serra do Mar coastal forests	73	95	6	270	44	53	33	34	49	189	98	280	180
687	1	-24.708	-47.555	2331.741	Tocantins/ Pindare moist forests	71	84	0	1	54	82	50	32	46	213	132	291	204
688	3	-1.445	-48.5	1402.345	Serra do Mar coastal forests	75	90	0		79	117	135	48	27	267	218	323	299

689	1	-23.778	-45.358	2392.687	Serra do Mar coastal forests	67	90	10		58	96	55	26	58	191	101	264	186
690	1	-14.8	-39.0333	2412.933	Bahia interior forests	67	71	0	1	50	45	61	55	45	244	186	297	252
691	3	-14.8	-39.05	2411.224	Campos Rupestres montane savanna	67	71	0	1	50	45	60	54	45	244	186	297	252
694	1	-24.586	-48.593	2260.72	Araucaria moist forests	75	97	3	159	43	66	33	25	41	193	104	277	176
695	1	-24.5833	-48.6	2260.078	Bahia coastal forests	75	98	3	266	42	65	32	25	41	192	102	277	174
696	1	16.3952	-86.3832	3926.998	Cerrado													
697	1	-19.6333	-43.2167	2253.928	Bahia interior forests	65	118	1	912	38	84	24	5	41	212	110	296	195
698	1	-20.253	-43.809	2244.931	Alto ParanÃƒÂ¡ Atlantic forests	65	116	6	927	40	90	20	5	41	196	97	276	178
699	1	-14.275	-38.9833	2400.647	Alto ParanÃƒÂ¡ Atlantic forests	67	72	0		50	40	64	55	41	247	188	301	254
700	1	-3.1333	-58.4333	474.4459	Alto ParanÃƒÂ¡ Atlantic forests	83	86	0	51	55	98	92	30	18	270	221	328	298
701	1	-2.9667	-58.9167	478.7825	Alto ParanÃƒÂ¡ Atlantic forests	82	85	0	88	56	94	93	31	23	270	222	327	298
702	1	-26.3333	-49.9	2359.741	Alto ParanÃƒÂ¡ Atlantic forests	78	114	9	926	41	50	28	30	48	177	72	273	166
703	1	-14.7894	-39.5247	2362.353	Alto ParanÃƒÂ¡ Atlantic forests	68	76	0	205	43	42	51	44	39	240	180	295	243
704	1	-23.102	-48.616	2124.307	Bahia coastal forests	71	111	1	784	37	63	23	15	41	203	105	290	173
705	1	-15.1167	-40.0667	2319.276	Purus varzeÃƒÂ¡	69	85	1	276	33	41	37	27	31	235	170	295	227
706	1	-23.2667	-47.3	2220.608	Serra do Mar coastal forests	75	99	0	607	41	74	27	15	42	203	113	283	180
707	5	-23.264	-47.299	2220.439	Serra do Mar coastal forests	75	99	0	605	41	75	27	15	42	202	113	283	181

712	1	-13.7333	-39.15	2366.608	Serra do Mar coastal forests	70	77	0	108	40	35	55	44	32	245	185	301	249
713	1	-8.3333	-65.7167	669.0909	Serra do Mar coastal forests	80	99	0	99	58	95	74	10	56	267	197	331	296
714	2	-24.693	-48.002	2304.186	Serra do Mar coastal forests	75	88	0	122	49	75	41	29	42	206	124	288	192
716	5	-26.486	-49.067	2414.763	Mato Grosso seasonal forests	75	92	4	224	45	61	35	31	48	195	107	283	187
721	1	-26.4833	-49.0833	2413.695	Madeira-TapajÃƒÂ³s moist forests	75	92	4	224	45	61	35	31	48	195	107	283	187
722	2	-26.3	-48.85	2407.863	Bahia coastal forests	75	87	2	159	47	67	38	31	47	200	116	285	192
724	1	-11.378	-58.741	473.8521	Bahia coastal forests	75	124	2	374	57	96	57	2	54	256	163	341	269
725	1	-21.7667	-43.35	2387.268	Mato Grosso seasonal forests	69	107	0	758	41	92	25	6	37	207	111	292	199
726	1	-21.764	-43.35	2387.076	Guianan freshwater swamp forests	69	107	0	758	41	92	25	6	37	207	111	292	199
727	1	-8.2667	-72.7833	1441.768	Cerrado	80	105	0	200	59	81	72	21	66	265	195	327	285
728	1	-12.85	-58.9333	629.8788	Cerrado	72	127	3	376	50	89	46	2	46	254	157	338	259
729	1	-10.3268	-58.5979	367.0824	Iquitos varzeÃƒÂ¡	76	120	2	200	60	99	66	2	58	255	168	336	274
731	2	-2.5833	-64.6667	747.522	Guianan savanna	81	91	0	44	68	79	95	49	54	267	215	321	305
732	1	-13.182	-39.425	2321.987	Guianan savanna	73	86	1	215	29	30	38	30	22	239	175	300	239
733	1	-9.751	-48.358	1285.799	Madeira-TapajÃƒÂ³s moist forests	68	121	0	148	46	79	53	1	56	266	177	352	261
734	1	5.8333	-55.0374	1534.97	Southwest Amazon moist forests	66	79	0	1	61	67	75	74	26	267	222	324	239

735	1	-22.5667	-47.4	2154.153	Serra do Mar coastal forests	74	104	0	610	41	77	27	13	45	209	115	288	181
736	1	-22.565	-47.402	2153.876	Serra do Mar coastal forests	74	104	0	610	41	77	27	13	45	209	115	288	181
737	1	-4.1381	-70.7265	1261.89	Serra do Mar coastal forests	82	96	0	90	73	94	97	41	77	261	206	316	301
738	1	0.0333	-51.0664	1254.156	Serra do Mar coastal forests	73	79	0	1	73	103	130	62	11	268	226	326	295
739	2	0.039	-51.066	1254.595	Serra do Mar coastal forests	73	79	0	1	73	103	130	62	11	268	226	326	295
741	1	-9.4396	-61.9837	347.6148	JapurÃƒÂ¡-Solimoes-Negro moist forests	78	107	2	197	57	96	71	5	56	259	181	331	282
742	1	-11.9442	-71.2831	1368.963	JapurÃƒÂ¡-Solimoes-Negro moist forests	67	105	0	310	87	135	81	46	95	241	166	304	240
743	6	-23.546	-47.183	2252.217	JapurÃƒÂ¡-Solimoes-Negro moist forests	75	96	2	887	42	75	28	17	42	196	109	275	177
749	1	-3.102	-60.025	455.6889	Cerrado	82	85	0	34	61	85	98	29	39	272	224	328	300
750	1	-3.1019	-60.025	455.6999	Cerrado	82	85	0	34	61	85	98	29	39	272	224	328	300
751	1	-3.0752	-60.3133	461.831	Cerrado	82	85	0	27	62	82	98	30	42	272	224	328	301
752	1	-6.1368	-61.7468	250.3422	Cerrado	82	95	0	79	62	90	91	14	57	266	206	328	302
754	2	-0.595	-47.5819	1536.745	Alto ParanÃƒÂ¡ Atlantic forests	75	84	0		78	101	155	57	9	266	219	322	293
756	1	-20.357	-43.345	2290.415	Alto ParanÃƒÂ¡ Atlantic forests	65	116	2	746	38	80	21	6	39	206	105	291	192
761	1	-21.6	-48.3667	2008.09	Cerrado	69	113	0	607	39	78	25	9	43	221	124	298	188
762	1	-13.533	-48.22	1443.063	Cerrado	64	116	0	336	43	91	39	2	44	254	163	339	229
763	1	-20.819	-49.521	1865.829	Cerrado	63	122	0	461	37	80	26	7	40	234	131	312	205
764	1	-20.8167	-49.5167	1865.901	Cerrado	63	122	0	461	37	80	26	7	40	234	131	312	205
765	1	-0.8667	-52.5283	1065.84	Cerrado	76	88	1	92	64	76	118	56	14	265	218	326	294
766	1	-26.5667	-54.7667	2206.094	Alto ParanÃƒÂ¡ Atlantic forests	55	121	2	149	46	52	53	32	55	208	97	319	197

768	1	14.3548	-83.877	3575.769	Uatuma-Trombetas moist forests	48	73	0	67	89	60	25	151	121	260	211	312	279
769	6	-14.474	-48.46	1472.394	Uatuma-Trombetas moist forests	65	114	1	736	45	94	40	2	48	243	153	323	214
775	1	-15.8315	-56.5281	1016.09	Tocantins/ Pindare moist forests	68	122	0	186	36	73	39	4	34	263	161	334	259
776	1	-22.2833	-43.5333	2410.157	Bahia interior forests	70	105	1	86	37	78	27	7	34	211	118	296	207
777	1	-14.673	-52.353	1155.177	Madeira-TapajÃƒÂ³s moist forests	67	124	1	345	48	97	38	1	50	256	155	338	243
778	1	-1.76	-55.86	741.9434	Guianan Highlands moist forests	76	89	0	15	55	70	97	30	22	269	221	332	296
779	1	-1.4648	-56.3675	738.5604	Caatinga Enclaves moist forests	76	87	1	27	56	66	95	38	21	271	223	333	296
780	1	-21.797	-50.89	1873.751	Alto ParanÃƒÂ¡ Atlantic forests	64	118	0	373	37	68	27	11	43	227	125	312	194
781	1	-21.8	-50.8667	1875.307	Ucayali moist forests	64	118	0	364	37	68	27	11	43	226	124	312	193
782	4	-1.5519	-47.1144	1535.914	Cerrado	76	92	0	37	69	85	130	53	14	264	213	326	290
786	1	-20.517	-43.7	2271.871	Madeira-TapajÃƒÂ³s moist forests	66	115	4	1171	39	88	21	6	40	196	98	278	181
787	1	-10.7481	-62.2158	475.3646	Mato Grosso seasonal forests	75	112	5	291	50	89	57	2	48	257	174	333	271
788	1	4.4827	-61.1491	1302.629	Mato Grosso seasonal forests	65	108	0	930	55	24	60	90	46	232	173	296	219
789	1	-4.1995	-38.9013	2333.566	Madeira-TapajÃƒÂ³s moist forests	67	83	0	608	28	29	73	14	3	263	208	320	257

790	1	10.217	-83.2662	3241.574	Madeira-TapajÃƒÂ³s moist forests	56	97	0	1	108	118	89	143	92	257	197	323	281
791	1	-16.8	-49.9167	1506.448	Central American montane forests	63	122	0	616	45	97	38	2	53	245	147	326	213
792	1	-9.6141	-74.9352	1692.456	Central American montane forests	76	113	2	200	64	87	60	35	75	245	174	310	241
793	1	-22.413	-50.576	1948.795	Bahia coastal forests	65	119	0	545	38	65	28	13	44	220	115	310	186
794	1	-12.615	-47.883	1431.992	Amazon-Orinoco-Southern Caribbean mangroves	64	120	0	279	40	85	38	0	41	259	164	348	236
795	1	-12.6	-47.8667	1432.955	Amazon-Orinoco-Southern Caribbean mangroves	64	120	0	279	40	85	38	0	41	259	164	348	236
796	1	-9.665	-56.477	451.4459	Amazon-Orinoco-Southern Caribbean mangroves	77	122	2	177	63	102	71	2	61	256	170	338	278
797	1	-9.65	-58.4667	304.514	Amazon-Orinoco-Southern Caribbean mangroves	77	117	2	184	62	101	73	3	60	257	174	336	279
798	2	-6.0667	-49.9	1097.107	Amazon-Orinoco-Southern Caribbean mangroves	79	111	3	184	55	93	90	5	43	260	190	334	285
800	1	-9.4656	-61.598	321.2595	Cerrado	78	109	3	311	57	96	71	4	56	258	180	332	281
801	1	-8.05	-61.9667	260.9297	Serra do Mar coastal forests	80	102	1	94	61	96	82	8	59	261	189	330	291

802	1	14.2665	-88.1771	3936.603	Serra do Mar coastal forests	49	110	3	1878	46	9	14	88	59	210	133	291	191
803	1	15.6189	-86.8622	3912.879	Serra do Mar coastal forests	45	89	3	1359	53	51	21	56	85	233	166	297	237
804	1	-15.4667	-39.65	2374.64	Madeira-TapajÃƒÂ³s moist forests	69	81	0	152	40	48	47	39	40	239	176	297	239
805	1	-1.2	-47.32	1531.825	Alto ParanÃƒÂ¡ Atlantic forests	76	91	0	10	71	87	138	56	12	263	214	326	290
806	4	-1.1919	-47.3122	1532.998	Alto ParanÃƒÂ¡ Atlantic forests	76	91	0	6	71	87	139	56	11	264	214	325	290
810	1	-21.42	-50.078	1885.194	Alto ParanÃƒÂ¡ Atlantic forests	63	122	0	444	37	73	25	9	40	232	127	316	200
811	1	-21.4167	-50.0833	1884.579	Central American dry forests	63	122	0	444	37	73	25	9	40	232	127	316	200
812	2	-24.32	-46.998	2331.217	Cerrado	68	86	1		61	93	58	32	62	209	124	285	202
814	1	-24.3167	-47	2330.804	Cerrado	70	86	1	48	58	89	54	31	57	211	126	288	202
815	1	-12.2	-61.0833	570.4112	Madeira-TapajÃƒÂ³s moist forests	71	120	5	289	46	84	46	1	43	253	162	333	259
816	2	-21.186	-48.907	1937.222	Madeira-TapajÃƒÂ³s moist forests	64	119	0	523	38	79	24	8	40	230	128	308	197
818	1	-21.1833	-48.9	1937.443	Cerrado	64	119	0	523	38	79	24	8	40	230	128	308	197
819	1	-23.2	-49.3833	2088.344	Uatuma-Trombetas moist forests	69	118	1	611	36	59	23	15	41	205	101	301	175
820	2	-23.194	-49.384	2087.752	Uatuma-Trombetas moist forests	69	118	1	504	36	59	23	15	41	206	102	301	175
822	1	10.1688	-85.8131	3469.737	Uatuma-Trombetas moist forests	51	115	0		49	0	10	58	112	269	202	350	282

823	1	-25.095	-50.162	2226.602	Uatuma-Trombetas moist forests	78	115	6	914	42	57	33	29	47	180	75	274	164
824	1	-9.588	-67.533	895.8383	Uatuma-Trombetas moist forests	79	103	0	144	55	95	62	11	56	264	188	331	288
825	1	-15.8482	-58.4677	965.3851	Uatuma-Trombetas moist forests	68	126	1	195	37	79	34	6	29	259	153	342	258
826	3	-8.762	-63.904	488.3529	Venezuelan Andes montane forests	79	101	0	81	58	96	73	8	56	264	190	331	290
829	1	-21.763	-52.116	1807.039	Cerrado	64	111	0	278	37	64	30	10	49	230	133	310	200
830	1	-2.0344	-60.025	573.5395	Cerrado	81	87	0	100	59	75	92	41	34	269	221	327	295
831	4	-1.8981	-59.4744	588.6563	Southwest Amazon moist forests	80	86	1	67	58	76	91	42	28	268	221	327	293
835	2	-1.8833	-59.4667	590.3363	Uatuma-Trombetas moist forests	80	86	1	67	58	76	91	42	28	268	221	327	293
837	1	8.9649	-70.4508	2146.777	Uatuma-Trombetas moist forests	73	99	13	1861	39	8	47	55	57	205	141	263	187
838	1	-5.1279	-61.7213	317.1016	Chiquitano dry forests	82	92	0	101	61	86	93	20	55	267	211	327	304
839	1	14.1487	-85.0676	3660.494	Chiquitano dry forests	45	92	2	245	62	33	19	111	83	236	175	300	237
840	1	-21.587	-48.071	2026.517	ChocÃƒÂ³-DariÃƒÂ©n moist forests	70	112	0	581	40	79	26	9	44	219	122	294	186
841	1	-21.5833	-48.0667	2026.49	Alto ParanÃƒÂ¡ Atlantic forests	70	112	0	581	40	79	26	9	44	219	122	294	186
842	1	-9.9667	-67.8	936.3197	Alto ParanÃƒÂ¡ Atlantic forests	78	105	0	165	53	92	61	12	55	263	186	331	283

843	1	-2.7	-59.5167	499.8607	Bahia interior forests	82	85	0	100	59	86	95	33	31	271	224	328	298
844	1	-2.699	-59.7	499.308	Bahia interior forests	82	84	0	80	60	83	95	34	33	272	224	328	299
845	1	-2.696	-59.7038	499.6347	Bahia interior forests	82	84	0	80	60	83	95	34	33	272	224	328	299
846	3	-2.4167	-59.7167	530.5033	Cerrado	81	85	0	100	59	81	94	36	32	271	223	328	297
849	1	-16.3756	-60.9547	1021.869	Bahia coastal forests	61	127	0	581	32	64	25	6	28	254	147	341	229
850	1	-16.3469	-60.9502	1018.657	Bahia coastal forests	61	127	0	544	32	64	25	6	28	254	147	340	229
851	1	4.0667	-77.0533	2291.107	Bahia coastal forests	79	82	1	42	154	105	147	150	200	251	208	299	272
852	1	-21.243	-48.804	1948.835	TapajÃƒÂ³s-Xingu moist forests	65	119	0	616	38	79	24	8	40	229	127	307	196
853	1	-21.2333	-48.8	1948.258	TapajÃƒÂ³s-Xingu moist forests	65	119	0	616	38	79	24	8	40	229	127	307	196
854	1	-19.9667	-43.4167	2258.557	TapajÃƒÂ³s-Xingu moist forests	65	116	2	804	39	85	22	5	40	207	108	290	190
855	2	-19.959	-43.415	2258.195	Serra do Mar coastal forests	65	116	2	804	39	85	22	5	40	207	108	290	190
857	1	-9.112	-45.922	1538.663	Purus varzeÃƒÂ¡	65	123	3	284	38	69	48	0	39	259	173	350	232
858	2	-3.667	-45.38	1640.383	Serra do Mar coastal forests	73	97	0	45	51	84	104	19	14	270	213	333	285
860	2	-20.025	-40.7417	2493.855	Cerrado	66	101	10	827	33	56	25	14	39	224	142	303	222
862	1	-19.9333	-40.6	2501.114	Tocantins/ Pindare moist forests	66	98	7	822	33	55	26	15	40	231	151	310	231
863	1	-2.443	-54.708	769.1747	Tocantins/ Pindare moist forests	66	92	0	10	55	61	105	35	15	266	213	329	292

864	2	-2.43	-54.69	771.6166	Tocantins/ Pindare moist forests	67	92	0	7	55	61	105	35	15	266	213	329	291
866	2	-23.664	-46.538	2304.02	Tocantins/ Pindare moist forests	76	91	3	770	45	81	35	19	44	197	111	274	184
868	1	-3.0833	-67.9333	1015.087	Tocantins/ Pindare moist forests	81	94	1	66	76	91	100	49	69	259	203	313	300
869	1	-23.961	-46.334	2342.588	Uatuma-Trombetas moist forests	71	86	1	1	62	98	60	31	65	207	121	280	200
870	1	-23.95	-46.3333	2341.699	Cerrado	71	86	1	1	62	98	60	31	65	207	121	280	200
871	1	-22.018	-47.891	2075.084	Cerrado	73	108	0	837	40	78	25	10	46	209	115	286	177
873	7	-1.675	-47.775	1463.466	Cerrado	75	93	0	23	74	101	130	49	22	265	214	326	294
880	1	0.9681	-59.9365	904.9831	Tocantins/ Pindare moist forests	67	94	1	211	50	34	67	75	24	266	214	327	271
881	2	-13.4333	-56.7333	763.3483	Tocantins/ Pindare moist forests	71	131	0	368	52	93	46	2	51	258	156	343	257
883	1	-22.75	-48.5667	2095.865	Tocantins/ Pindare moist forests	71	111	1	730	38	67	23	13	42	208	111	293	177
884	1	-22.731	-48.571	2093.913	Tocantins/ Pindare moist forests	71	111	1	674	38	68	23	13	42	209	112	294	177
885	1	-23.529	-47.135	2253.814	Uatuma-Trombetas moist forests	75	96	2	914	42	75	28	16	42	196	109	275	177
886	1	-8.1667	-70.7667	1219.337	Monte Alegre varzeÃƒÂ¡	82	105	0	199	60	91	71	21	65	260	188	323	292
887	1	-3.5802	-64.8041	688.8039	Cerrado	82	90	0	45	67	84	95	40	56	269	215	322	306

888	1	-3.354	-64.711	695.5855	Trinidad and Tobago moist forests	82	90	0	44	68	83	95	42	55	269	216	322	306
889	1	15.7748	-87.4569	3973.733	Tocantins/ Pindare moist forests	47	88	1	7	71	78	30	66	117	252	187	315	263
890	6	-2.419	-48.152	1391.718	Tocantins/ Pindare moist forests	76	98	0	62	69	104	119	38	28	267	212	326	299
896	1	0.8833	-52	1242.392	Alto ParanÃƒÂ¡ Atlantic forests	73	80	1	97	73	97	127	65	11	263	220	321	288
897	1	-6.9947	-62.6811	324.1139	Alto ParanÃƒÂ¡ Atlantic forests	81	97	0	58	61	91	88	11	58	264	198	329	298
898	1	-20.7833	-51.7	1734.13	Caatinga Enclaves moist forests	61	119	0	339	36	70	28	9	42	245	140	324	216
899	1	10.71	-61.22	1988.734	Serra do Mar coastal forests	62	86	1	499	48	21	16	79	71	256	199	306	281
900	6	-3.768	-49.673	1180.27	Serra do Mar coastal forests	79	102	1	34	64	108	127	17	24	269	210	331	310
906	1	-3.6833	-49.7	1180.57	Bahia coastal forests	79	102	1	32	64	108	127	18	24	269	210	331	311
907	1	-21.935	-50.514	1907.438	Bahia coastal forests	64	120	0	517	37	68	26	12	42	225	121	312	192
908	1	-21.9333	-50.5167	1907.129	Bahia coastal forests	64	120	0	517	37	68	26	12	42	225	121	312	192
909	1	-3.854	-40.921	2119.354	Tocantins/ Pindare moist forests	68	100	6	719	37	49	100	9	2	257	196	327	238
910	5	-23.434	-45.071	2384.736	Tocantins/ Pindare moist forests	72	93	14	114	53	94	49	22	51	189	97	262	185
915	1	-7.3343	-75.2045	1706.008	Amazon-Orinoco-Southern Caribbean mangroves	81	112	0	158	48	57	62	21	56	266	196	331	273

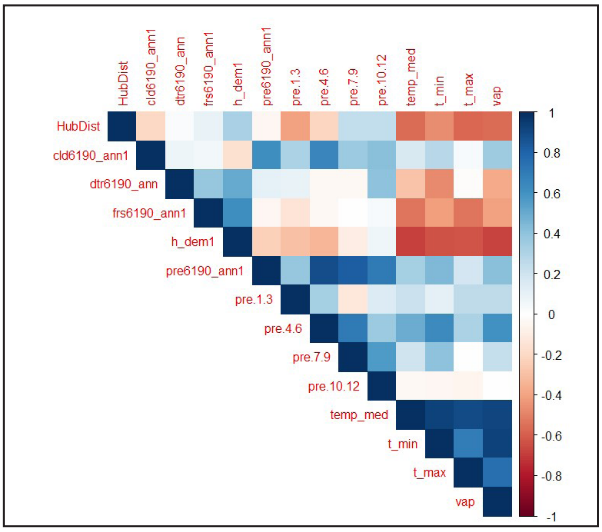
916	1	-3.2406	-43.4222	1862.827	Amazon-Orinoco-Southern Caribbean mangroves	68	85	0	58	52	71	125	24	4	272	219	328	283
917	1	-14.5917	-39.2833	2380.206	Amazon-Orinoco-Southern Caribbean mangroves	68	72	0	98	48	42	58	51	41	244	185	298	251
920	3	-0.8583	-48.1417	1468.116	Amazon-Orinoco-Southern Caribbean mangroves	68	86	0	4	80	112	146	52	18	267	219	322	296
923	1	-20.873	-48.297	1951.138	Amazon-Orinoco-Southern Caribbean mangroves	66	114	0	547	41	82	27	7	44	228	129	297	197
924	1	-20.8667	-48.2833	1951.544	Amazon-Orinoco-Southern Caribbean mangroves	66	114	0	547	41	82	27	7	44	228	129	297	197
925	1	-1.3	-46.2667	1633.376	Amazon-Orinoco-Southern Caribbean mangroves	75	84	0	4	66	75	132	55	8	265	217	321	289
926	28	-1.1967	-46.14	1650.91	Amazon-Orinoco-Southern Caribbean mangroves	75	82	0	1	66	74	133	56	7	265	217	320	289

Apéndice 3

Resultados de análisis de correlación entre variables continuas

Script

```
# Cargar los datos
df <- read.csv("Variables_climaticas.csv", stringsAsFactors =
FALSE)
# Visualizar estructura de datos
str(df)
# Eliminar columna de abundancia
numeric_vars <- df[, sapply(df, is.numeric)]
numeric_vars <- subset(numeric_vars, select = -c(abundancia))
# Cargar librería
library(corrplot)
# Calcular matriz de correlación
cor_matrix <- cor(numeric_vars, use = "complete.obs")
# Visualizar
corrplot(cor_matrix, method = "color", type = "upper", tl.cex
= 0.8)
# Encontrar correlaciones altas
high_corr <- which(abs(cor_matrix) > 0.7 & abs(cor_matrix)
< 1, arr.ind = TRUE)
unique_pairs <- unique(t(apply(high_corr, 1, sort)))
for (i in 1:nrow(unique_pairs)) {
  cat(colnames(cor_matrix)[unique_pairs[i, 1]], " - ",
      colnames(cor_matrix)[unique_pairs[i, 2]], "\n")
```



Principales correlaciones altas:

temp_med y t_max: r = 0.97
temp_med y t_min: r = 0.97
pre6190_ann1 y pre_10_12: r = 0.88
pre_1_3 y pre_4_6: r = 0.89

Grupo de variables correlacionadas	**Conservar solo una**
temp_med, t_max, t_min	temp_med
pre6190_ann1, pre_10_12	pre6190_ann1
pre_1_3, pre_4_6, pre_7_9	pre_1_3
vap, temp_med	temp_med

Resumen de variables seleccionadas para el GAM

Correlación < 0,7

Variable	Descripción
HubDist	Distancia al centroide de la distribución
temp_med	Temperatura media anual
pre6190_ann1	Precipitación total anual
h_dem1	Altitud promedio
ECO_NAME	Ecorregión WWF (variable categórica)

Apéndice 4

Sript para R para modelo GAM

Variables continuas

```
# Cargar paquetes
library(tidyverse)
library(mgcv)
library(gratia)
library(performance)
# Cargar archivo CSV
data <- read.csv("Abundancia_por_coordenada.csv")
# Revisar nombres
str(data)
# Convertir ecorregión a factor
data$ECO_NAME <- as.factor(data$ECO_NAME)
# Modelado GAM
gam_model <- gam(
 abundancia ~
  s(HubDist, k = 10) +
  s(temp_med, k = 10) +
  s(pre6190_ann1, k = 10) +
  s(h_dem1, k = 10) +
  ECO_NAME,
 family = nb(),  # Distribución negativa binomial (para sobre-
    dispersión)
 data = data,
 method = "REML"
)
# Resumen del modelo
summary(gam_model)
# Graficar efectos parciales (variables contínuas)
draw(gam_model, residuals = TRUE)
```

Variables categóricas

```
# Cargar paquetes
library(mgcv)
library(dplyr)
data <- read.csv("Abundancia_por_coordenada.csv")
data$ECO_NAME <- as.factor(data$ECO_NAME)
gam_model <- gam(
  abundancia ~ s(HubDist, k=10) +
    s(temp_med, k=10) +
    s(pre6190_ann1, k=10) +
    s(h_dem1, k=10) +
    ECO_NAME,
  data = data,
  family = nb(link = "log")
)
summary(gam_model)
library(ggplot2)
coefs <- summary(gam_model)$p.table
```

Principales correlaciones altas:

temp_med y t_max: r = 0.97
temp_med y t_min: r = 0.97
pre6190_ann1 y pre_10_12: r = 0.88
pre_1_3 y pre_4_6: r = 0.89

Grupo de variables correlacionadas	**Conservar solo una**
temp_med, t_max, t_min	temp_med
pre6190_ann1, pre_10_12	pre6190_ann1
pre_1_3, pre_4_6, pre_7_9	pre_1_3
vap, temp_med	temp_med

Resumen de variables seleccionadas para el GAM

Correlación < 0,7

Variable	Descripción
HubDist	Distancia al centroide de la distribución
temp_med	Temperatura media anual
pre6190_ann1	Precipitación total anual
h_dem1	Altitud promedio
ECO_NAME	Ecorregión WWF (variable categórica)

Apéndice 4

Sript para R para modelo GAM

Variables continuas

```
# Cargar paquetes
library(tidyverse)
library(mgcv)
library(gratia)
library(performance)
# Cargar archivo CSV
data <- read.csv("Abundancia_por_coordenada.csv")
# Revisar nombres
str(data)
# Convertir ecorregión a factor
data$ECO_NAME <- as.factor(data$ECO_NAME)
# Modelado GAM
gam_model <- gam(
 abundancia ~
  s(HubDist, k = 10) +
  s(temp_med, k = 10) +
  s(pre6190_ann1, k = 10) +
  s(h_dem1, k = 10) +
  ECO_NAME,
 family = nb(),  # Distribución negativa binomial (para sobredispersión)
 data = data,
 method = "REML"
)
# Resumen del modelo
summary(gam_model)
# Graficar efectos parciales (variables contínuas)
draw(gam_model, residuals = TRUE)
```

Variables categóricas

```
# Cargar paquetes
library(mgcv)
library(dplyr)
data <- read.csv("Abundancia_por_coordenada.csv")
data$ECO_NAME <- as.factor(data$ECO_NAME)
gam_model <- gam(
  abundancia ~ s(HubDist, k=10) +
    s(temp_med, k=10) +
    s(pre6190_ann1, k=10) +
    s(h_dem1, k=10) +
    ECO_NAME,
  data = data,
  family = nb(link = "log")
)
summary(gam_model)
library(ggplot2)
coefs <- summary(gam_model)$p.table
eco_coefs <- as.data.frame(coefs[grep("^ECO_NAME", rownames(coefs)), ])
eco_coefs$ECO_NAME <- gsub("^ECO_NAME", "", rownames(eco_coefs))
colnames(eco_coefs) <- c("Estimate", "StdError", "zvalue", "pvalue", "ECO_NAME")
eco_coefs <- eco_coefs %>%
  mutate(
    lower = Estimate - 1.96 * StdError,
    upper = Estimate + 1.96 * StdError
  )
ggplot(eco_coefs, aes(x = reorder(ECO_NAME, Estimate), y = Estimate)) +
  geom_point() +
   geom_errorbar(aes(ymin = lower, ymax = upper), width = 0.3) +
  coord_flip() +
  theme_minimal() +
  labs(
   title = "Efecto de la ecorregión sobre la abundancia relativa",
    x = "Ecorregión",
    y = "Estimación del efecto (log)"
  )
```

Trabajo

Cuad. herpetol. 40 (1): 73-108 (*2026*)

Morphological evolutionary acquisitions in the specialized genus of lizards *Phymaturus* (Iguania: Liolaemidae). The origin of herbivory and saxicolous mode of life in liolaemid lizards

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ABSTRACT
With few exceptions, there are still not enough studies on the origin of herbivory and the saxicolous mode of life in lizards of the Liolaemidae family, nor on the possible morphological adaptations that may have favored these traits. In the present study, we recorded external measurements and collected data from skeletons representing all major clades of *Liolaemus* and *Phymaturus*, as well as *Ctenoblepharys*. To identify modifications that could explain the different body shapes and their possible relationship with modes of life, we studied seventeen body measurements, the lengths of the bony and inscriptional ribs, and the number of trunk vertebrae. ANOVA and principal component analysis were performed, and the evolution and origin of these characters were analyzed in a metatree of the family. We found that *Phymaturus* and herbivorous species of *Liolaemus* exhibit the largest abdominal volume and body size. Greater abdominal capacity, trunk height, and head height characterize the herbivorous saxicolous clades, which is reasonable for accommodating larger viscera and plant contents, as well as providing a flattened head shape important for using rock crevices as refuges. On average, *Phymaturus* species possess at least two additional vertebrae, and their inscriptional ribs are elongated, contributing to their greater abdominal volume. We also observed pseudo-valvules in the small intestine, which may favor slower movement of plant material along the digestive tract. According to our analysis, herbivory and the saxicolous mode of life were acquired by *Phymaturus* independently within the Liolaemidae family. Our phylogenetic statistics indicate that the body measurements studied have a strong phylogenetic imprint. Thus, in the phylogeny of Liolaemidae, the origin of herbivory and saxicoly can be traced to the ancestors of different lineages (at least eight and seven cases, respectively) and was later inherited by almost all descendants.

Key words: Abdominal Capacity; Intestines; Skeletons; Diet; Saxicoly.

RESUMEN
Con pocas excepciones, aún no existen suficientes estudios sobre el origen de la herbivoría y el modo de vida saxícola en lagartijas de la familia Liolaemidae, ni sobre las posibles adaptaciones morfológicas que pudieron haber favorecido estos rasgos. En el presente estudio, registramos medidas externas y recolectamos datos de esqueletos que representan a todos los clados principales de *Liolaemus* y *Phymaturus*, así como en *Ctenoblepharys*. Para identificar modificaciones que pudieran explicar las diferentes formas corporales y su posible relación con los modos de vida, estudiamos diecisiete medidas corporales, las longitudes de las costillas óseas e inscripcionales, y el número de vértebras del tronco. Se realizaron análisis de ANOVA y de componentes principales, y se analizó la evolución y el origen de estos caracteres en un meta-árbol de la familia. Encontramos que *Phymaturus* y las especies herbívoras de *Liolaemus* exhiben el mayor volumen abdominal y tamaño corporal. Una mayor capacidad abdominal, altura del tronco y altura de la cabeza caracterizan a los clados saxicolas herbívoros, lo cual les permite albergar vísceras y contenido vegetal de mayor tamaño, además de proporcionar una forma de cabeza aplanada, importante para usar las grietas de las rocas como refugio. En promedio, las especies

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de *Phymaturus* poseen al menos dos vértebras adicionales, y sus costillas inscripcionales son alargadas, lo que contribuye a su mayor volumen abdominal. También observamos pseudo-válvulas en el intestino delgado, lo que podría favorecer un tránsito más lento del material vegetal a lo largo del tracto digestivo. Según nuestro análisis, la herbivoría y el modo de vida saxícola fueron adquiridos por *Phymaturus* de forma independiente dentro de la familia Liolaemidae. Nuestras estadísticas filogenéticas indican que las medidas corporales estudiadas tienen una fuerte impronta de la filogenia. Por lo tanto, en la filogenia de Liolaemidae, el origen de la herbivoría y la saxicolía se pueden rastrear hasta los ancestros de diferentes linajes (al menos ocho y siete casos, respectivamente) y fue heredado posteriormente por casi todos los descendientes.

Palabras claves: Capacidad Abdominal; Intestinos; Esqueletos; Dieta; Saxicolía.

Introduction

Contemporary studies on the relationship between animal morphology and mode of life are based on analyses that consider the group's evolutionary history. The central question is whether the modifications observed in certain organisms constitute adaptations to their mode of life or whether, on the contrary, they have been inherited from a common ancestor. The prediction of an association between form and function is evidenced by the study of morphological traits linked to modes of life in each animal lineage (Feilich and López-Fernández, 2019; Kennedy *et al*., 2020). In recent decades, numerous approaches and methodologies have been developed to analyze eco-morphology in a phylogenetic context, demonstrating the need to always consider the evolutionary relationships of the organisms studied (Felsenstein, 1985; Martins and Hansen, 1997; Freckleton *et al*., 2002; O'Meara, 2012, among others). In reptiles, morphology is closely linked to ecological mode of life (feeding, habitat, locomotion) through adaptive evolution. This often leads to phenomena of evolutionary convergence between distant lineages, although always under the strong influence of phylogenetic history. Among the main factors driving these changes are habitat-specific body shape (e.g., flattened versus slender bodies), mandibular modifications associated with diet, and limb length in relation to locomotion (Pianka 1969, 1986; Losos 1990, 1994; Vitt and Caldwell, 2013).

Several studies have addressed these issues from multiple perspectives. For example, Bauwens *et al.* (1995) analyzed the evolution of running speed in lacertid lizards, relating limb length to locomotor function and microhabitat. Losos (1990, 1994) demonstrated strong links between morphology and microhabitat in *Anolis* lizards, showing that long limbs are associated with open habitats and short limbs with closed habitats. For a comprehensive review of the relationship between form and habitat in reptiles, including the ecomorphological importance of scale structure, see Vitt and Caldwell (2013). Klaczko *et al.* (2016) identified a strong association between the cranial morphology of xenodontine snakes and their dietary preferences, while Hudry and Herrel (2025) showed that head morphological patterns reflect ecological differences: fossorial species have compact heads that widen posteriorly, aquatic species exhibit hydrodynamic profiles, and arboreal species tend to have elongated heads for maneuvering in complex habitats.

These examples illustrate that, although related species often share traits due to phylogenetic inertia, they can diverge rapidly by occupying different ecological niches or converge with distant species in similar habitats.

The present study aims to analyze the general body morphology of a large and representative sample of Liolaemidae species, exploring its relationship with three biological and ecological characteristics that could have influenced their current form: diet, microhabitat/roof preference, and reproductive mode. To fully understand morphological evolution and its link to lifestyle, it is essential to optimize these traits in phylogenetic trees (for example, using parsimony). This approach allows us to elucidate the origin of traits and the sequence of changes that have led to the morphological configuration observed in different lineages. The genus *Phymaturus* includes species of iguana-like lizards distributed mainly in Patagonia, the foothills, the Andean mountain ranges, and the Puna region of Argentina and Chile. They inhabit areas from 200 to 4200 meters above sea level, facing extreme environmental conditions such as large daily temperature ranges, strong winds, high solar radiation, and limited resources. They are characterized by a wide and robust body, relatively short limbs, slow movements, and a marked preference for rocky environments, where they use crevices as refuges (strictly saxicolous) (Fig. 1A). They are viviparous, with small litters of large offspring (Valdecantos *et al*., 2019) (Fig. 1B), and strictly herbivorous, feeding on leaves, fruits, and flowers (Castro *et al*., 2013; Corbalán and Debandi, 2014; Córdoba *et al*., 2015), and possess a well-developed anterior cecum (Figs. 1C and D). In the last 20 years, 41 of the 52 known species have been described, significantly enriching our knowledge of their taxonomy and phylogeny (Lobo and Barrasso, 2021). *Liolaemus*, for its part, is the most diverse genus in the family, with 288 species distributed from Peru to Patagonia (Argentina and Chile). This diversity is reflected in the variety of diets (herbivores, omnivores, insectivores) and in the occupation of different substrates (terrestrial, psammophilous, saxicolous, and even semi-arboreal). *Liolaemus* species can be viviparous or oviparous; viviparity

Figure 1. The genus *Phymaturus* comprises lizards with a very restricted mode of life; they are saxicolous, viviparous, and herbivorous. A) *Phymaturus extrilidus* in a rock crevice in the Sierra de la Invernada mountains, San Juan, Argentina. Photo: R. Espinoza. B) Dissected female of *P. verdugo* (MCN-UNSa 1973, SVL=101,7 mm) with two full developed fetuses (FE). C) *Phymaturus extrilidus* consuming flowers. Photo: R. Espinoza. D) Dissected female of *Phymaturus* sp. (*gualcamayo*) (MCN-UNSa 3538, SVL=93,0 mm) notice the large anterior colon (=*caecum*, ac) fulfilled of plant material.

is associated with adaptation to high-altitude, cold regions or high latitudes (Schulte *et al*., 2000). The evolutionary analysis of the family is now more accessible thanks to numerous cladistic contributions on the phylogeny of both genera (Quinteros, 2013; Lobo *et al*., 2016, 2018; Esquerre *et al*., 2019, 2022; Abdala *et al*., 2020), which allows for a comparative evaluation of the origin and evolution of traits both between genera and within *Phymaturus*.

Compared to most *Liolaemus species*, *Phymaturus* has a noticeably wider body (Figs. 2A and B). While this characteristic has been repeatedly noted in the literature, it had not previously been evaluated through large-scale comparative studies. Preliminary observations of osteological preparations have revealed that the characteristic body width of *Phymaturus* could be due to the elongation of a series of post-xiphysternal ribs with free cartilaginous ends (inscriptional ribs), although these are also present in *Liolaemus*, but arranged differently.

Given that *Phymaturus* combines biological characteristics, preferences, and modes of life (herbivorous, saxicolous, viviparous), it is essential to determine how these factors have shaped their morphology and what their influence has been. It is also relevant to consider whether the origin of these morphological changes preceded and favored the emergence of these modes of life. Were they initially herbivorous, and did this lead to changes that facilitated the other traits? Or was viviparity or a saxicolous mode of life the initial factor?. To address these questions, we must first review the background of each case and its particular problems that have arisen over time; therefore, we will do so in separate sections below, under the following subtitles: viviparity and litter size, saxicoly, herbivory, origin of characters and evolutionary tracking in trees, and morphological aspects studied to date.

Viviparity and litter size

Recent studies examined both, size and shape of body in *Phymaturus* have indicated that these dimensions may respond to certain selective regimes (Reaney *et al*., 2018; González Marín *et al*., 2018, for the *Phymaturus patagonicus* group). However, these studies do not specifically identify which aspect of the mode of life of these animals may be involved (e.g. herbivory, saxicoly), as there are no specific tests that evaluate this. Valdecantos *et al.* (2019) explicitly assessed fecundity and sexual dimorphism, revealing that species exhibiting sexual size dimorphism (female biased SSD) there is a positive relationship between brood size and brood mass with body size and body mass (respectively) of gravid females giving strength to the fecundity advantage hypothesis. Furthermore, the relationship between litter size and mass with body size and mass, respectively, was positive, providing additional support for the fecundity advantage hypothesis. In *Phymaturus*, litter size is reduced (mean 1.9) compared to most *Liolaemus* species, where litter size is generally larger. Pincheira-Donoso and Tregenza (2011) collected data from 72 *Liolaemus* species and found that only 10 species have an average of 2–2.5 offspring, while in the remaining 62 species, litter size varies from 3 to 14.5, with an average of 4.6. This reduction in litter size does not appear to be related to reproductive mode, as only 3 of those 10 *Liolaemus* species are viviparous. One might wonder whether reproductive mode, the number or size of eggs/offspring, is related to the widening of the abdomen and the increase in its capacity. In these viviparous animals, could the possession of a reduced litter size but larger fetuses have been favored by the acquisition of greater abdominal volume? Preliminary evidence suggests, for example, that *L. magellanicus* or *L. vulcanus*, both viviparous, have an average of six offspring but reach a smaller size than *Phymaturus* fetuses. Despite having elongated ribs, their arrangement has not produced the same widening effect. To clarify this, a better understanding of the phylogenetic origin of viviparity in liolaemids, as well as litter size, is needed. This should be addressed within a broader framework involving phylogenetic analysis. Previous studies have found incongruent results regarding the origin and evolution of viviparity (Pincheira Donoso *et al*., 2013; Esquerre *et al*., 2018). The main differences being that in the first case reversals are prohibited and an oviparous origin is forced on the group, in the second case the origin in the liolemids is ambiguous and it is proven that there were numerous reversal events between both modes of parity.

Saxicoly

Previous studies on saxicolous lizards have shown that they often are characterized by having acquired longer limbs and a more flattened head and body (Doughty and Shine, 1995; Vanhooydonck and Van Damme, 1999; Revell *et al*., 2007; Goodman *et al*., 2008). However, it has been indicated that despite being saxicolous species, their use of that environment may not be the same (Revell *et al*., 2007).

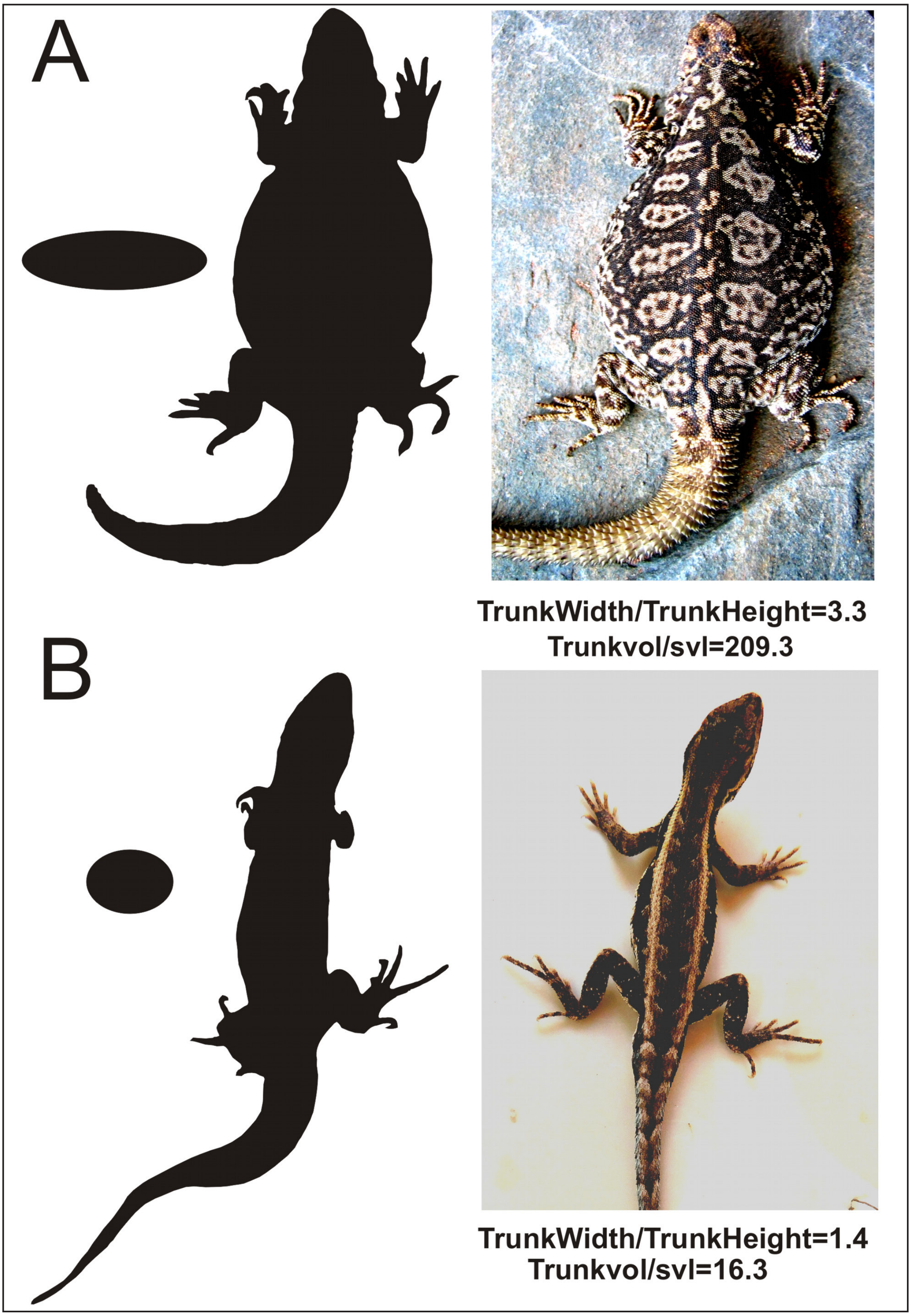


Figure 2. The body shape and trunk volume of a species of the genus *Phymaturus* and a species of *Liolaemus*. A) the strict herbivorous *Phymaturus roigorum* (MCN-UNSa 1962, SVL= 95,2 mm). To the left its body shape with a cross section at mid-trunk indicated. B) the insectivorous *Liolaemus chacoensis* (IBIGEO 6879, SVL= 39,2 mm) one of the smallest species of the genus and the minimal trunk volume/svl index value. The two individuals are shown on the same scale for comparative purposes. Trunk in *Phymaturus roigorum* is almost three times wider than the trunk of *Liolaemus chacoensis*. Trunk volume is calculated using the elliptic cylinder equation following Goodman et al. (2009).

For example, while many species move and utilize practically vertical rock walls, this behavior may not be the case for *Phymaturus*. The feet are comparatively somewhat shorter relative to the snout vent length than those of species in the Chilean group of *Liolaemus* (unpublished data) of different modes of life (not only saxicolous). Perhaps the traction and general locomotor work on the surface of the rocks and inside the cracks in our case would be reflected more in certain segments of the limb and not in all. Tulli *et al.* (2011) found that arboreal and saxicolous species of liolaemids exhibited greater resistance to mechanical traction effects across all substrates compared to generalists and psammophilous species. These species showed a positive relationship between forelimb dimensions (length of the humerus and length of the claw of finger 5) and the maximum force exerted. The distribution of species in this genus is very restricted in the most of species, to small rocky outcrops of little extension (20-30 km) to a very few that are distributed in a larger range (i.e. *P. palluma*) Lobo *et al.* (2010), Corbalán *et al.* (2011). Often, these outcrops consist of small rocks protruding from the ground, no more than 1.5 to 2 meters high, characterized by cracks of different sizes where *Phymaturus* individuals seek refuge. It is worth asking whether the body of *Phymaturus* is indeed flattened (which would be advantageous for entering their shelters) and to what extent compared to other lineages, to verify the hypothesis of longer limbs and if this body shape originated as an adaptive response to their mode of life. In a group of "flattened" lizards (family Scincidae) with saxicolous mode of life, it was initially postulated that their clutch size would be affected by a depressed body (Goodman *et al.*, 2009), *Phymaturus* in comparison to most *Liolaemus* exhibits a reduced "output" (Boretto and Ibargüengoytía 2006, 2009; Boretto *et al.*, 2007; Valdecantos *et al.*, 2019). It is viviparous and develops one to two large offspring on average (Fig. 1B), is the reduced reproductive output observed in this lineage, relative to other Liolaemidae, associated with the evolution of its distinctive body shape?. First of all, in order to answer this question, it should be known if they are flattened and to what extent (as there is currently no specific study comparing this genus to other related ones), and whether their abdominal volume differs from that of other liolaemids, and if the reduced litter size was either a novelty for *Phymaturus* or if this condition was already present in the ancestor of the family. We also do not know if other saxicolous lineages of *Liolaemus* exhibit morphological characteristics like *Phymaturus*, and if they have responded in their history in the same way.

Herbivory

Atwood *et al.* (2020) demonstrated that trophic level and body size are significant factors influencing extinction risk across all amniote species. Specifically, herbivorous reptiles and large-bodied herbivores consistently exhibit the highest proportions of threatened species. Given that the family Liolaemidae includes an entire genus of herbivores (*Phymaturus*) and several lineages of *Liolaemus* with herbivorous species, it is essential to expand our knowledge about these clades, including the origin of their dietary preferences, morphological characteristics, evolutionary history, and other related topics.

In past contributions, the researchers sought to study the evolution of herbivory in liolaemids, as well as its relationship with body size, length of the digestive tract, and the presence of parasites (Espinoza *et al.*, 2004; O'Grady *et al.*, 2005 and more recently Ocampo *et al.*, 2022); however, some conclusions in those contributions are somewhat contradictory, which warrants a reassessment. In Espinoza *et al.* (2004), it was found that within the Liolaemidae family, herbivory has evolved more frequently than in all other squamate reptiles combined. Furthermore, in contrast to other herbivorous lizards and according to existing theory, most herbivorous liolaemids are small-bodied and live in cold climates. Herbivory is generally believed to evolve only in reptile species that are large-bodied, inhabit hot climates, and maintain high body temperatures. These three well-known "rules" of herbivory are the basis of the physiological constraints that explain the scarcity of herbivorous reptile species. O'Grady *et al.* (2005) compared a variety of digestive tract specializations among different diet categories within the family Liolaemidae (18 *Liolaemus* spp and 3 *Phymaturus* spp) to test the hypothesis that herbivores require greater intestinal complexity to process plant matter, and that herbivory favors the evolution of larger body size. Herbivorous liolaemids were found to be larger relative to their omnivorous and insectivorous counterparts, resulting in larger viscera. The herbivorous species examined in this study lacked the morphological specializations observed in herbivores of the families Iguanidae and Agamidae (see Iverson, 1982). O'Grady *et al.* (2005) found that the length of the small intestine of herbivorous liolaemids was longer than that of others. However, Hoppe *et al.* (2021) found that the large intestine is longer in the case of herbivores. Nevertheless, other modifications, not necessarily as drastic as those observed in iguanids, could be present in herbivorous liolaemids, which deserves a more detailed study (in Lobo *et al.*, 2016, folds were described in the walls of the most posterior end of the large intestine in species of *Phymaturus*).

The first to study the relationship between body size and diet in liolemids were O'Grady *et al.* (2005), although their taxonomic sample was limited in terms of the representation of the different groups (21 species out of 338 species recognized for the family, Abdala *et al.*, 2021). In fact, only a single example of the *montanus* group was included, a clade consisting of more than 60 species inhabiting the puna and cordillera by Abdala *et al.* (2020) (*L. dorbignyi* probably *L. vulcanus*; in O'Grady's study, data on the species used were not indicated). Examples of small-sized herbivores that contradict the herbivory-greater body size hypothesis have been described in subsequent studies, such as Valdecantos *et al.* (2012), who found that *L. poecilochromus* (now *L. kunza*, see Abdala *et al.*, 2021) is mainly herbivorous (>80% plants in the diet; Cooper and Vitt, 2002; Espinoza *et al.*, 2004), which is surprising for several reasons. Firstly, the old "rules" of herbivory for lizards stipulate that herbivores must be large-bodied (Pough, 1973) (*L. kunza* males: 63.5mm, mean SVL females: 62.8 mm).

Herbivorous species of liolaemids seem to be an exception to the "rule" of body size, although within liolaemids herbivorous species according to O'Grady *et al.* (2005) are generally larger than non-herbivorous species. Herbivory would also be present in other small altitude *Liolaemus* species. Olivera Jara and Aguilar (2020) presumably raise to 9 the species of the *L. montanus* group that primarily feed on plants (although only a few works are specific diet investigations, Olivera Jara and Aguilar, 2020; Valdecantos *et al.*, 2012). On the other hand, another aspect not yet studied is that referred to the volume or capacity of the abdominal cavity. Does a greater volume favor the development of larger digestive organs?. The body shape of *Phymaturus* seems to offer greater abdominal capacity (volume) compared to an insectivorous species of *Liolaemus* (Fig. 2), but trunk volume has not been measured until now. Clauss *et al.* (2017) proved that, in mammals, herbivores generally have a larger body cavity volume than carnivores, although they included other tetrapods in the study (including some reptiles), and their conclusions are not decisive for those groups. Hoppe *et al.* (2021) found that the large intestine is longer in the case of herbivores.

Being *Phymaturus* a strict herbivorous animal, one might wonder if this characteristic is evident when we compare it with species of the sister genus *Liolaemus* where omnivory and insectivory predominate, with herbivory occurring only in some lineages. Another character obviously related to diet and not considered in all these studies is dental morphology that would be related to eating habits. Etheridge (1995), Lobo and Abdala (2001) and Lobo *et al.* (2012) studied the morphology of the teeth in *Ctenoblepharys*, *Liolaemus* and *Phymaturus* for systematic or phylogenetic reconstruction purposes only. However, dental morphology has not yet been studied comparatively between herbivores of both genera (*Phymaturus* and *Liolaemus*) to assess the existence of similar adaptations. The studies conducted by Parsons and Cameron (1977) and Iverson (1980, 1982) represent the most important contributions to date, and no similar studies have been conducted on liolaemids.

About the modifications in the digestive tract related to the herbivorous diet in reptiles. In fact, there is a lack of knowledge about the morphology of the digestive tract that should be addressed. In a recent contribution, Ocampo *et al.* (2024) found that herbivorous species have evolved larger heads, shorter hindlimbs, and a small difference between forelimb and hindlimb length, while omnivores and insectivores exhibited smaller heads and longer hindlimbs. Their conclusions were based on a set of seven measurements and the reconstruction of ancestral states. The evolution of diet was carried out using probabilistic methods, finding percentages of probabilities about the origin expressed in pie charts see Fig. 1 from Ocampo *et al.* (2024).

The origin of characters and evolution tracking on trees (and their problems)

The studies published so far have used disparity of criteria when reconstructing ancestral states or analyzing the evolution of these aspects (ML, Bayesian analysis and parsimony) so they are not completely comparable, and in all cases the comparisons with outgroups are restricted to just one or completely null (e.g. Pincheira-Donoso *et al.*, 2013; Esquerre *et al.*, 2018). Hence the need to reevaluate the origin and evolution of these aspects. The limited use of outgroups or the arbitrary use of only one significantly affects the result regardless of the method used, whether probabilistic methods or parsimony (Grant, 2019). Schulte *et al.* (2000) optimized viviparity using parsimony, but with wrong assignment of reproductive modes in outgroups, while Pincheira-Donoso *et al.* (2013) applied a Bayesian analysis of ancestral reconstruction but forced the analysis in the root of Liolaemidae in the oviparous mode without considering the distribution of these characters in the outgroups and those related to Liolaemidae. Esquerre *et al.* (2018) employed Bayesian analyses, utilizing information from a single outgroup, leaving the explanation with a high degree of uncertainty at the basal nodes (indicated by probabilities pie chart at nodes). Regarding herbivory, Espinoza *et al.* (2004) optimized a Liolaemidae tree using maximum likelihood and parsimony for 91 species across three diet categories, while, more recently, Ocampo *et al.* (2022), found results that are not consistent with those of Espinoza *et al.* (2004), employing Bayesian methods and their ancestral reconstructions are uncertain/ambiguous (probability percentages pie charts at nodes) (furthermore, they did not consider the use of multiple outgroups, which can also influence the analyses.). The definition of the diet categories is problematic, as there are few detailed studies of the diet of species involving the analysis of the contents of a large sample of individuals (information is available for only about 10% of species). In several cases, it has been reported that diet can be affected by seasons, ontogeny, and sexual dimorphism. In the case of the saxicolous mode of life, it has not been explicitly studied. Blankers *et al.* (2013) did it for Iguania including representatives of all families, although they used an extremely limited sample of liolaemids (5 spp.).

Morphological aspects studied so far that raise questions

Cei *et al.* (2003) found that females of viviparous *Liolaemus* species have a greater trunk length than those of oviparous species, although the effect of phylogeny was not evaluated at that time. O'Grady *et al.* (2005) indicated that, in their sample of liolaemids, the small intestine is longer in herbivores. However, the results of this work are not entirely conclusive and exhibit some contradictions with other studies. Hoppe *et al.* (2021), studying the length of intestines in reptiles and mammals, found that the large intestine is longer in herbivores. Previous studies on *Liolaemus* did not find any relationship between morphology and habitat use, but they did find correlations between morphology and escape behavior (Jaksic and Núñez, 1979; Jaksic *et al.*, 1980; Schulte *et al.*, 2004; Pincheira-Donoso *et al.*, 2009). Tulli *et al.* (2011) found a positive relationship between grip strength and forelimb length in saxicolous and arboreal species. Additionally, Tulli *et al.* (2012) studied the effects of different substrates on the locomotor performance of various species, finding that most morphological characters would be restricted by phylogeny, considering the morphology of liolaemids as highly conservative. Toyama (2017) analyzed morphology relationships with habitat use in Tropidurinae, incorporating a sample of liolaemids and relating them to genera of Tropiduridae following Pyron (2013). However, it is currently known that the relationships of this family are different (Burbrink *et al.*, 2020), and their results are not very significant for the liolaemids. Regarding some morphological relationships and habitat use, he finds similar results to those found previously (longer forelimbs, narrower bodies in arboreal, Sinervo and Losos, 1991; Kohlsdorf *et al.*, 2004; length of toes and nails greater in arboreal species than in terrestrial ones, Ribas *et al.*, 2004; Tulli *et al.*, 2009). For saxicolous species, Revell *et al.* (2007) and Toyama (2017) find flattened heads and bodies, and long extremities. Anyway, Revell *et al.* (2007) indicated that for some taxa, this rule would not apply, possibly due to different uses of the same habitat.

In the present contribution, our aim was to analyze the origins of viviparity, herbivory, and the saxicolous mode of life in liolaemid lizards, as well as the possible morphological changes related to these characteristics. Since during the evolution of the group the three aspects have interacted in some way simultaneously and not independently of each other, although we do not know which has prevailed over the others or to what extent, it is inevitable to study them together. For example, a hypothesis to illustrate this problem could state that "in *Phymaturus* a greater abdominal volume allowed having larger viscera for the herbivorous diet, thereby facilitating the development of larger offspring, but this greater volume and size was conditioned by the saxicolous mode of life, using cracks as shelters for which more flattened bodies were needed". However, to confirm this hypothesis, we must first study the morphologies of the different lineages, relating them to their modes of life within the context of their phylogenetic history. What came first, viviparity, herbivory, or the saxicolous mode of life? Which morphological characters were influenced in each case? In summary, as a general hypothesis, it is considered that the mode of birth, diet, and the use of preferred habitat are reflected in specific body measurements (such as head, trunk, and extremities) that will be the result from the interaction of the three aspects of the mode of life mentioned, without one prevailing over another. Characters not influenced by mode of life are surely due to phylogenetic inheritance.

The first step needed to study the origin and evolution of any feature and to advance any kind of interpretation is to optimize it in a phylogenetic tree. To have a broad look at these issues indicated above, we decided to study these data applying both conventional statistics (ANOVA, PCA) and tests where the phylogenetic relationships of the analyzed species are considered. We also consider it important to specify our considerations about the categories assigned to species regarding diet and mode of life before studying their evolution.

Materials and methods

Character mapping

The optimization of characters was performed solely for the purpose of establishing their origin and changes at the root of the liolaemids and the nodes of *Phymaturus* and *Liolaemus,* as well as their two large clades. The optimization of the three characters, herbivory, viviparity and saxicolous use of habitat were performed using TNT Goloboff *et al.* (2008) on a meta tree (315 spp.) based on the last topologies of *Phymaturus*, *Liolaemus,* and their major clades compiled by Quinteros (2021), and following also (in part) Portelli and Quinteros (2018), Lobo (2001, 2005), Abdala (2007), Abdala *et al.* (2020), Lobo *et al.*, (2012, 2016, 2018), Lobo and Barrasso (2021) and Esquerre *et al.* (2019, 2022). This metatree and the complete optimizations can be seen in the supplementary files S1-S3. That metatree is also shown in Fig. 8. Since many of the relationships within the terminal clades of *Liolaemus* remain unresolved, as well as the existence of alternative hypotheses, we only focus on the origin of these characters at the basal nodes. We employed maximum parsimony as criterion (preferred because provides rejectable hypothesis with decisive assignations to ancestral nodes instead of probability pie assignations to nodes as other methods do). Additionally, we utilized all pleurodont families as outgroups (based in the last hypothesis of Squamate phylogenetic relationships available in literature, Reeder *et al.* 2015, Burbrink *et al.* 2020). Squamate relationships for outgroup optimizations were made considering Reeder *et al.* (2015) (combined hypothesis of molecules and morphological information), the use of Burbrink *et al.* (2020) (molecular only analysis) didn´t change conclusions in our analysis because the peculiar distribution of the three characters, which are rare in most other families (Fig. 1). We consider it important to include a large sample of outgroups in the analysis, unlike in previous studies (i.e. Pincheira Donoso *et al.*, 2013, Esquerre *et al.*, 2018), because the limited use of outgroups or the arbitrary use of only one significantly affects the result regardless of the method used, whether probabilistic methods or parsimony (Grant, 2019).

Necessary clarifications to be made before the analysis of the diet in liolaemids

Because there exist only a very limited number of contributions to the diet of liolaemids, it is quite difficult, or at least somewhat risky, to estimate or generalize about its evolution and rates of changes, transitions etc. (as in Ocampo *et al.*, 2022). In fact, only 37 articles (see Appendix 1) have been published with detailed diet analysis of 32 species (in a total of more than 330 spp of Liolaemidae, Abdala *et al.*, 2021). Most diet assignments to species come from occasional observations of feces, the dissection of one or a few individuals, behavioral observations made in the field, or are taken from the original taxonomic descriptions, which introduce a commentary on the natural history of animals. None of these assignments consider the existence of ontogenetic variation, seasonal variation, and even sexual dimorphism related to diet, that are only detected after the study/examination of a numerous series of individuals, of both sexes, ages and samples taken in different seasons (Rocha 1998, 2000; Valdecantos *et al.*, 2012; Semhan *et al.*, 2016, among others). With the purpose of providing comparable results with previous studies, we considered that the current classification of the three categories of diet used for liolaemids in the literature: herbivorous, omnivorous, insectivorous, but for mapping character evolution we preferred in the present study a more conservative analysis considering just herbivorous versus non-herbivorous.

Different ways of considering a lizard to be saxicolous

With respect to the definition of saxicolous, it is important to make some distinctions, i.e. species of the *Liolaemus elongatus* clade are traditionally considered to be saxicolous in their vast majority (Cei, 1986), but for example *Liolaemus ceii* in Lonco Luan (Neuquén province, Argentina) can be seen on rocks, but they always take refuge under holes located under the same rocks they use for basking, it is not the same as a *Liolaemus heliodermis* in Tucumán that always takes refuge in cracks (like *Phymaturus*) (Robles and Halloy, 2011). Lizards have different reasons for carrying on their activities over rocks, sunbathing, social communication, hunting prey (in case of insectivorous species), mating etc., having their preferred refuges in rock crevices or not, which one of these activities can affect morphologies during their evolution?. The species that we find on the rocks could be differentiated by 1) exclusive use of cracks as shelter (*Phymaturus*, some spp. of the subclade of *Liolaemus capillitas*, some spp. of the clade of *Liolaemus dorbignyi*) 2) use of cracks in the rocks as well as hollows and caves in the earth or under rocks as shelter (majority of spp. of the *Liolaemus elongatus* clade, some spp. of the *Liolaemus dorbignyi* clade, some spp. of the *Liolaemus nigroviridis* clade), and 3) use of hollows and caves in the ground as refuge (most of *Liolaemus* spp. that are indicated many times as saxicolous). We think that making the differentiation of saxicolous modes of life would be more informative about their evolution and morphological adaptations (if there exist). However, this knowledge is null along liolaemid literature, and we are unable to conduct analyses with a new criterion. We optimized the saxicolous mode of life occurrence following the traditional and actual literature for assigning this feature to each species. But for the PCA analysis combining diet and lifestyles versus morphological characters we did make a difference, as is explained below.

Anatomical observations

All specimens studied are listed in Appendix 1. We studied 322 skeletons of 61 spp of *Liolaemus*, *Ctenoblepharys*, 29 spp of *Phymaturus,* and 73 skeletons of pleurodont outgroups. Data were obtained from cleared and stained specimens prepared following Wassersug (1979), which are deposited at MCN-UNSa and IBIGEO herpetological collections, and from RX images taken by Richard Etheridge, currently stored at IBIGEO library.

To compare whether the number of trunk vertebrae between the genera *Liolaemus* and *Phymaturus* is statistically significant, a Wilcoxon test was performed (the distribution was not normal, according to the Shapiro-Wilks test). To compare whether the length of the inscriptional ribs between *Liolaemus* and *Phymaturus* is statistically significant a T-test was performed (the distribution was normal according to the Shapiro-Wilks test).

Additionally, we dissected and studied the digestive tract of 54 *Phymaturus* and 49 *Liolaemus* specimens, six and eight species respectively. For everyone, the sex was recorded, and the snout-vent length (SVL) was taken. The observation and analysis of the digestive tract were also carried out using a longitudinal section of the same (dissection) to determine the presence/absence of folds, valves and/or sphincters (following Parsons and Cameron, 1977; Iverson, 1982; Srichairat *et al.*, 2018). Detailed observations of the interior of the tract were performed using a binocular magnifying glass. The different morphological characteristics of the internal mucosa were photographed using a digital camera coupled to an Olympus stereoscopic magnifying glass, as well as a Nikkon Coolpix B B500 compact camera with macro settings for submerged material.

Body measurements and statistical comparisons

External measurements were made based on alcohol-preserved specimens deposited in the following herpetological collections: MCN-UNSa (Museo de Ciencias Naturales de la Universidad Nacional de Salta, Argentina), IBIGEO (Instituto de Bio y Geociencias del NOA, Salta, Argentina) and FML (Herpetological collection of Fundación Miguel Lillo, Tucuman, Argentina). External morphology data were collected from a sample comprising 123 spp of *Liolaemus* (n= 882) and 33 spp of *Phymaturus* (n=309), in addition to *Ctenoblepharys adspersa* (n=5). Measurements taken to estimate trunk volume of species included trunk length, trunk width, and trunk height (measured at mid-trunk), and the ellipsoidal cylinder formula was applied (following Goodman *et al.*, 2009) ($V=\Pi Rrh$) (R = half the width of the trunk measured at half its trunk length, r = half the height at half its trunk length, and h = interlimb length). According to Goodman *et al.* (2009), applying this formula yields similar results to those obtained using water displacement (Archimedes principle). The advantage of using that formula is the collection of individual measurements that are analyzed for other purposes (i.e., trunk height for revealing the potential flattened shape of bodies of saxicolous species). Also, we measured: height, width, and length of the head; hand, length and width of radio-ulna, humerus; thigh and tibia, and foot length (from ankle to the tip of the IVth toe).

To have a broad look at these issues indicated above, we decided to study the morphology of liolaemids using both conventional statistical methods and phylogenetic tests. For comparisons of body measurements, we utilized INFOSTAT software (Di Rienzo *et al.*, 2012) for all statistical analyses. The analyzed characters represent morphometric variations, including trunk length (tl), trunk width (tw), trunk height (th), head height (hh), head width (hw), head length (hl), femur length (fe), femur width (few), tibia length (ti), tibia width (tiw), foot length (fo), hand length (ha), humerus length (hu), humerus width (huw), radius length (ra), radius width (raw), and trunk volume (tv). Since the trunk cavity contains the viscera, and this could make a difference for herbivores, we decided to measure the volume of the trunk. Given species variability in body size, which can affect all morphometric measurements, we conducted a regression for these characters using SVL as the independent variable, and the residuals were used for ANOVA and PCA. We performed an ANOVA (analysis of variance), followed by Fisher's LSD (Least Significant Difference) test for multiple comparisons to analyze external morphology; we used the conventional categories of herbivorous, omnivorous, and insectivorous (being cautious in our interpretations due to the lack of information in the literature as we detailed above). We use non-parametric tests when the data does not follow a normal distribution (Kruskal-Wallis). Comparisons by mode of life are made discriminating between species classified as: "psammophilous", "strict psammophilous", "terrestrial", "saxicolous" and "strict saxicolous". We performed two different PCA analyzes (variance-covariance matrix), one comparing the lineages of *Liolaemus* and *Phymaturus* for the morphometric variables. The second analysis was based on known combinations of diet and lifestyle assigned to the species sample included in this study (these were: strict saxicolous-insectivorous, strict saxicolous-omnivorous, strict saxicolous-herbivorous, terrestrial-insectivorous, saxicolous-insectivorous, saxicolous-omnivorous, saxicolous-herbivorous, terrestrial-omnivorous, terrestrial-herbivorous, strict psammophilous-insectivorous, strict psammophilous-omnivorous, psammophilous insectivorous, psammophilous omnivorous, psammophilous herbivorous, pseudo-arboricolous-omnivorous). This combination is made considering that both biological aspects evolved together, and their interaction may have affected morphological aspects of the animals to different degrees. Strict saxicolous species were distinguished from saxicolous species based on the former exclusively requiring cracks in rocks as shelter, whereas the latter can utilize other types of shelters. Strict psammophilous species dive into dunes and have restricted use of the environment, while psammophilous species have a wider range of environmental utilization and do not exhibit specialized burrowing behavior in sand (see Halloy *et al.*, 1998), described differences in behavior between members of the *L. wiegmannii* group and the *L. fitzingerii* complex. To evaluate the degree of independence/dependence of these morphological characters on the phylogenetic history of the group, we performed a phylogenetic ANOVA (Garland *et al.*, 1993) using the residuals of regression of log10 transformed characters with Log10svl as the regressor variable. Because the distribution of habitat preference was not normal, the Kruskal-Wallis test was performed. Statistical significance in the phylogenetic ANOVA was assessed using a permutation test with 1,000 permutations. P-values for post-hoc comparisons were adjusted using the Holm method (Holm, 1979) to account for multiple testing. We also calculated the lambda paramether of phylogenetic signal (Pagel, 1999). These tests were performed in R 4.3.0 (R Core Team, 2023) applying the "phytools" (Revell, 2012) and "ape" (Paradis and Schliep, 2019) packages.

Results

1-Origin and evolution of viviparity, herbivory, and saxicolous mode of life.

Viviparity (Fig. 3A and Fig. S1) occurs in only two families of pleurodontans: Phrynosomatidae and Liolaemidae. Zuñiga-Vega *et al.* (2016) reported five instances of the origin of viviparity in Phrynosomatidae (within *Phrynosoma* and *Sceloporus*), with oviparity being the ancestral parity mode of this family. In Liolaemidae, the common ancestor of *Liolaemus* and *Phymaturus* is recovered as viviparous. Within *Liolaemus* further changes to oviparity (13 times) are found 2 times in the *alticolor-bibroni* group, and eleven in the *nigroviridis*, *lemniscatus*, *gravenhorsti*, *nigromaculatus*, *tenuis*, *punmahuida*, *kriegi*, *monticola*, *capillitas* and *petrophilus* groups and in the subgenus *Eulaemus* in the *boulengeri* group. Terminal re-acquisitions of viviparity seem to be more restricted, occurring only 6 times, once in the *nigroviridis* group, 3 times in the *alticolor-bibroni* group, and twice in *Eulaemus* (*L. xanthoviridis* and the *ornatus* clade). The size of the litter was also optimized; most pleurodonts have an average litter size of 4.8–5.8. There was a reduction in litter number among pleurodonts, at the node of leiosaurids and liolaemids, to 3.7–4.7. Subsequently, there was a further reduction for the ancestral node of *Liolaemus* and *Phymaturus* (1–2.5 eggs or offspring). Within *Liolaemus,* the number increased in certain lineages. In summary, both viviparity and reduced litter size are primitive and did not represent anything new in *Phymaturus*.

Within pleurodontans the herbivorous diet arises twice: in Iguanidae and in liolaemids (Fig. 3B). This occurs independently in *Phymaturus* and at least 18 times within *Liolaemus (kriegi ceii* group, *lineomaculatus* group, 9 times within the *montanus* group, 4 times in the *boulengeri* group*, L. araucaniensis, punmahuida* group, and *nigromaculatus* group) (Fig. S2). Saxicoly in Pleurodonta arose several times: Iguanidae, Tropiduridae, Phrynosomatidae, Opluridae and Liolaemidae (Fig. 3C and Fig. S3). Iguanas are arboreal or terrestrial, except for *Sauromalus*; the root of Iguanidae is non–saxicolous. Blankers *et al.* (2013) found in their optimization of saxicoly the non-saxicolous mode of life as the ancestral state for Tropiduridae; because *Microlophus* and several species of *Stenocercus* and *Tropidurus* are saxicolous and relationships among genera are not very well resolved currently, we prefer to assign a more conservative ambiguous state for the family root. Within the family Phrynosomatidae, a saxicolous mode of life, occurred in *Petrosaurus* and several species of *Sceloporus*. We follow Blankers *et al.* (2013) that assign at the root of the family a non–saxicolous state. In Opluridae, *Chalarodon madagascariensis* is terrestrial, while *Oplurus* consists of both arboreal and a saxicolous clade. The root of this family is non–saxicolous. In liolaemids, the saxicolous mode of life occurred in *Phymaturus*, while the ancestor of *Liolaemus* was non–saxicolous. Within *Liolaemus,* saxicolous mode of life arises at least 13 times; this includes seven times in the subgenus *Eulaemus* (*L. kolengh*, *L. robertoi*, *L. orientalis*, *L. chlorostictus, L. dorbignyi, L. jamesi* and *L. qalaywa* species or species groups) and six times in *Liolaemus* sensu stricto (within the *alticolor-bibroni*, *nigromaculatus*, *elongatus*, *nigroviridis*, and the *altissimus* groups once, and in *L. nitidus*) (Fig. S3).

2-Body shape and trunk volume

The characteristic body shape of *Phymaturus,* which sets it apart from other liolaemids, is clearly given by the shape of its trunk, they are wider. When examining a cross-section of the middle of the trunk, the cutting surface is an oval, with its long axis greater than the vertical one. In fact, the width of the trunk is more than three times its height (Fig. 2), while in most *Liolaemus* and *Ctenoblepharys* this relationship is much less pronounced. It is known from previous studies that herbivorous animals tend to reach greater sizes than those that are not (see, for example, Espinoza *et al.*, 2004). The most common explanation is that this would allow them to contain larger viscera to better process plant–origin food.

In Figure 4, we present the distribution of the trunk volume to SVL ratio across 156 species of *Phymaturus*, *Ctenoblepharys adspersa* and *Liolaemus*. As evident, the *Phymaturus* species in this sample are located at the far left of the graph, exhibiting the largest volumes of the trunk, especially the species of the *palluma* group, surpassing even the *patagonicus* group (Fig. 4). Our estimations of trunk volume indicate that *Phymaturus,* with a few species of *Liolaemus* (*kriegi* and *montanus* groups), have the highest values of trunk volume/SVL. Figure 4 illustrates that *Phymaturus* display 2–10 times greater trunk volumes than insectivorous *Liolaemus* species. Below a trunk volume/SVL =100, only 7 out of 112 species are herbivorous. Above this value, 87% are herbivorous (with only 6 *Liolaemus* omnivorous species); there are no insectivorous species surpassing trunk volume/SVL= 100.

In Figure 4B, we show the number of herbivorous species across different lineages. All species within the *palluma* and *patagonicus* groups of *Phymaturus* exhibit herbivory, along with the species of the *Liolaemus kriegi* subclade (5 spp) (after our own dissections of *L. buergeri*, *L. kriegi*, and *L. ceii*, and the report for *L. tregenzai* and *L. zabalai* of Pincheira-Donoso and Scolaro, 2007 and Troncoso Palacios *et al.*, 2015). Herbivory occurred at a low frequency

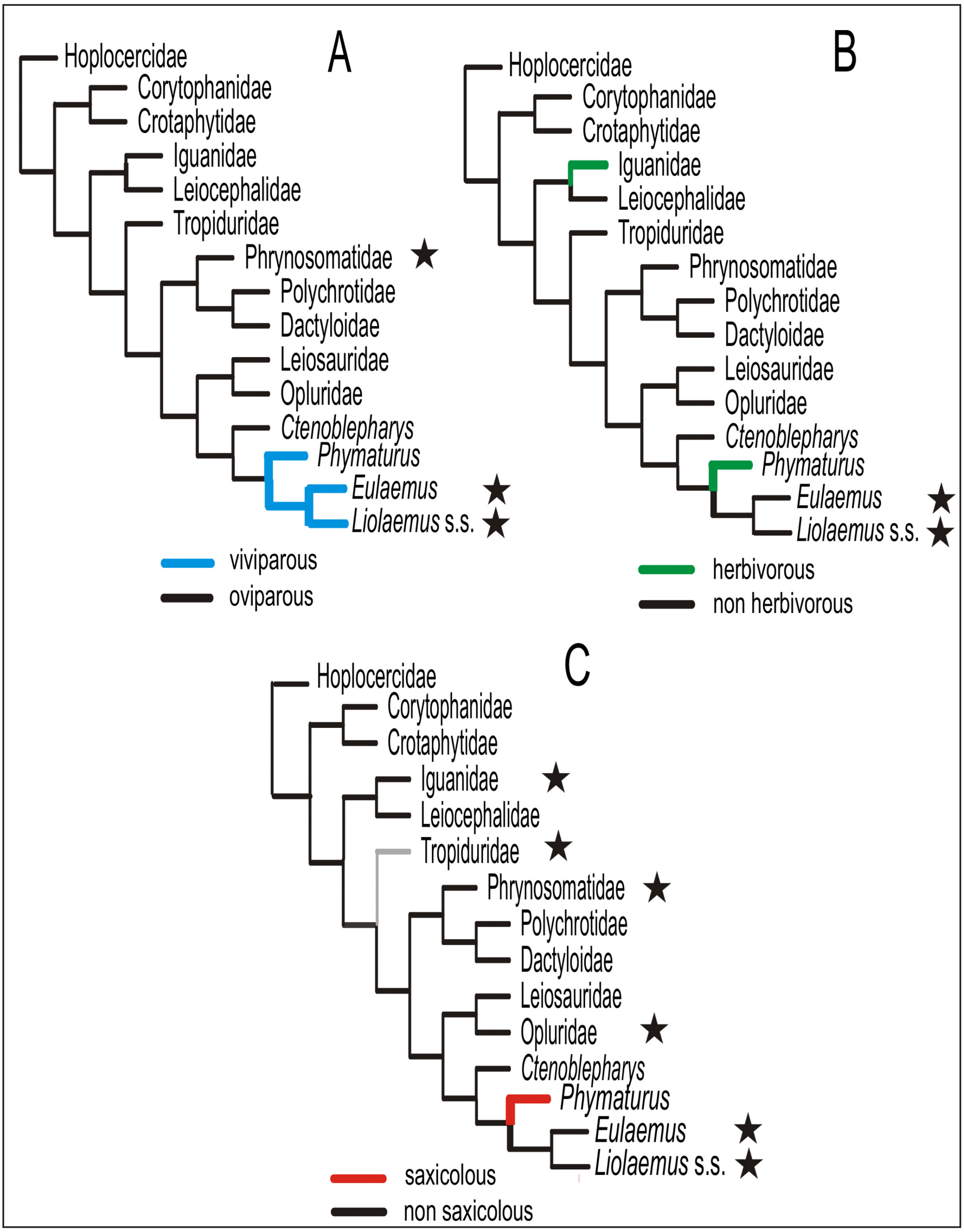


Figure 3. Liolaemid genera and their pleurodont relatives. Optimizations were made on the tree topology of squamates recovered by Reeder et al. (2015) based on an analysis of total evidence. A) Viviparity was acquired in the ancestor of *Liolaemus* and *Phymaturus* and was lost numerous times during evolution (within both subgenera of *Liolaemus*). With the star we indicate the origin of viviparity within Phrynosomatidae (within *Phrynosoma* and *Sceloporus* at least five times according to Zuñiga-Vega et al., 2016), oviparity being the ancestral parity mode of this family. B) Herbivory evolved twice, in Iguanidae and in *Phymaturus*, the basal condition for *Liolaemus* is non herbivorous, different lineages within both subgenera of *Liolaemus* got the condition independently (indicated by stars). C) The saxicolous mode of life occurred several times within pleurodonts (indicated with a star), within Iguanidae (*Sauromalus*) Phrynosomatidae (*Petrosaurus* and spp. of *Sceloporus*), Tropiduridae (*Microlophus* and spp. of *Stenocercus* and *Tropidurus*), Opluridae (saxicolous species of *Oplurus*) and Liolaemidae (*Phymaturus* and at least 11 eleven times within *Liolaemus*, the basal condition for *Liolaemus* is non saxicolous). In Liolaemidae *Phymaturus* and several lineages of *Liolaemus* are saxicolous. For more detail and discussion see in the text.

within the larger clades: *L. montanus* (69 spp), *L. elongatus-petrophilus* (30 spp), and *L. boulengeri* (74 spp) groups. Two species within the small *L. lineomaculatus* group (7 spp) are herbivorous, while two are omnivorous, and the diet of the remaining three remain unknown (Abdala *et al*., 2021).

3-Changes on *Phymaturus* anatomy

After studying the skeleton of 322 individuals of *Phymaturus*, *Liolaemus* and *Ctenoblepharys*, (Figs. 5 and 6) we found three important characteristics to mention. Analysis of the trunk skeleton in liolaemids revealed that the inscriptional ribs are more elongated in *Phymaturus,* averaging 50.3% (SD= 0.06; n=54; 28 spp) of the total rib length; whereas in *Liolaemus,* this measurement reaches only 26.2% (SD= 0.09; n= 69; 26 spp) (Figs. 5A and B). Consequently, the elongation of the inscriptional ribs, and not the bone portion, contributes to the increased trunk width observed in *Phymaturus*. Indeed, the difference between the lengths of the inscriptional ribs of *Liolaemus* and *Phymaturus* is statistically significant (T test, p< 0.0001). However, the position of the postxiphysternal ribs in *Phymaturus* differs, being situated at a lower angle relative to the anteroposterior axis of the vertebral column compared to the other genera (Fig. 5B). This elongation of the ribs, added to their more perpendicular location than in *Liolaemus*, gives the typical silhouette of a widened body observed in species of this genus, as depicted in Figure 2. At the same time, we observed that, on average, the genus *Phymaturus* possesses more trunk vertebrae compared to *Liolaemus* and *Ctenoblepharys*, as well as most other pleurodonts (Fig. 5C), (mean= 26.32; versus 24.19 of *Liolaemus* and 25 of *Ctenoblepharys*). Running the Wilcoxon test, we found that the differences between *Liolaemus* and *Phymaturus* genera in the number of trunk vertebrae are significant (p< 0.0001).The combination of having more vertebrae in the trunk and longer inscriptional ribs has facilitated an increase in the volume or resulting capacity of the trunk in *Phymaturus*, making it possible to carry larger viscera, which is important in relation to its strictly herbivorous diet. Our review of 64 digestive tracts across 9 species of *Liolaemus* and 6 of *Phymaturus* has allowed us to appreciate interesting characteristics in the internal relief of the digestive tract. The small intestine in *Phymaturus* species of the *palluma* group has sections with smooth walls forming dilated chambers separated by 1–3 pseudo–valves (Fig. 6). In *Liolaemus*, the walls feature conspicuous longitudinal folds along most of their length, lacking chambers (except in herbivorous forms, which can exhibit pseudo–valves contrary to insectivorous species). These pseudo–valves were found in individuals of herbivorous species of *Liolaemus*: *L. buergeri*, *L. kriegi*, *L. albiceps*, and *L. kunza* representing different lineages of the genus. In the case of *Liolaemus kunza*, every individual exhibits these pseudo–valves; their diet was studied by Valdecantos *et al.* (2012), which includes lizards of small size and with reduced trunk volume, unlike the large size observed in most herbivorous species (Fig. 4). The anterior colon has smooth internal walls in most of the species studied, both in *Liolaemus* and *Phymaturus*. It may present small transverse or oblique folds, but not in the entire sample of individuals; they were found in three species of *Phymaturus* (*P. palluma*, *P. indistinctus*, and *P. yachanana*) and two of *Liolaemus* (*L. buergeri* and *L. tulkas*). Other differences found in the morphology of the digestive tract include the middle region of the stomach, where most species of *Phymaturus* (except *P. aguanegra* and *P. zapalensis*) have longitudinal folds, while in most *Liolaemus* species it lacks folds (except for the herbivorous *L. kriegi* and *L. buergeri*). The pyloric region is externally differentiated from the rest of the stomach; it is more tubular and elongated in shape in *Phymaturus*, while being short and inconspicuous in *Liolaemus*. The duodenal bulb is conspicuous in *Liolaemus* species but indefinite in *Phymaturus*. Measurements and proportions of the different sections of the digestive tract and their analysis are part of another ongoing research.

4-Head, trunk and limb measurements, phylogenetic signal

Our observations indicate that herbivorous species are larger (ANOVA, F=656.49, P <0.0001) than omnivores or insectivorous species. Herbivores (average adult svl: 85.4 mm) were 14.7% larger than omnivores species (73.8 mm) and omnivores were 19% larger than insectivores (59.5 mm). In Table 1, we found that the measurements showing significant differences in the ANOVA regarding herbivory are tl (trunk length), tw (trunk width), head length (hl), foot length (fo), humerus length and width (hu an huw), and tv (trunk volume). Herbivores exhibit greater trunk length (tl) and trunk width (tw) compared to omnivores and insectivores. Head height (hh) is lower in herbivores than in the other two groups. Head length (hl) is higher in insectivores than in omnivores, and in turn, omnivores have higher head length than herbivores. Additionally, in herbivores, the foot (fo) is shorter than in omnivores and insectivores. Both humerus length (hu) and width (huw) are greater in herbivores compared to omnivores and insectivores. The trunk volume of an

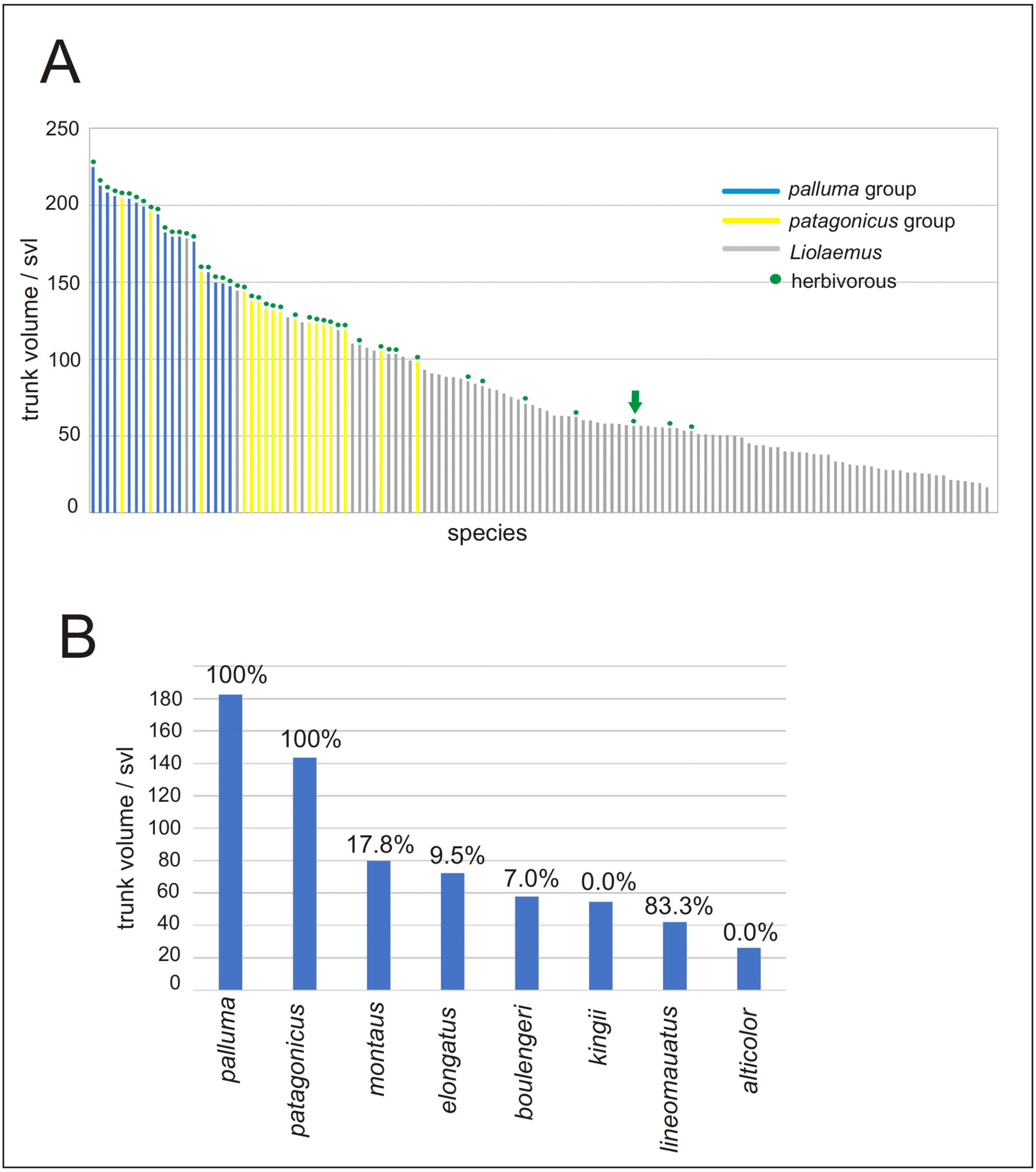
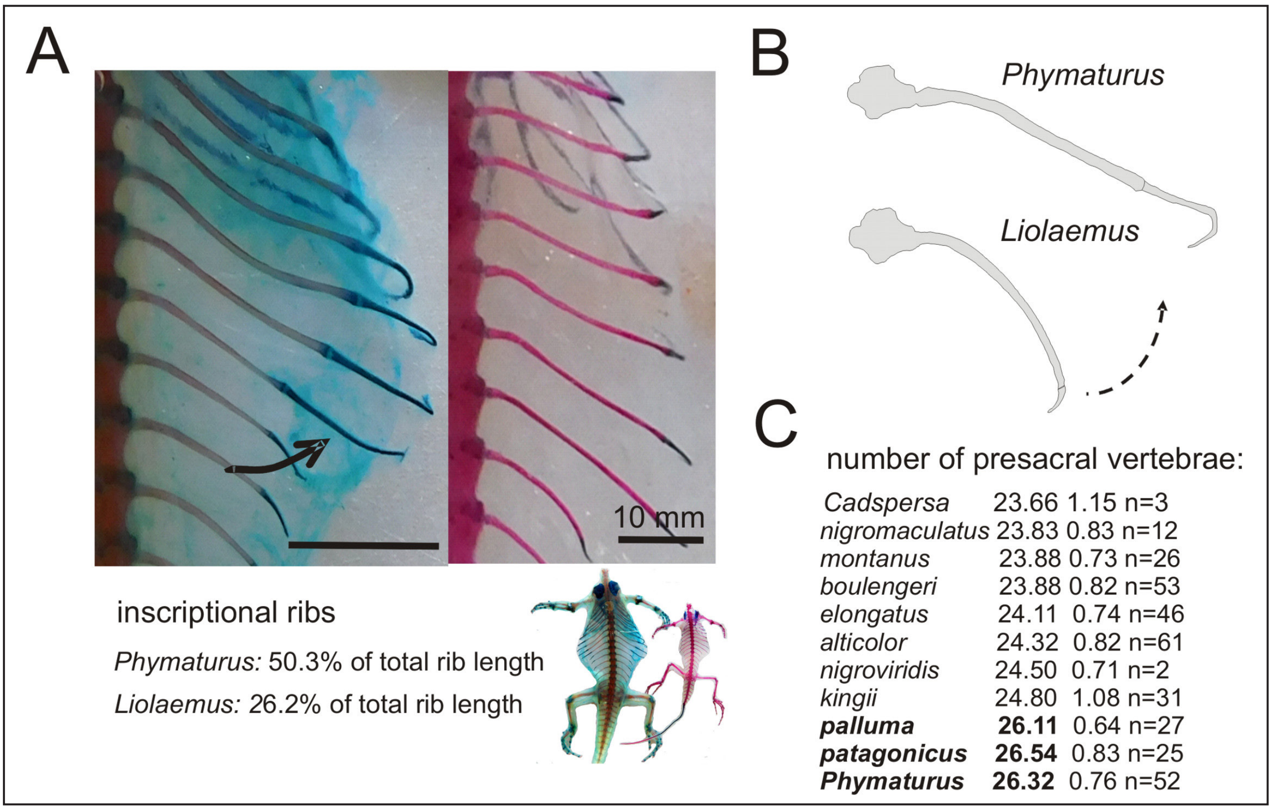


Figure 4. Herbivory in liolaemids and its relationship with trunk volume and body size. A) The distribution of trunk volume/svl index along the studied sample (156 spp.) showing the enlarged trunk capacity found in *Phymaturus* and some species of *Liolaemus* (values are the trunk volume/svl index). In blue *P. palluma* group species of *Phymaturus*, in yellow species of the *P. patagonicus* group, in gray are indicated *Liolaemus* species. Green dots indicate herbivory. Below trunk volume/SVL =100 only 7 species among 112 are herbivorous. Above this value 87% are herbivorous (only 6 *Liolaemus* omnivorous species), there are no insectivorous species above 100. B) percentage of herbivorous species within main clades of *Phymaturus* and *Liolaemus*. The arrow indicates the position of *Liolaemus kunza*, with low trunk volume/svl but with pseudo-valves in the small intestine as in most *Phymaturus*.

herbivore is 80.1% greater than that of an insectivore and 57.4% greater than that of an omnivore. The differences between them are more conspicuous than those indicated by SVL. As we mentioned above, the correlation between an herbivorous diet and trunk volume is somewhat greater than that found between herbivory and SVL. Changes in some of the dimensions comprising the volume (length, width, or height of the trunk) have significant consequences, as observed in tl and tw (Table 1).

Regarding saxicoly, the measures considered in the literature include head and trunk depression and longer hindlimbs according to Toyama (2017), Revell *et al.* (2007), among others. Comparisons made among different habitat uses reveal significant differences in trunk length, height, and width (tl, th, tw), head height and length (hh, hl), femur length and width (fe, few), foot, hand, and humerus length (fo, ha, hu), radius length and width and trunk volume (ra, raw, tv). The trunk length is greater in strict terrestrial saxicoles, while the trunk width is greater in strict saxicoles and strict psammophilous. The trunk height is higher in strict psammophilous. In strict saxicoles, the head height is lower than in all the other groups. Additionally, the head length is shorter in strict saxicoles. Foot length in strict and terrestrial saxicoles is shorter than in psammophilous. The length of the humerus is greater in strict saxicoles than in saxicoles and terrestrials. Furthermore, in the strict saxicoles, the forearm is wider than in saxicoles. The comparisons made between the modes of life (Table 1) reveal several differences between the species classified as strict saxicolous and the saxicolous, demonstrating that a too general definition of saxicolous, which includes all the species, is wrong or uninformative.

The results of the phylogenetic ANOVA indicate the non-independence of these morphologies from the phylogenetic history, with the P–values obtained being higher than those of the conventional ANOVA. There is a strong influence of phylogeny on morphologies; in fact, out of the 17 variables



inscriptional ribs

Phymaturus: 50.3% of total rib length

Liolaemus: 26.2% of total rib length

number of presacral vertebrae:

Cadspersa	23.66	1.15	n=3
nigromaculatus	23.83	0.83	n=12
montanus	23.88	0.73	n=26
boulengeri	23.88	0.82	n=53
elongatus	24.11	0.74	n=46
alticolor	24.32	0.82	n=61
nigroviridis	24.50	0.71	n=2
kingii	24.80	1.08	n=31
palluma	**26.11**	0.64	n=27
patagonicus	**26.54**	0.83	n=25
Phymaturus	**26.32**	0.76	n=52

Figure 5. Skeletal innovations acquired by lizards of the genus *Phymaturus* that favored achieving a greater trunk volume. A) Cleared and stained skeletons of *Phymaturus cacivioi* (larger) and *Liolaemus quilmes*. Posxiphisternal ribs of *Phymaturus* and *Liolaemus*. There is no significant difference between the bony sections of both genera but in *Phymaturus* their cartilaginous free ending (inscriptional ribs) is longer and curved at its tip. B) In *Liolaemus* the terminal cartilage is shorter and ventrally curved. In *Phymaturus* are articulated in a lower degree respect to vertebral column. C) In *Phymaturus* there is on average one pair more presacral vertebrae than in *Liolaemus* which explain differences in trunk length. Even when *Phymaturus* exhibit a more flattened body than most *Liolaemus*, its larger capacity of trunk needed for is strict herbivory is ensured by the other two dimensions (length and width).

studied, only four present phylogenetic signals below 50%, these are trunk height (th), humerus and radius width (hw and raw), and trunk volume (tv) (see Table 1).

In Figure 7A (Table 2), our PCA of body measurements versus major liolaemid lineages revealed that trunk length and trunk width contribute to the morphological differentiation of the *Phymaturus palluma* group, *P. patagonicus* group, and the *Liolaemus lineomaculatus* group. In the first two cases, all *Phymaturus* are strict herbivores, while most species of the *lineomaculatus* group are reported as herbivorous. When we perform a PCA combining habitat preference and diet (Fig. 7B, Table 2), we found that the strict saxicoly and herbivorous species (including *Phymaturus* species and a few of *Liolaemus*) are better explained by measurements of the trunk, mainly: tv (trunk volume), tl (trunk length), tw (trunk width) and th (trunk height). But also, hh (head height), tiw (tibia width), and huw (humerus width). All analyses were performed considering residuals to avoid the effect of SVL differences. Measurements directly related to herbivory, recovered in the first analysis, along with trunk height, which have direct explanation on their strict saxicolous mode of life (utilizing rock crevices exclusively as refuge). Trunk volume is built by all three dimensions, but trunk width and trunk length are more related.

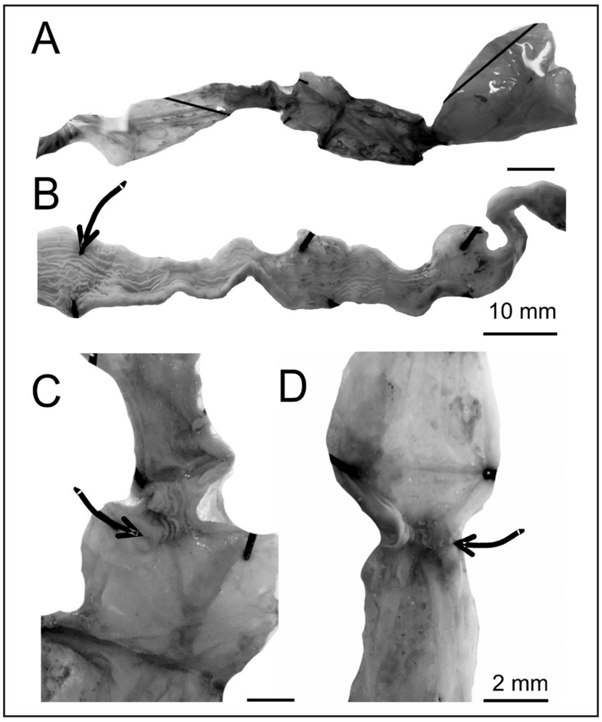


Figure 6. Modifications inside the digestive tract of *liolaemids*. Internal relief of the small intestine of A) small intestine of *Phymaturus aguanegra* (MCN 982, SVL=92.9 mm) showing its smooth walls; B) *Liolaemus mapuche* (MCN-UNSa 4803, SVL= 68.2 mm) the arrow indicates longitudinal folds typically present in insectivorous *Liolaemus*; C) *Phymaturus aguanegra* MCN 982 and D) *Liolaemus kunza* (MCN 1788, SVL= 63.1mm) with an arrow indicating the position of a pseudo-valve.

When we make comparisons between clades, we can make some interesting observations. In our study, although no significant differences were found (Table 3), there is a trend. The head and trunk are rather depressed in both groups of *Phymaturus* (Table 3), and the forelimbs are relatively long compared to the other clades. However, in the case of the hindlimbs, they are different between the *P. patagonicus* and *P. palluma* groups (there are significant differences between them in the length of the tibia and foot). In the first case, they are elongated, while in the *P. palluma* group, they are rather short. Greater trunk volume can be achieved in herbivores, but in a different way; in the *Liolaemus lineomaculatus* clade and in *Phymaturus*, it is achieved by increasing the length and width of the trunk, both have a rather depressed trunk. However, in the *L. kriegi* clade, the greatest volume is achieved by increasing the width and height of the trunk, but not the length of the trunk (Table 3).

Discussion

Given that *Phymaturus* exhibits a combination of biological characteristics, preferences, and mode of life (herbivorous, saxicolous, viviparous), and considering that we were unsure whether any of these traits were new in the origin of *Phymaturus* and if they had any effect on the current morphology of the group, we analyzed their origin and occurrence in the genus. According to our results, viviparity and reduced litter size are primitive characters already present in the ancestor of *Phymaturus* and *Liolaemus* together, whereas herbivory and saxicoly being novel in *Phymaturus* (Fig. 3). Below, we discuss the results obtained in relation to each of these three characteristics.

On liolaemid herbivory

Our comparisons among the three classical categories reveal that herbivores are 14.7% larger than omnivores, while omnivores are 19% larger than insectivores (O'Grady *et al.*, 2015, found herbivores to be 33% larger than omnivores, while omnivores were 18% larger than insectivores). Comparisons made in the present study found a smaller difference between

Table 1. ANOVA results obtained after comparisons across 157 Liolaemid species for seventeen measurements for diet and Kruskal-Wallis test for habitat preference (in this case the distribution was not normal). Different capital letters following mean ± standard error between species indicate a significant difference. Characters that showed significant differences are indicated in bold. For each case, the phylogenetic ANOVA was calculated using a permutation test with 1,000 permutations. P-values for post-hoc comparisons were adjusted using the Holm method. The phylogenetic signal (lambda index of Pagel, 1999) is also indicated for all characters. Abbreviations: Her= herbivore, Omn= omnivorous, Ins= insectivorous, Psa= psammophilous, Strict psa= strict psammophilous, Sax= saxicolous, Strict sax= strict saxicolous, Ter= terrestrial, tl= trunk length, tw= trunk width, th= trunk height, tv= trunk volume, hh= head height, hw= head width, hl= head length, fe= femur length, few= femur width, ti= tibia length, tiw= tibia width, fo= foot length, ha= hand length, hu= humerus length, huw= humerus width, ra= radius length, raw= radius width.

	Her	Omn	Ins	P value	Phylo Anova	Psa	Strict psa	Sax	Strict sax	Ter	Test: Kruskal W	Phylo Anova	Phylo signalλ
tl	B	A	A	**<0.0001**	0.568	AB	AB	A	B	B	**0.0199**	0.967	0.700523
tw	B	A	A	**<0.0001**	0.525	A	B	A	B	AB	**0.0001**	0.715	0.781915
th	-	-	-	-	-	AB	B	A	A	A	**0.0040**	0.904	**0.251346**
hh	A	B	A	**0.0001**	0.603	BC	C	AB	A	BC	**0.0001**	0.765	0.621969
hw	-	-	-	-	-	-	-	-	-	-	-	-	0.85829
hl	A	B	B	**<0.0001**	0.434	AB	B	B	A	AB	**0.0208**	0.936	0.895781
fe	-	-	-	-	-	AB	AB	A	B	A	**0.0026**	0.929	0.820286
few	-	-	-	-	-	BC	C	A	B	AB	**0.0084**	0.949	0.62415
ti	-	-	-	-	-	B	AB	A	A	A	**0.0444**	0.935	0.914291
tiw	-	-	-	-	-	-	-	-	-	-	-	-	0.589477
fo	A	B	AB	**0.0125**	0.825	B	AB	AB	A	A	**0.0176**	0.928	0.8212
ha	-	-	-	-	-	-	-	-	-	-	-	-	0.824825
hu	B	A	AB	**0.0005**	0.663	AB	AB	A	B	A	**0.0002**	0.783	0.726085
huw	AB	B	A	**0.0255**	0.875	-	-	-	-	-	-	-	**0.436747**
ra	-	-	-	-	-	AB	B	AB	B	A	**0.0060**	0.905	0.872795
raw	-	-	-	-	-	B	B	A	B	AB	**0.0134**	0.944	**0.358359**
tv	B	A	A	**0.0001**	0.629	AB	C	A	B	B	**0.0025**	0.874	**0.463064**

herbivores and omnivores than O'Grady *et al.* (2015). This difference may be due to the different sample sizes studied (135 spp versus 21). An important distinction between the herbivory of *Phymaturus* and *Liolaemus* is that in the former it is strict, with only vegetable content found, while in *Liolaemus* there is always a percentage of material of animal origin (insects). In only two cases, some insect remnants were reported in the gut of *Phymaturus* (in *P. zapalensis* Boretto and Ibargüengoytía, 2018; *P.* sp. related to *P. yachanana*, Obregón Streitenberger *et al.*, 2018), but it has not been proven at this time if they are a frequent item (not accidental) of their diet. Not much discovery has been made since Espinoza *et al.* (2004) regarding the evolution of herbivory in liolaemids. Ocampo *et al.* (2022, 2024) conducted an ancestral reconstruction of dietary diversification throughout the Liolaemidae evolutionary history, shown in pie charts at nodes representing posterior probabilities of each diet class. Even though they suggested an insectivorous origin (Ocampo *et al.*, 2022), their optimizations are not decisive (because the method performed). In their analysis, they found that herbivory exhibited a higher rate of diversification than insectivory and omnivory. It's possible that their result was influenced by *Phymaturus* radiation, consisting of 52 species, all inheriting herbivory from their ancestor. Within *Liolaemus,* herbivory is rare (see their own Fig. 1), as reported for 30 out of 288 species of *Liolaemus* according to Abdala *et al.* (2021). In Ocampo *et al.* (2024), the most likely ancestor of Liolaemidae was found to be omnivorous. We traced the evolution of herbivorous versus non–herbivorous species, avoiding more precise optimizations. However, due to the limited number of contributions on the diet of liolaemids (full diet studies only focused on 32 out of more than 330 spp. of liolaemids, see list of diet literature in Appendix1), assigning a specific diet type to species is somewhat risky. Most diet assignments to species come from

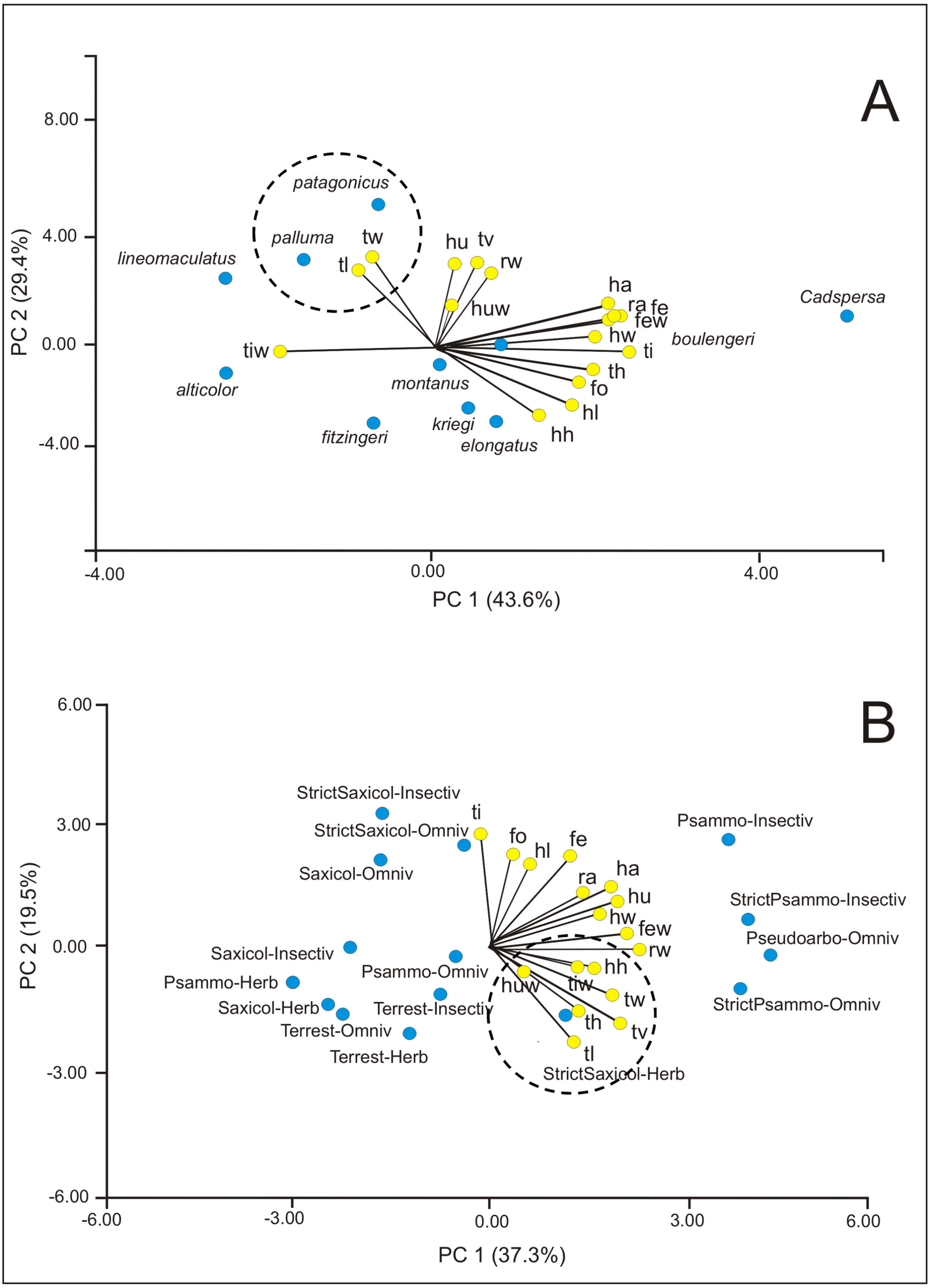


Figure 7. Spatial relationship of the studied body measurements and their relationship with groups of *Phymaturus* species and other Liolaemids and modes of life. A) PCA of Clades / body measurements: PCA1 vs PCA2 represents 73% of information. The *palluma* and *patagonicus* species groups of *Phymaturus* informed by tl (trunk length) and tw (trunk width). B) PCA of diet-habitat preference / body measurements: PCA1 vs PCA2 represent 56.8% of information. The combination strict saxicolous-herbivorous (all *Phymaturus* and few species of *Liolaemus*) is informed mainly by trunk dimensions: tv (trunk volume), tl (trunk length), tw (trunk width) and th (trunk height). But also, hh (head height), tiw (tibia width) and huw (humerus width). All analyses performed considering residuals to avoid the effect of SVL differences.

occasional observations of feces, dissections of one or a few individuals, behavioral observations made in the field, or are taken from the original taxonomic descriptions, which include commentary on the natural history of animals. None of these assignments consider the existence of ontogenetic variation, seasonal variation, and even sexual dimorphism related to diet, which are only detected after studying/examining a numerous series of individuals, of both sexes, ages, and samples taken in different seasons (Rocha 1998, 2000; Valdecantos *et al*., 2012; Semhan *et al*., 2016, among others, see full diet literature of Liolaemidae in Appendix 1). Only 12 *Liolaemus* diet studies (out of 37 published) addressed any of these aspects (ontogenetic variation, sexual dimorphism, and seasonal variation) of a genus of 288 species. Due to the fragmentary nature of the information, we considered it inappropriate to estimate or generalize, calculate rates of changes and transitions considering the three state-categories (insectivorous, omnivorous, herbivorous) (as Ocampo *et al*., 2022 did). Instead, we preferred, in certain cases, a more conservative approach, emphasizing comparisons between herbivores and non-herbivores.

Ocampo *et al.* (2024) found that herbivorous species have evolved larger heads, shorter hindlimbs, and a minimal difference between forelimb and hindlimb length, whereas omnivores and insectivores displayed smaller heads and longer hindlimbs. However, comparing these findings with ours becomes difficult since, in our case, 16 measurements versus 7 (Table 1) were taken (including the three related to the trunk) also estimating the trunk volume. Our results support that in the case of herbivores, they have greater length and width of the trunk than in non-herbivores (contrary to Ocampo *et al*., 2024). We demonstrate that in the case of *Phymaturus,* this is explained by the addition of two presacral vertebrae and the elongation of the inscriptional ribs (Fig. 5). We found (contrary to Ocampo *et al*., 2024) that heads are smaller (we found significant differences in head height and head length). The length of the head is shorter (shorter snout), consistent with previous studies on a broader scale in squamates by Vitt *et al.* (2003). In insectivorous species, the snout tends to be longer; see also Metzger and Herrel (2005). This is related to the need for a more elongated snout and its ability to capture prey. Ocampo *et al.* (2024) found that the total length of hind limbs is shorter in herbivores, our individual measurements of the limb segments show us that the difference lies in the feet (which are shorter in herbivores), with no differences in femurs and tibias.

In the context of pleurodontan clades, the occurrence of herbivory is rare, much like viviparity, as we previously highlighted (Fig. 3B). Unlike *Phymaturus*, where herbivory and saxicolous habitat preference are strictly combined, which was a clear novelty in the origin of the genus (Fig. 3), within *Liolaemus* this combination is exceptional. Only 3 species belonging to the subgenus *Eulaemus* are known to be herbivorous and saxicolous simultaneously (*L. chlorostictus*, *L. orientalis*, *L. aymararum*), compared to 20 other herbivorous species that are not saxicolous. Within the *Liolaemus* sensu stricto subgenus, the *L. kriegi* group (*L. buergeri*, *L. zabalai*, *L. ceii*) and *L. tregenzai* are herbivorous and saxicolous at the same time versus two other herbivorous–only species. Herbivory is generally quite exceptional in the *Liolaemus* sensu stricto subgenus. Independent changes have occurred along independent lineages. In fact, we show that a greater trunk volume can be achieved in herbivores, but in a different way. In the *L. lineomaculatus* clade and in *Phymaturus*, this is accomplished by increasing the length and width of the trunk. Both have a rather depressed trunk. However, in the *L. kriegi* clade, the greatest volume is achieved by increasing the width and height of the trunk, but not its length (Table 3).

Saxicolous mode of life

In the *palluma* group of *Phymaturus,* the hind limbs are shorter compared to those in the *patagonicus* group (and these latter ones do not present significant differences with *Liolaemus* clades). Perhaps this is linked to the fact that the species in the *P. palluma* group are slightly larger, have a greater volume of the trunk (heavier), and the fact of having shorter limbs and a lower center of mass ensures better balance on inclined surfaces. Climbers should have rather strong and short limbs to maintain their center of gravity closer to the substrate, along with trunks that are flatter and closer to the surface (Van Damme *et al*., 1997). *Phymaturus* species from both groups have longer forelimbs compared to most *Liolaemus* species (Table 3). According to Tulli *et al.* (2011), the challenge presented by rocky environment for lizards is solved with longer forelimbs, taller nails, and a shorter distance between limbs. These adaptations contribute to improved clinging performance in these animals. Our results agree with this last statement, except for "shorter distance between

Table 2. Principal component scores based on 17 continuous characters (measurements). The values shown correspond in the upper case to the PCA displayed in Figure 7A, in the lower case to the PCA displayed in Figure 7B.
Values above 0.30 were arbitrarily considered here (in bold) for description of results and discussion purposes. Species vary in body size, and this can affect all morphometric measurements; hence, a regression was performed for these characters using SVL as the independent variable, and the residuals were used for the PCA.

PCA Clades/measurements					**PCA Diet-mode of life/measurements**				
(Figure 7A)					(Figure 7B)				
measurements	pc1	pc2	pc3	pc4	measurements	pc1	pc2	pc3	pc4
RDUO LOG10tl	-0.14	**0.35**	-0.07	-0.22	RDUO LOG10tl	0.21	**-0.37**	-0.14	-0.27
RDUO LOG10tw	-0.12	**0.41**	-0.05	0.10	RDUO LOG10tw	**0.30**	-0.18	-0.24	0.28
RDUO LOG10th	0.28	-0.10	-0.09	0.23	RDUO LOG10th	0.21	-0.23	0.38	0.02
RDUO LOG10hh	0.19	**-0.31**	-0.23	0.28	RDUO LOG10hh	0.08	-0.08	0.52	-0.10
RDUO LOG10hw	0.29	0.06	-0.40	0.15	RDUO LOG10hw	0.23	0.19	0.20	0.48
RDUO LOG10hl	0.25	-0.25	-0.19	0.08	RDUO LOG10hl	0.09	**0.31**	0.29	0.45
RDUO LOG10fe	**0.32**	0.13	0.27	-0.14	RDUO LOG10fe	0.21	**0.37**	-0.25	0.09
RDUO LOG10few	**0.32**	0.14	0.21	0.06	RDUO LOG10few	**0.33**	0.05	0.03	-0.18
RDUO LOG10ti	**0.35**	-0.01	0.20	0.02	RDUO LOG10ti	- 0.03	**0.43**	0.15	-0.29
RDUO LOG10tiw	-0.28	-0.01	0.30	0.38	RDUO LOG10tiw	0.21	-0.08	0.25	-0.24
RDUO LOG10fo	0.26	-0.15	0.45	0.04	RDUO LOG10fo	0.05	**0.35**	0.24	-0.26
RDUO LOG10ha	**0.32**	0.19	2.0E	-0.21	RDUO LOG10ha	0.29	0.23	-0.20	-0.03
RDUO LOG10hu	0.03	**0.37**	0.30	0.02	RDUO LOG10hu	0.27	0.12	-0.32	0.05
RDUO LOG10huw	0.02	0.18	0.13	0.69	RDUO LOG10huw	0.26	-0.08	0.17	0.12
RDUO LOG10ra	**0.34**	0.14	-0.02	-0.19	RDUO LOG10ra	**0.31**	0.17	-0.06	-0.36
RDUO LOG10raw	0.10	**0.33**	-0.40	0.07	RDUO LOG10raw	**0.37**	-0.01	-0.04	-0.09
RDUO LOG10vol	0.07	**0.38**	-0.13	0.22	RDUO LOG10vol	**0.32**	**-0.30**	0.07	0.11

limbs" aspect. In the present contribution, we show that trunk length in *Phymaturus* exceeds that of all other *Liolaemus* lineages. The combination of longer and wider trunks in these herbivores animals has allowed them to increase their abdominal capacity. Toyama (2017, Fig. 2) illustrated in a PCA analysis of different variables that *Phymaturus* separates from other genera, with the width of the abdomen and the length of the trunk being the related characteristics. This fact (more evident changes of the trunk dimensions) would be evidence that herbivory has predominated over their saxicolous mode of life. This is evident in their trunk measurements, which deviate more from those expected for a life on rocks (even though we found significant differences, they are not flatter than terrestrial or psammophilous species; see Table 1). However, the saxicoly did manifest itself in a measurement of the head; in fact, the height of the head is lower than in all other categories. The longer forelimbs appear to be the most important evidence regarding saxicolous life (as previously found by Tulli *et al.*, 2011). Longer forelimbs would provide greater adhesion force to the substrate, primarily due to the longer forelimbs (Tulli *et al.*, 2011) (see humerus, radius and hand length in Table 1 and Table 3). In this work, we found that the length of the hindlimbs differs between both clades of *Phymaturus* (Table 3), being longer in the *P. patagonicus* group and more in accordance with what would be expected for a saxicolous clade. Tulli *et al.* (2016) found a correlation between muscle-tendinous morphology and habitat use; strict saxicolous lizards tend to exhibit wider flexor digitorum longus aponeurosis (they studied two species of the *P. patagonicus* group). However, species of the *L. kriegi* clade, although saxicolous, do not strictly use cracks as shelter (they can take refuge in holes under rocks as well) as the *Phymaturus* species do; for them the height of the trunk is not a limitation. Species of the *L. lineomaculatus* group, such as *L. kolengh,* sometimes take refuge under slabs equivalent to cracks in the preferred environments of *Phymaturus*. Strict psammophilous exhibit smaller trunk volume than all other categories; according to Halloy *et al.* (1998), these are the unique liolaemids that exhibit specialized diving behavior in sand dunes, and a larger trunk volume could mean being an obstacle to this.

The phylogenetic distribution of herbivory and saxicoly

The results of the phylogenetic ANOVA indicate the non-independence of these morphologies from the phylogenetic history, with the P–values obtained being higher than those of the conventional ANOVA. These results may appear contradictory to those found with traditional statistics; however, we believe that they complement them. If we observe the distribution of herbivory and saxicoly (and the related morphology) in the phylogenetic tree, we notice that herbivory and strict saxicoly were acquired at the origin of *Phymaturus* (Fig. 8). Subsequently, this genus underwent important

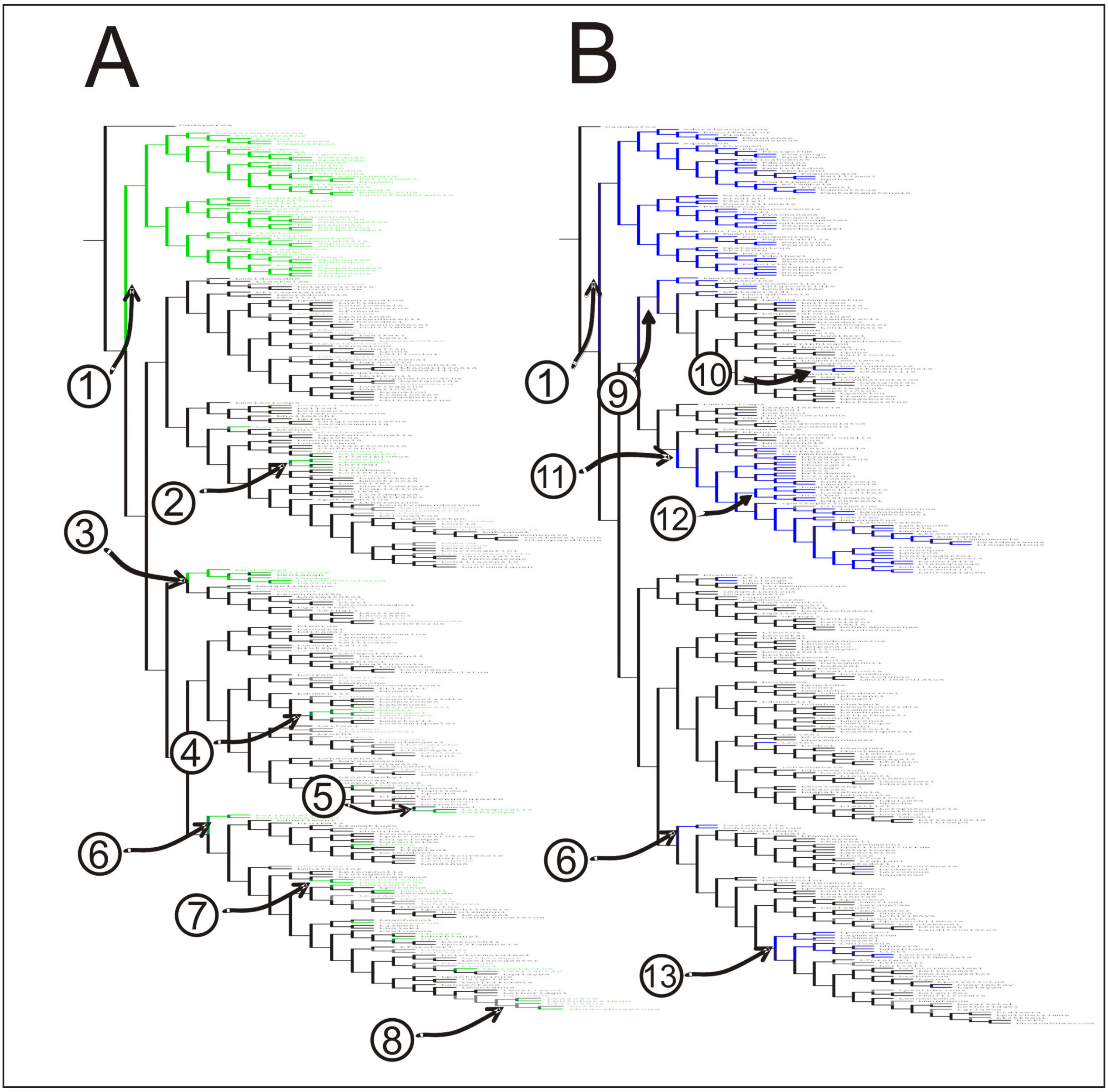


Figure 8. The persistence of modes of life in different lineages of Liolaemidliolaemids: the occurrence of herbivory (A) and saxicoly (B). Arrows indicate the lineages where herbivory or saxicoly were originally acquired (ancestor) and this characteristic remained conserved in all its descendant species. Therefore, it is expected that these characteristics and their associated morphology will be found in phylogenetic tests as due to a phylogenetic effect. 1- *Phymaturus* (herbivorous and strict saxicolous) 2- *Liolaemus kriegi* subclade (herbivorous), 3- *L. lineomaculatus* clade? Group? (herbivorous), 4- *L. fitzingerii* complex (herbivorous/omnivorous), 5- *L. albiceps-L. irregularis* (herbivorous), 6- *L. orientalis- L. chlorostictus* (herbivorous and strict saxicolous) 7- *L. cazianiae* (herbivorous), 8- *L. pulcherrimus* (herbivorous) 9- *L. nigroviridis* and *L. belli* subclades (saxicolous),10- *L. saxatilis-tandiliensis* (saxicolous), 11- *L. elongatus-petrophilus* group (saxicolous) ,12- *L. capillitas* subclade (strict saxicolous) 13- *L. dorbignyi* and *L. jamesi* subclades (strict saxicolous).

Table 3. ANOVA results obtained after comparisons across ten liolaemid lineages. The raw (actual) values for each case are presented, as they may be useful to other researchers (but not the residuals). Since differences were found in SVL between the analyzed species, the residuals of the regression of each measurement character versus SVL were used to remove the possible effects of size across analyses. Data are given in millimeters, except for tv, which is given in milliliters. Different capital letters following the mean ± standard error between species indicate a significant difference ($p < 0.05$). For each lineage, the sample size is indicated above, with the number of species recorded per lineage shown below. The *Liolaemus fitzingeri* complex is nested within the *boulengeri* group and the *Liolaemus kriegi* subclade nested within the *elongatus-petrophilus* group, were analyzed separated because are omnivorous or herbivorous lineages different from the rest of species of the groups they belong. Abbreviations: the same as Table 1. The *Phymaturus patagonicus* and *palluma* species groups are highlighted to show their morphology in comparison with *Liolaemus* and *Ctenoblepharys* lineages. *Phymaturus* species groups share similar head and trunk height (somewhat depressed) and the longest forelimbs among Liolaemid lizards. Hindlimbs exhibit differences (foot and tibia are longer in the *patagonicus* group).

	elongatus **n=162 14**	***kriegi*** **n=423**	***montanus*** **n=171 19**	***Cadspersa*** **n=51**	***fitzingerii*** **n=334**	***boulengeri*** **n=284 28**	***alticolor*** **n=138 15**	***lineomaculatus*** **n=222**	***patagonicus*** **n=167 18**	***palluma*** **n=124 13**	**Test**	**P**
tl	33.47+-5.96 A	47.3+-3.96 A	36.98+-5.59 AB	31.83+-2.22 ABC	38.96+-6.49 ABC	30.39+-7.12 ABC	25.22+-3.06 BCD	30.87+-6.74 BCD	44.29+-4.55 CD	52.62+-5.97 D	F=35.39	<0.0001
tw	19.50+-3.93 ABC	28.20+-2.72 BC	22.50+-4.79 C	15.93+-3.38 ABC	21.25+-2.96 A	16.17+-4.05 BC	11.43+-1.99 BC	18.42+-1.58 D	33.89+-2.84 D	38.61+-3.93 D	F=74.64	<0.0001
th	9.47+-2.20 AB	13.93+-3.82 CD	10.12+-1.90 ABC	10.32+-2.00 D	10.03+-2.95 BCD	8.43+-2.30 BCD	6.26+-2.83 A	7.26+-3.08 AB	9.71+-2.60 AB	10.90+-2.20 AB	F=17.60	<0.0001
hh	7.86+-0.92 BC	9.68+-1.52 D	8.48+-1.67 CD	7.75+-1.48 D	8.70+-2.31 CD	7.09+-1.56 CD	5.20+-0.87 AB	5.74+-0.05 AB	7.62+-0.73 A	8.68+-0.92 AB	F=68.49	<0.0001
hw	12.74+-1.76 BC	15.26+-3.03 C	13.72+-2.87 C	12.53+-2.13 D	12.16+-2.13 A	10.35+-2.15 C	7.71+-1.04 A	9.38+-0.49 C	13.88+-1.10 AB	16.65+-1.76 BC	F=32.39	<0.0001
hl	16.34+-1.72 CD	18.62+-3.02 CD	16.16+-2.64 C	14.90+-1.87 D	15.70+-1.69 B	13.24+-2.28 C	10.72+-1.23 AB	11.39+-0.46 AB	15.08+-0.79 A	17.53+-1.72 B	F=102.01	<0.0001
fe	12.91+-2.18 C	15.17+-2.11 AB	12.77+-2.58 BC	12.56+-1.33 D	12.84+-0.51 AB	10.15+-2.33 BC	7.93+-1.33 AB	8.18+-0.14 A	15.86+-1.59 C	16.88+-2.18 ABC	F=23.25	<0.0001
few	6.33+-1.21 AB	7.40+-1.40 AB	6.58+-1.81 AB	6.14+-0.85 C	7.32+-1.75 AB	5.16+-1.40 BC	3.60+-0.63 A	4.08+-0.39 AB	8.19+-0.87 BC	9.05+-1.21 AB	F=16.28	<0.0001
ti	14.50+-1.71 D	18.50+-3.29 BC	14.12+-2.62 BCD	15.25+-1.61 E	15.59+-3.01 CD	12.16+-2.55 CD	9.06+-1.04 A	9.36+-1.19 AB	13.31+-1.22 CD	17.04+-1.71 AB	F=56.52	<0.0001
tiw	4.27+-0.69 BC	5.40+-0.93 BC	4.22+-0.88 BC	2.69+-0.28 A	4.94+-1.23 BC	3.68+-1.04 BC	2.58+-0.54 B	2.88+-0.32 BC	5.44+-0.72 C	5.64+-0.69 BC	F=14.92	<0.0001
fo	21.70+-2.89 E	25.70+-4.84 CD	20.38+-2.87 ABCD	19.99+-2.05 E	24.10+-2.27 DE	18.11+-3.35 DE	14.49+-1.65 ABC	14.14+-0.95 AB	24.05+-1.19 DE	23.45+-2.89 A	F=44.74	<0.0001
ha	12.58+-1.67 BC	13.85+-1.99 AB	12.12+-2.18 ABC	14.62+-1.54 D	13.04+-1.03 A	9.82+-1.75 ABC	8.45+-1.10 AB	8.64+-0.25 ABC	15.23+-1.06 C	16.25+-1.67 ABC	F=20.81	<0.0001

hu	10.52+-1.32 BCD	12.52+-2.09 ABC	10.42+-1.85 BCD	9.01+-1.08 BCD	11.78+-0.61 A	8.59+-1.42 CD	6.88+-0.97 ABC	7.44+-0.92 ABC	13.89+-1.06 E	15.58+-1.32 DE	F=43.26	<0.0001
huw	4.07+-0.97 ABCD	5.48+-1.41 ABC	4.89+-1.09 D	3.48+-0.60 ABCD	4.80+-0.68 ABCD	3.52+-1.12 CD	2.33+-0.34 A	2.72+-0.15 BCD	5.71+-0.80 BCD	6.36+-0.97 ABCD	F=20.75	<0.0001
ra	8.50+-1.20 BC	9.86+-1.83 ABC	8.95+-1.86 ABC	10.48+-1.11 D	9.82+-1.54 AB	6.99+-1.37 ABC	5.37+-1.03 AB	6.55+-1.20 ABC	10.87+-0.95 C	11.77+-1.20 BC	F=20.78	<0.0001
raw	3.75+-0.74 AB	5.47+-1.46 ABC	4.14+-1.02 BCD	3.64+-0.39 DE	3.84+-0.99 A	3.25+-0.83 BCD	2.28+-0.56 AB	3.21+-0.50 E	5.21+-0.68 CDE	5.80+-0.74 CDE	F=18.46	<0.0001
tv	5462.37+-2603.95 AB	15119.60+-6398.69 CD	7009.87+-3300.43A BCD	4215.05+-1673.94 CD	7007.84+-3787.20 ABC	3779.16+-2761.25 BCD	1531.39+-1053.95 ABC	3482.74+-2372.91 D	11431.49+-3624.37 D	17269.31+-3823.02 D	F=25.83	<0.0001

diversification in Argentina and Chile, and all its descendants retained these same characteristics. That is why both the phylogenetic ANOVA and the lambda index suggest that these characters would be explained by phylogeny (common ancestry). We can say that the same principle applies for the origin of saxicoly in the *Liolaemus elongatus* clade and all the species it encompasses inheriting those characteristics (Fig. 8), where the strict saxicoly of species in the *L. capillitas* subclade occurred in their ancestor and was inherited by all its descendants (*L. heliodermis*, *L. capillitas*, *L. umbrifer*, *L. tulkas*, *L. fiambala* and *L. galactostictos*). The same can be said for the herbivorous *Liolaemus kriegi* subclade. Therefore, conventional ANOVA describes the novelties of those diets and modes of life at the origin of these different clades, which were conserved in subsequent diversifications (Fig. 8).

Skeletal novelties in *Phymaturus*

In the broader context of squamate reptiles, according to Bergmann and Irschick (2011), a higher number of vertebrae has been reached by several lineages, mainly including Serpentes, Amphisbaenia, Pygopodidae, and some lineages of Scincidae and Anguidae. Bergmann and Irschick (2011) have shown that increased rates of evolution in vertebral numbers have coincided with increased rates and disparity in body shape evolution. But at the same time, they also found that the evolution of many vertebrae has not inhibited body shape or taxonomic diversification, and they concluded that increased vertebral number is not a key innovation. Small changes vertebral number can indeed contribute to achieving a particular body shape configuration in cooperation with other anatomical changes as we explain below. Bergmann and Irschick (2011) findings demonstrate that lineage attributes, such as the relaxation of constraints on vertebral number, can facilitate the evolution of novel body shapes. However, they also remarked that various factors are responsible for body shape and taxonomic diversification. We agree with this latter statement. For instance, a higher number of vertebrae has facilitated, for example, the acquisition of a snake-like body shape multiple times, especially in those lineages adapted to a fossorial mode of life. But, in our case, *Phymaturus* increased (but moderately) their vertebral number, this, combined with a widened body due to the disposition of their postxiphysternal ribs and elongation of the inscriptional ribs (Fig. 5), favored a general increase in their trunk volume (needed for their strict herbivorous diet).

Most iguanids possess 24 presacral vertebrae (including the atlas and axis), with a range spanning from 21 to 26. Hoffstetter and Gasc (1969) tabulated presacral vertebral numbers for most lizard families, noting a modal number of 26 in gekkotan and scincomorphan, and 29 in anguimorphan, with even higher numbers in snake body shape clades. Romer (1956) previously considered the primitive condition to be the one found in rhynchocephalian 23–25. Etheridge and De Queiroz (1988) also regarded these numbers as primitive in their analyses of iguanian lineages relationships. Considering the current relationships of squamate lineages, within Toxicophora, we had a clade conserving primitive condition (pleurodonts), with a modal number of 24. In this context, in a clade highly conservative, *Phymaturus* increased a little bit just the needed to increase abdominal volume. Within the pleurodonts, only Polychrotidae have been found to possess 26 to 27 presacral vertebrae, as in *Phymaturus*.

Digestive tract novelties in *Phymaturus*

The occurrence of pseudo–valves in the small intestine, which is convergent with herbivorous species of *Liolaemus*, could have meant a specific strategy to slow down the transit of food along the tract. To date, these structures have not been found in other lizards, perhaps they went unnoticed in previous studies. In the case of small species (such as *L. kunza*) which lack a significant trunk volume to contain larger viscera (Fig. 4) and do not have marked partitions in the cecum like iguanids, this might have led them to develop a different strategy. The occurrence of these pseudo–valves (Fig. 6D) in the small intestine to facilitate optimal transit and digestion of plant material. The caecum shows smooth walls in most species of *Phymaturus* and *Liolaemus*, with only a few exceptions showing oblique and transverse folds, but never developing very conspicuous partitions like those described for iguanids (Iverson 1980, 1982). In most species of *Phymaturus* (except *P. aguanegra* and *P. zapalensis*), the middle region of the stomach has longitudinal folds, while in most *Liolaemus* species it lacks folds (except the herbivorous *L. kriegi* and *L. buergeri*). The pyloric region is differentiated, it is tubular and elongated in shape in *Phymaturus*, while being short and inconspicuous in *Liolaemus*. The duodenal bulb is conspicuous in *Liolaemus* species, but indefinite in

Phymaturus. However, the functional implications of these last two structures remain unknown.

Comments on the origin and evolution of viviparity

Our parsimony reconstructions provide a decisive assignment (unambiguous) along a Liolaemidae tree. The use of all pleurodont families as outgroups reveals that viviparity is rare (only occurring within Phrynosomatids and in the ancestor of *Liolaemus-Phymaturus*, with later changes inside *Liolaemus* (Fig. 3, see also Fig. S1). This hypothesis differs from previous studies in two aspects: the use of multiple outgroups, a parsimony analysis, and the use of an updated topology of Liolaemidae. Schulte *et al.* (2000) were the first authors to study the origin and evolution of viviparity in *Liolaemus*. They performed a parsimony analysis based on 60 species of *Liolaemus*, two *Phymaturus* species, and three outgroups. Depending on whether they considered viviparity as reversible or irreversible, different interpretations were made regarding the tree: six gains of viviparity or a combination of three gains and three losses of viviparity within *Liolaemus*. Their study was pioneering in suggesting the correspondence between the occurrence of viviparity and high elevations of the Andes at areas located at high latitude (then cold climate). However, their conclusions were not decisive, which provoked later studies to address the same topic. Pincheira-Donoso *et al.* (2013), influenced by previous authors who stated that for squamates in general, viviparity is regarded as predominantly irreversible, and that oviparity is unlikely to re-evolve (they cited Lee and Shine, 1998; Shine and Lee, 1999; and Shine, 2005), conducted their analyses in consistency with this criterion. They performed likelihood reconstructions of character evolution with Mesquite v.2.01 (Maddison and Maddison, 2011) and applied phylogenetic methods to evaluate the transitions between oviparity and viviparity in *Liolaemus* topology. Pincheira *et al.* (2013) remarked that the unidirectional oviparity–viviparity evolutionary transition was found in their analyses to be most likely among competing hypotheses. But their results are clearly influenced by the methods they applied, as reported in the methods section: "*For these two irreversible models of trait evolution to exhibit both character states in the tips, a tree root fixed to character state 0 (i.e. oviparity) is required. Therefore, we fixed the tree root to an oviparous state, using a modified version of the Diverse package of Mesquite (v.2.01) developed by R.G. FitzJohn (Goldberg & Igic, 2008).*" So, what are the chances that they will find a transition from viviparity to oviparity more frequently? By not using outgroups and fixing the ancestral state and then applying a method to analyze the oviparous-viviparous transition, we ensure that our results are consistent regardless of the model used. Schulte *et al.* (2000) remarked that different studies have addressed the issue of the reversibility of parity mode in squamate reptiles and agree that there is no strong evidence exists for the irreversibility of viviparity (Benabib *et al.*, 1997; Lee and Doughty, 1997; Lee and Shine, 1998). More recently, Esquerre *et al.* (2018) analyzed the evolution of parity mode in Liolaemidae applying a Bayesian MCMC routine. They considered only one outgroup, and their results fell into a significant degree of uncertainty regarding the ancestral condition for liolaemids. Esquerre *et al.* (2018) analysis provided a pie charts representation of probabilities for both parity modes for each node of the tree, so the nature of their analysis avoids contributing any decisive hypothesis of ancestry. Any future study that modifies the assignment of parity mode to any terminal taxa or update the tree topology, or employs different outgroups, will always represent probabilities of both parity modes at each node. Consequently, these hypotheses become un-rejectable, offering no alternatives of new discoveries. Their assignment of transitions between parity modes along the tree was based on a qualitative assessment of node state likelihoods, inferring transitions when the likelihood of a node's state exhibited a different, most likely state than its ancestor. A positive result of this study was demonstrated that viviparity is reversible, and the transition viviparity to oviparity occurred several times during *Liolaemus* diversification, in opposition to the hypothesis of Pincheira *et al.* (2013). Parsimony optimizations provide rejectable hypotheses and dissipate uncertainties on ancestral reconstructions. Our optimization brings a full hypothesis for all nodes of the tree that are refutable; animals are either oviparous or viviparous, not 30% of oviparous and 70% viviparous at the same time, the same is for all internal branches of the tree. The evolutionary explanation for liolaemids is recovered here with the simplest path: the novelty of viviparity occurred in the ancestor of *Liolaemus-Phymaturus* (different to Schulte *et al.*, 2000; Pincheira *et al.*, 2013; Esquerre *et al.*, 2018) and reverted several times to oviparous (as in Esquerré *et al.*, 2018). Here we recovered a hypothesis of evolution of parity mode in liolaemids, implying 13 transitions from viviparous to oviparous and only 6 transitions from oviparous to viviparous (Fig. S1). Retake viviparity in more terminal clades was rare or more unlikely. Esquerré *et al.* (2019) recovered 8 transitions from oviparity to viviparity and 7 from viviparity to oviparity.

Conclusions

Viviparity was the ancestral condition for the *Phymaturus-Liolaemus* node, along with reduced litter size. The novelties in the origin of *Phymaturus* were the herbivorous diet and the saxicolous life with exclusive use of crevices as shelter. Our phylogenetic statistics (phylogenetic ANOVA and lambda test of phylogenetic signal) indicate a strong phylogenetic imprint on the body measurements studied. All lineages showing characters with significance regarding diet and mode of life would have acquired them early, with all their descendants inheriting them (Fig. 8).

Phymaturus, with respect to the large clades of *Liolaemus*, differed mainly in the width of the abdomen and length of the trunk, which helped to considerably expand its abdominal capacity. This expansion is important for its herbivorous diet and, secondarily, it favored the development of large fetuses, the accumulation of fat more than in the tail, and the defensive behavior of "inflating" in the cracks. In *Phymaturus* the head is larger than *Liolaemus* but is smaller in relation to the body. Its snout is shorter unlike what occurs in most omnivorous and insectivorous *Liolaemus*. The herbivory generated the necessary changes such as greater abdominal volume to contain larger viscera due to herbivory, expressed in greater trunk length and width. Secondarily, this would have allowed these animals to develop larger fetuses (with reduced litter numbers ancestral for both *Phymaturus* and *Liolaemus*; see Fig. S1) and to contain larger fat deposits, more in the abdominal region rather than the tail (the reverse in *Liolaemus*, Paz, 2017), and possibly the ability to inflate inside the cracks (behavior not yet tested or studied in these animals) (like what has been described for *Uromastyx* and *Sauromalus*, Deban *et al.*,1994, Cooper *et al.*, 2000). In the *palluma* group of *Phymaturus*, the modifications were a little more extreme compared to the *P. patagonicus* group, including larger volumes of the trunk and somewhat larger body sizes, resulting in heavier individuals with shorter hind limbs (perhaps thus obtaining a lower center of mass, see Ting *et al.*, 1994; Clemente *et al.*, 2008; Foster *et al.*, 2018). Longer posterior extremities are more related to better runners in saxicolous species (Revell *et al.*, 2007), maybe the use of habitat is a little different between species of the *P. patagonicus* (longer hindlimbs) and *P. palluma* groups. In *Phymaturus,* as in other saxicolous liolaemids, the adherence force of forelimbs was proved by Tulli *et al.* (2011) their fore limbs are longer, we recovered same result. Longer forelimbs would provide greater adhesion force to the substrate, mainly due to their longer forelimbs (Tulli *et al.*, 2011). According to Tulli *et al.* (2016), there exists a correlation between muscle-tendinous morphology and habitat use, suggesting that strict saxicolous lizards tend to exhibit wider flexor digitorum longus aponeurosis, which might be explained by the higher resistance imposed by clinging to rocks. We add this greater grip force by the forelimbs as an anti-predatory mechanism, as described by Cooper *et al.* (2000) for other lizards, to prevent their extraction from crevices. *Phymaturus* species, when they try to avoid being extracted from the cracks, go as deeply as possible into the cracks, pressing their bodies against the crevice roof and extending their legs to exert pressure against it. The disposition of the spiny tails against the predator adds another strategy (Cooper *et al.*, 2000, Ramm *et al.*, 2020). The genus *Phymaturus* exhibit a series of exclusive features that differentiate them from the other two liolaemid genera: the monotypic *Ctenoblepharys* and the highly diverse *Liolaemus* (circa 288 spp.). These characteristics could be related to their diet and lifestyle. The teeth of *Phymaturus* have been described as tricuspid, with their crowns rounded, the central one being larger than the other two (Etheridge, 1995), which is convergent with members of the *Liolaemus fitzingerii* group (Lobo and Abdala 2001, 2002; Abdala, 2007). Additionally, the acquisition of pseudovalves in the small intestine, which we think serves to slow down the transit of plant material along the tract (Fig. 6). The anterior colon (= intestinal cecum) is particularly developed, see Fig. 1B (statistical validation is still needed, as the measurements and proportions of the different sections of the digestive tract of liolaemids are the subject of another study currently in progress). Greater trunk length and abdomen width generating abdominal capacity several times greater than most *Liolaemus* (evidenced in the length of inscriptional ribs and the number of presacral vertebrae). Short hind limbs in the *P. palluma* group are the largest and most voluminous species (lower center of body mass for life on slopes). Differences between the lengths of the hind limbs of the *palluma* and *patagonicus* groups of *Phymaturus* (Table 3) could represent a different use of the environment between the two species groups.

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Supplementary files

Supplementary materials cited in this article are available upon request from FL. Figure S1: Optimization of viviparity in the Liolaemidae tree and clutch/litter size. Figure S2: Optimization of Herbivory. Figure S3: Optimization of saxicoly.

Appendix I

Materials

Acronyms. CMNH: Carnegie Museum of Natural History, Pittsburgh, United States; IBA: Instituto de Biología Animal, Mendoza, Argentina; IBIGEO: Instituto de Bio y Geociencias del NOA, Salta, Argentina; FML: Fundación Miguel Lillo, Tucumán, Argentina; LACM: Los Ángeles County Museum, Los Ángeles, United States; MCN–UNSa: Museo de Ciencias Naturales de la Universidad Nacional de Salta, Salta, Argentina; MNHN: Museo Nacional de Historia Natural, Santiago, Chile; MVZ: Museum of Vertebrate Zoology, Berkeley, United States; SDSU: San Diego State University, San Diego, United States. AMNH (American Museum of Natural History, New York, United States), MCZ (Museum of Comparative Zoology, Harvard University, United States), SDSU (San Diego State University), USNM Unites States Natural Museum, Smithsonian Institution, Washington, United Sates), CAS (California Academy of Sciences, San Francisco, United States) UNSJ (Universidad Nacional de San Juan, San Juan, Argentina). Deposited at IBIGEO: fbc Felix B. Cruz collection, ptf Pamela T. Fierro collection. Pt "proyecto *Tupinambis*" materials.

Preserved in alcohol:

Ctenoblepharys adspersa (5): FML 3781, 368; LACM 94145–46. *Phymaturus aguanegra* (10): MCN–UNSa 970–72, 974,976, 979, 981–82, 990, 994. *Phymaturus antofagastensis* (7): MCN–UNSa 309–310, 1432–33, 1436, IBIGEO 7218–19. *Phymaturus castillensis* (11): IBA 869–1, 869–2, MCN–UNSa 3961–64, 3967, 3969, 3975–76, 3978. *Phymaturus ceii* (10): MCN–UNSa 910, 912–15, IBIGEO 6223–27. *Phymaturus chenqueniyen* (8): IBIGEO 6184–86, 6197–00. *Phymaturus damasense* (9): MNHN 1630–33, 1640, 1642, 1645, 3503. *Phymaturus delheyi* (8): MCN–UNSa 4970–74, 4980–81, 4932. *Phymaturus denotatus* (12): MCN–UNSa 3161, 3176, 3181, 3183, 3186, IBIGEO 5206, 5211, 5213–14, 5217, 5222–23. *Phymaturus dorsimaculatus* (12): MCN–UNSa 1581, 3727–29, 3733–36, 3738–40, 3779. *Phymaturus etheridgei* (6): MCN–UNSa 3109–13, 4308. *Phymaturus excelsus* (13): MCN–UNSa 1582–90, 1385–88. *Phymaturus extrilidus* (12): MCN–UNSa 2664, 2669, 2671, 2710–12, 2714–15, 2725–26, 2735, 2737. *Phymaturus felixi* (9): MCN–UNSa 1279–82, 3979–80, 3983, 3988, 3991. *Phymaturus fiambala* (12): IBIGEO 5757–60, 5762–68, 5774. *Phymaturus indistinctus* (11): MCN–UNSa 667, 682–684, 685, 1274, 1277, 3943–45, 3955. *Phymaturus katenke* (7): IBIGEO 6165–69, 6171–72. *Phymaturus laurenti* (14): MCN–UNSa 306, 313, 316, 324, 325, 1910–11, 1919, 2849, 2851, IBIGEO 5131–33, 5135. *Phymaturus mallimaccii* (7): IBIGEO 5987–92, 6031. *Phymaturus nevadoi* (10): 3647, 3652–57, 3659–3661. *Phymaturus palluma* (8): MCN–UNSa 3130–31, 3612–13, 3619–22. *Phymaturus patagonicus* (10): IBA 789–1, 789–2, 789–3, 789–4, 789–5, 789–6, 789–7, SDSU 1980, MCN–UNSa 1284, 1286. *Phymaturus payuniae* (12): MCN–UNSa 2878–79, 3648–49, 3651, 3665–66, 3668–72. *Phymaturus punae* (5): MCN–UNSa 3116, 3118–19, 3589–90. *Phymaturus querque* (12): MCN–UNSa 3854–57,3860–63, 3865, 4876–77, 4899. *Phymaturus rahuensis* (5): IBIGEO 5539–42, 5576. *Phymaturus sitesi* (13): MCN–UNSa 4757–4761, 4765–69, 4771, 4792–93. *Phymaturus spurcus* (7): MCN–UNSa 1239–40, 1244, 1246–48, 1596. *Phymaturus tenebrosus* (8): MCN–UNSa 1270, 1273,3934, IBIGEO 5588–89, 5591–92, 5594. *Phymaturus verdugo* (7): MCN–UNSa 1958, 1960–61, 1973–75, 1977. *Phymaturus videlai* (5): MCN–UNSa 4203–07. *Phymaturus williamsi* (7): MCN–UNSa 2808–11, 2815,2821, 3262. *Phymaturus yachanana* (9): 4314, 4319–20, 3272, 3274, 3276, 3278, 3280–81. *Phymaturus zapalensis* (10): MCN–UNSa 3844–49, 3851–53, IBIGEO 6251. *Liolaemus abdalai* (13): MCN–UNSa 2735, 2740, 2742–50, fbc 1102–03. *Liolaemus albiceps* (12): ptf 1,3,5,7,10, 12–13, 16, 18, 20, 22, m. *Liolaemus austromendocinus* (14): MCN–UNSa 3698, 3702,3706,3708–11, 2022, 2027–29, 604, 606, 608. *Liolaemus bibroni* (7): MCN–UNSa 763, 768–70, 772, pmc291. *Liolaemus boulengeri* (4): MCN–UNSa 3367, IBIGEO 6122, 6130, 6181. *Liolaemus buergeri* (10): MCN–UNSa 2023–24, 3783–84, 3814, 3828–29, 3882–84. *Liolaemus canqueli* (8): MCN–UNSa 288, 1289–95. *Liolaemus capillitas* (8): IBIGEO 5835–37, FML 2029 (4 indiv.). *Liolaemus cazianiae* (10): MCN–UNSa 2521–22, 2528, 2530, 2537, 2539–40, 2553, 2555, 2568. *Liolaemus ceii* (15): MCN–UNSa 3746, 3750, 3753, 3768–70, 4912–13, 4915, 4918, 4931, 5543–46. *Liolaemus chacoensis* (7): PT 2575–77, 2782, 2784–86. *Liolaemus chaltin* (11): MCN–UNSa 2221, 2225, 2229–31, 2924, IBIGEO 6691–93, 6758, 6761. *Liolaemus chlorostictus* (9): IBIGEO 5452, MCN–UNSa 2499, 2502–03, 3476–80. *Liolaemus coeruleus* (12): 3723–26, 3793–99, 3801. *Liolaemus cuyanus* (5): MCN–UNSa 800–806. IBIGEO 5084. *Liolaemus cyanogaster* (4): CMNH 133118, 133733, MVZ 188724–25. *Liolaemus darwinii* (16): MCN–UNSa 4783–84, 4843–47, 4852–53, 4856–62. *Liolaemus dorbignyi* (5): MCN–UNSa 2119–21, 2132, 2136. *Liolaemus elongatus* (35): IBIGEO 7220–25. MCN–UNSa 780, 1236, 1322, 1325, 1343–44, 1389–92, 3811, 3956–57, 4005, 4209–11, 4213, 4766, 4775, 4782, 4785, 4787, 4900, 4914, 4921, 4986, 5001–02. *Liolaemus escarchadosi* (10): 1519–23, 1529–30, 1533, 1535–36. *Liolaemus espinozai* (6): MCN–UNSa 212–214, 3168–70. *Liolaemus famatinae* (5): IBIGEO 6014–18. *Liolaemus fiambala* (13): MCN–UNSa 2134–35, IBIGEO 5720–24, 5726, 5729–30, 5736–38. *Liolaemus fitzgeraldi* (3): MCN–UNSa 2595, 2597–98. *Liolaemus galactostictos* (13): FML 1794. *Liolaemus gracilis* (6): MCN–UNSa 4820, 4849, 4851, 4854, 4864, 5684. *Liolaemus halonastes* (9): 2523, 2527,2556, 2558, 2560–61, 2565–67. *Liolaemus heliodermis* (9): MCN–UNSa 3998–99, IBIGEO 5363–66, 6023–25. *Liolaemus inacayali* (9): MCN–UNSa 1226–28, IBIGEO 7235–3940. *Liolaemus irregularis* (17): MCN–UNSa 2242, 2251, 2255, 2279, 2285, 2294–95, 2300, 2308, 2312, 2315, 2760, 2767, 2783–85, 2787. *Liolaemus josei* (5): MCN–UNSa 3696–97, 3699, 3700, IBIGEO 7234. *Liolaemus kingii* (15): 6114–16, 6118–21, 6123–29, 6131. *Liolaemus kriegi* (17): MCN–UNSa 690, 1219–20, 3324,3366, 3868–69, 4328, 4890–93, IBIGEO 6153, 6192, 6194, 7079–80. *Liolaemus kolengh* (14): IBIGEO 5864–68, 5872–77, 5945, 5947–48. *Liolaemus koslowskyi* (15): pt3937,3939, fbc 084, MCN–UNSa 1397–98,1406–07,1409, 1411–15, 3292–93. *Liolaemus kunza* (12): 1839–40, 1860, 1936, 2014,2057–58, 2074,4376–78, 4380. *Liolaemus lavillai* (7): IBIGEO 5602–04, 5606–08, 5618. *Liolaemus lineomaculatus* (8): FML 1797 (3), 2118, 2731, 3356, 10098–99. *Liolaemus loboi* (7): 4551–57. *Liolaemus lutzae* (6): FML 1287. *Liolaemus magellanicus* (5): MCN–UNSa 855,859, 867–68, 872. *Liolaemus mapuche* (13): MCN–UNSa 4825–27,4830–34, 4836,4848–51. *Liolaemus martorii* (6): IBIGEO 6823–6828. *Liolaemus melanops* (5): MCN–UNSa 1297, 1300–01, 1305. *Liolaemus messii* (11):

IBIGEO 6694–04. *Liolaemus morenoi* (14): FML 17020–28, 22206–10. *Liolaemus multicolor* (10): IBIGEO 6728–37. *Liolaemus multimaculatus* (14): FML 1596. *Liolaemus neuquensis* (7): FML 3548, 7846–48, 9457, 22343–44. *Liolaemus nigriceps* (15): FML 1632(4), 24717–27. *Liolaemus olongasta* (8): FML 2669(4), MCN–UNSa 3328–30, IBIGEO 6057. *Liolaemus orientalis* (13): FML 2036. *Liolaemus ornatus* (12): MCN–UNSa 3595–00, IBIGEO 6722–27. *Liolaemus pacha* (13): FML 2399(6), 3094(7). *Liolaemus pachecoi* (10): FML 28835–40, 28891–92, 28894, 28898. *Liolaemus pagaburoi* (14): MCN–UNSa 472, 477–80, 620–627, 629. *Liolaemus parvus* (10): IBIGEO 6085–90, 6092, 6108–10. *Liolaemus patriciaiturrae* (9): FML 1189(2), 28730, 25949–54. *Liolaemus petrophilus* (9): pt 4841, 4846, MCN–UNSa 787, 1352, 4325, IBIGEO 6150–52, 6257–58. *Liolaemus pictus* (9): FML 1780(5), 7772–75. *Liolaemus pleopholis* (3): FML 26020–22. *Liolaemus porosus* (9): FML 1649(3), 1650(6). *Liolaemus pseudoanomalus* (8): FML 2087(5), 19011–12, 19015. *Liolaemus pulcherrimus* (9): 18238–45, 18247. *Liolaemus puna* (9): MCN–UNSa 2496–97, 2514–16, 3203–04, 3239–40. *Liolaemus puritamensis* (9): FML 983, 985, 18150, 28955–58, 29065–66. *Liolaemus pyriphlogos* (12): FML 1463. *Liolaemus quilmes* (15): FML 2445(4), 2451(6), 2291(5). *Liolaemus ramirezae* (6): MCN–UNSa 468, 519, 524, 2576–77, 2579. *Liolaemus robertmertensi* (13): FML 1308(3), 1488(7), 1847(3). *Liolaemus rosenmanni* (14): FML 29212–14,25936–39,25943–44, 25947–48, 25955–57. *Liolaemus rothi* (11): FML 1037, 10071–72, 17060, 17118–22, 23789–90. *Liolaemus ruibali* (15): IBIGEO 5271–78, 5280–84, 5286, 5289. *Liolaemus sagei* (6): FML 1637(4), 21536, 22426. *Liolaemus salinicola* (14): FML 1912(7), 16782–86, 16788–89. *Liolaemus sanjuanensis* (10): UNSJ 736,738–39, 740, 742–43, 746, 748–49, 766. *Liolaemus sarmientoi* (12): MCN–UNSa 1496, 1500, 1502, 1504–05, 1507–13. *Liolaemus saxatilis* (5): MCN–UNSa 903–05, IBIGEO 6782–83. *Liolaemus scapularis* (16): IBIGEO 5089–99, 5101–05. *Liolaemus scrocchii* (7): MCN–UNSa 2136–38, 4046, IBIGEO 5341–43. *Liolaemus shehuen* (6): 4321–24, 4326, 4330. *Liolaemus talampaya* (6): MCN–UNSa 2031–36. *Liolaemus tandiliensis* (13): MCN–UNSa 1604–16. *Liolaemus tromen* (6): MCN–UNSa 3780–82, 3812–13, 3830. *Liolaemus tulkas* (10): IBIGEO 5804–12, 5814. *Liolaemus umbrifer* (7): IBIGEO 5227–32, 5234. *Liolaemus vulcanus* (9): IBIGEO 5120–22, 5125–27, 5129, 5168–69. *Liolaemus wiegmannii* (12): MCN–UNSa 3139, 3151, 4742–48, IBIGEO 5839–41. *Liolaemus yanalcu* (12): MCN–UNSa 535–36,705, 726, 729, 955–56, 1038–39, 1635, 2237–38. *Liolaemus zullyae* (15): IBIGEO 5931–44.

Skeletons studied from Richard Etheridge´s RX plates collection (each RX plate is called CASE).

CASE L8R *Urostrophus torquatus* CAS 85234–36. *Urostrophus torquatus* CAS 85237. *Anolis* sp. MCZ 85247. CASE L 9R *Liolaemus lutzae* CAS 96881–82. CASELO9R *Plica umbra* CAS 95142, 93241–42. *Morunasaurus groi* CAS 98001. CASE L 10 R *Liolaemus multiformis multiformis* CAS 80903–04, 809042, 80901. *Liolaemus tenuis* CAS 85240, 85249, 85238, 84717. *Stenocercus humeralis* CAS 94112. *Stenocercus humeralis* CAS 94111. CASE L 11 R *Liolaemus chiliensis* CAS 85233.*Tropidurus duncanensis* CAS 12206. *Tropidurus duncanensis* CAS 12200–02. CASE L 12 R *Liolaemus occipitalis* CAS 87093–94. *Liolaemus fuscus* CAS 84747–49. CASE L19R *Liolaemus pictus* CAS 85241, 85243–44, 85246–251, 84719. CASE L 66 R *Liolaemus chiliensis* 85233, *Liolaemus fuscus* 84747. CASE77 *Anolis mirus* 1910.7.11.5 *Leiocephalus apurimata* 62253. *Leiocephalus macropus koopmanni* 55541type. *Leiocephalus fimbriatus* 61226. *Leiocephalus personatus vinculum* 61059–60. CASE L–108–R *Liolaemus alticolor* MCZ 7287. *Liolaemus a. altissimus* MCZ 30611, 38612–13. *Liolaemus hatcheri* MCZ 11828. *Liolaemus schroederi* MCZ 51948–49. *Stenocerus juninensis* MCZ 45820–21. *Stenocerus nigromaculatus* MCZ 1797545820. CASE 110: *Phymaturus palluma* MCZ 2033. CASE L110 *Tropidurus praeornatus* MCZ 33582.*Tropidurus praeornatus* MCZ 33581. *Urocentron flaviceps* MCZ 37270. *Enyalius* sp. CAS9 6826. CASE 111 *Phymaturus patagonicus* MCZ 14914–15. *Stenocercus chrysopygus* MCZ 45833. *Stenocercus chrysopygus* MCZ 8073. *Stenocercus chrysopygus* MCZ 45835. *Diplolaemus bibroni* MCZ 14918–19. *Stenocercus chrysopygus* MCZ 45834. CASE 120 *Pristidactylus scapulatus* MCZ 33584. *Liolaemus elongatus* MCZ 14929–30, 14927. *Enyalioides heterolepis* MCZ 39911. *Enyalioides heterolepis* MCZ 24959. / SDSCCOLL *Enyalius pictus*. *Urocentron* sp. MCZ 12440MA. CASE 123 *Liolaemus lenzi* MCZ 7264. *Liolaemus wiegmannii* MCZ 57402–03, 61219–20. *Liolaemus chacoensis* MCZ 86603–04, 49520–21. *Liolaemus fuscus* MCZ 38622, 38624–26. *Liolaemus signifer* MCZ 86598–01. CASE 125 *Liolaemus schroederi* MCZ 65404. *Liolaemus fitzingeri* MCZ 15901–02. *Liolaemus villaricensis* MCZ 86310–12. *Liolaemus monticola* MCZ 21212–13. *Liolaemus boulengeri* MCZ 14939, 149397. CASE 126 *Liolaemus bisignatus* MCZ 7270 1–4, *Liolaemus lineomaculatus* MCZ 11819–22, *Liolaemus cyanogaster* MCZ 2051, 2051, 2051, *Liolaemus chiliensis* MCZ 19979, 19985. CASE 127 *Liolaemus kingii* MCZ 11839–40, 11837. *Liolaemus lutzae* MCZ 79136–37, 79139–40. *Liolaemus walkeri* MCZ 45816–18, 45813, 45813. *Ctenoblepharys adspersa* MCZ 70228. /SDSC COLL *Pristidactylus torquatus* SDSU. CASE 128 *Liolaemus darwini* MCZ 86620–27, 866291. CASEL128 *Tropidurus torquatus* MCZ 66943.*Tropidurus torquatus* MCZ 80879. CASE 135 *Enyalioides praestabilis* USNM7797. *Enyalioides praestabilis* USNM 7798. *Enyalioides praestabilis* USNM7796. CASE 136 *Liolaemus altissimus altissimus* USNM 1463133–34. *Liolaemus wiegmannii* USNM 70477, 70473–74, 70481. *Liolaemus fitzgeraldi* USNM38937, *Liolaemus tenuis* USNM 5518 (7). CASE 137 *Liolaemus kingii* USNM 36918–23. *Liolaemus lineomaculatus* USNM 36985, 36893–94, 36901, 36896–99. CASE 138 *Liolaemus elongatus* USNM 13954–57. *Liolaemus fitzingeri* USNM 36934–38. CASE 143 Gifts *Liolaemus multiformis* SDSU, SDSU SDSU, SDSU… *Tropidurus boicardi* CASE143 *Tropidurus boicardi*. CASE143 *Tropidurus boicardi*. CASE144 *Tropidurus boicardi*. CASE144 *Tropidurus boicardi* CASE144 *Tropidurus boicardi* CASE144 *Tropidurus boicardi*. *Liolaemus pictus* (6 uncatalogued). CASEL148 *Urocentron flaviceps* AMNH 56409. *Stenocercus azureus* AMNH 17013. *Stenocercus azureus* AMNH 37558. *Stenocercus azureus* AMNH 37559. *Stenocercus azureus* AMNH 37557. *Stenocercus ornatissimus* AMNH 27136–37. *Stenocercus ornatissimus* AMNH 28783. *Urocentron flaviceps* AMNH 57206–08. CASE 156 *Liolaemus lineomaculatus* AMNH 17010, *Liolaemus bibroni* AMNH 80051, *Liolaemus lemniscatus* AMNH 88325, *Liolaemus wiegmannii* AMNH 64806, 12009. *Liolaemus gravenhorsti* AMNH80054–55, *Liolaemus simonsi* AMNH 13491, 13496–98. *Liolaemus* *magellanicus* AMNH 80043–45, *Liolaemus cyanogaster* AMNH 38065–67. CASE157 *Liolaemus fitzingeri* AMNH 80047–49. *Liolaemus chiliensis* AMNH 80052–53. *Liolaemus alticolor* AMNH 79935–39, 38068–70. *Urocentron* sp. MCZ 84247. CASE 158 *Liolaemus nitidus* AMNH 37810–11, 37523, 37808, 37804, 37571–72. CASE 159 *Liolaemus platei* AMNH 37574–75, 37377–78, 37579, 37587–88, 37581. CASE124 *Liolaemus nitidus* MCZ 65402. *Liolaemus nigroviridis* MCZ 86303. *Liolaemus tenuis* MCZ 65401, 65485. *Ctenoblepharys adspersa* MCZ 70228. *Liolaemus lemniscatus* MCZ 21214, 65398. *Liolaemus magellanicus* MCZ 67910–11. *Liolaemus goetschi* MCZ 51950. CASE160 *Enyalioides praestabilis* AMNH 37554–55. CASE170 *Plica umbra* MCZ 101799,101748. CASE173 (no collection data) *Stenocercus doellojuradoi* CASE173 *Stenocercus scapularis*. CASE 173 R (no collection data) *Liolaemus schroederi. Liolaemus nigroviridis. Liolaemus ornatus* (2). *Liolaemus fitzingeri. Liolaemus darwini. Liolaemus jamesi. Liolaemus bibroni. Liolaemus magellanicus.*

Cleared and stained specimens:

Phymaturus aguanegra MCN–UNSa 965–69, 984–85. *Phymaturus cacivioi* MCN–UNSa 3901, 3936, 3903. *Phymaturus calcogaster* MCN 4302–03. *Phymaturus castillensis* MCN–UNSa 3977. *Phymaturus ceii* MCN–UNSa 908–09. *Phymaturus damasense* MCN–UNSa 1643. *Phymaturus delheyi* MCN–UNSa 4976. *Phymaturus denotatus* MCN–UNSa 319, 321. *Phymaturus dorsimaculatus* MCN–UNSa 921, 923, 1577–78. *Phymaturus etheridgei* MCN–UNSa 4306. *Phymaturus excelsus* MCN–UNSa 922. *Phymaturus extrilidus* MCN–UNSa 2665, 2713. *Phymaturus felixi* MCN–UNSa 3990. *Phymaturus indistinctus* MCN1481–82. *Phymaturus laurenti* MCN–UNSa 318, 326. *Phymaturus nevadoi* MCN–UNSa 3658. *Phymaturus niger* IBIGEO 5578, 5568. *Phymaturus palluma* MCN–UNSa 3639. *Phymaturus patagonicus* MCN–UNSa 1285. *Phymaturus payuniae* MCN–UNSa 3673. *Phymaturus querque* MCN–UNSa 3858. *Phymaturus roigorum* MCN–UNSa 2113, 2115. *Phymaturus sitesi* MCN–UNSa 4763. *Phymaturus spurcus* MCN–UNSa 1249. *Phymaturus tenebrosus* MCN–UNSa 1489, 1491. *Phymaturus williamsi* MCN–UNSa 2813, 2817. *Phymaturus yachanana* IBIGEO 7226. *Phymaturus zapalensis* MCN–UNSa 1485–86, 3850. *Liolaemus kolengh* MCN–UNSa 579. *Liolaemus kriegi* MCN–UNSa 1218. *Liolaemus ceii* IBIGEO 6671–72. *Liolaemus austromendocinus* FML 3422–3. *Liolaemus petrophilus* MCN–UNSa 1347. *Liolaemus elongatus* MCN–UNSa 4609. *Liolaemus capillitas* FML 1229–21. *Liolaemus vulcanus* MCN–UNSa 1863, IBIGEO 5119. *Liolaemus ruibali* FML 02574–1, MCN–UNSa 3132. *Liolaemus multicolor* MCN–UNSa 1463,1444. *Liolaemus quilmes* MCN–UNSa 3524–25, 3528. *Liolaemus koslowskyi* MCN–UNSa 573– 574, 576. *Liolaemus albiceps* MCN–UNSa 402, 453, 2585, 457,1452. *Liolaemus irregularis* MCN–UNSa 2446. *Liolaemus ornatus* MCN–UNSa 3547. *Liolaemus lavillai* MCN–UNSa 2686, 4351. *Liolaemus scapularis* MCN–UNSa 283, 253. *Liolaemus inacayali* MCN–UNSa 498. *Liolaemus pseudoanomalus* MCN–UNSa 526. *Liolaemus chaltin* MCN–UNSa 235, 2238, 2222, 2226, 2223. *Liolaemus abdalai* MCN–UNSa 493. *Liolaemus bibroni* MCN–UNSa 491. *Liolaemus sanjuanensis* UNSJ 737,747, 7341. *Liolaemus nigroviridis* MCN–UNSa 569–70, 572.

Digestive tracts studied:

Phymaturus aguanegra MCN–UNSa 970–74, 976–83, 986–87, 989–91, 993–95. *Phymaturus dorsimaculatus* MCN–UNSa 1581, 3729–3736, 3779. *Phymaturus indistinctus* MCN–UNSa 682, 684–85, 687, 1274,1277. *Phymaturus* cf. *palluma* MCN–UNSa 2111–12, 3623–25, 3516. *Phymaturus* cf. *yachanana* MCN–UNSa 3272, 3274, 3276, 3280, 3282, 3277–79. *Phymaturus zapalensis* MCN–UNSa 3844–49; 3851–53. *Liolaemus albiceps* MCN–UNSa 423, 4569–70, IBIGEO 6280, 6284–85. *Liolaemus buergeri* MCN–UNSa 3783–84, 3814, 3828–29. *Liolaemus ceii* MCN–UNSa 3752, 3755, 3758, 3764. *Liolaemus* cf. *ceii* MCN–UNSa 4895, 4897, 4901. *Liolaemus kriegi* MCN–UNSa 690, IBIGEO 7079–80. *Liolaemus kunza* MCN–UNSa 1763–88, 1771,1786; 1859–60,1868–70,1936, 2040, 4376–77, 4380. *Liolaemus mapuche* MCN–UNSa 4800, 4803. *Liolaemus tulkas* IBIGEO 5805–08, 5812. *Liolaemus umbrifer* MCN–UNSa 2865, IBIGEO 5113, 5115, 5228, 5230.

DIET LITERATURE FOR LIOLAEMID LIZARDS

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Trabajo

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Dimorfismo sexual morfométrico en una población de *Cercosaura parkeri* (Squamata: Gymnophthalmidae)

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ABSTRACT

Sexual morphometric dimorphism was analyzed in *Cercosaura parkeri*. Males exhibited significantly larger values in all head-related measurements (width, length, and height), as well as in neck width and length of the neck and in radio-cubit length. These traits may be associated with increased bite force, potentially used during male–male combat and copulatory behavior. Although cephalic differences are often linked to dietary divergence between sexes—thereby reducing intersexual competition—this aspect was not assessed in the present study. Males showed a higher number of femoral pores, which suggests that they may 'invest' in chemical signaling to become more attractive to females, to indicate their presence in a territory, and/or to inform other males about their status and competitive ability. In contrast, females exhibited greater trunk length compared to males, which may provide increased abdominal space for carrying larger eggs. No significant sexual differences were observed in snout–vent length, limb measurements (forelimbs and hindlimbs), or tail length.

Key words: Morphometric; Lizards; Sexual Selection; Natural Selection.

RESUMEN

Se estudió el dimorfismo sexual morfométrico en *Cercosaura parkeri*. Se encontraron valores significativamente mayores de todas las variables cefálicas (ancho, largo y alto de la cabeza), ancho y largo del cuello y en longitud radio-cúbito en machos, lo que podría estar relacionado con una mayor fuerza de mordida y sujeción, utilizadas tanto en encuentros antagónicos con otros machos, como en el momento de la cópula. Las diferencias cefálicas también se relacionan en muchas especies con la dieta, evitando la competencia entre los sexos. Los machos presentaron mayor número de poros femorales, por lo que estos podrían "invertir" en señales químicas para volverse más atractivos hacia las hembras, o indicar su presencia en un territorio y/o informar a otros machos sobre su estatus y capacidad competitiva. Por otro lado, las hembras presentaron mayor longitud del tronco que los machos, lo que podría conferir un mayor espacio para albergar huevos más grandes. No se encontró diferencias en la longitud hocico-cloaca, en la mayoría de las variables tomadas en miembros anteriores y posteriores ni en el largo de la cola.

Palabras claves: Morfometría; Lagartijas; Selección Sexual; Selección Natural.

Introducción

El dimorfismo sexual (DS), definido como una diferencia fenotípica entre machos y hembras de una especie, es un rasgo común en los animales, y según varios autores, la mayoría de las especies son dimórficas en lugar de monomórficas (Schoener, 1977; Mouton y Van Wyk, 1993; Andersson, 1994). Se han propuesto diferentes mecanismos evolutivos para el desarrollo del dimorfismo sexual en diversos taxones animales, pudiéndose resumir en tres fuerzas principales, que actúan de forma diferencial sobre machos y hembras de una población: la selección sexual, la selección por fecundidad y la selección natural (Cox *et al*., 2003). En aquellas especies donde los machos compiten con otros por

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el acceso a hembras, la selección sexual puede actuar a través de combates entre machos o/y la elección de las hembras, favoreciendo así un mayor tamaño corporal de los machos, mientras que la selección por fecundidad puede favorecer un mayor tamaño corporal de las hembras, lo que les permite albergar mas huevos o embriones en desarrollo (Shine, 1989; Fairbain, 1997; Zamudio, 1998; Olsson, 2002; Kratochvíl y Frynta, 2002; Cox *et al.*, 2003; López Juri *et al.*, 2018; Naretto y Chiaraviglio, 2020). Por otro lado, la selección natural actúa sobre ambos sexos pudiendo limitar la evolución de algunos caracteres, por ejemplo, mediante el uso del hábitat. Estas tres fuerzas pueden actuar simultáneamente, haciendo evidente que las diferentes presiones selectivas que actúan sobre miembros de ambos sexos, pueden producir diferencias sexuales (Slatkin, 1984; Heuring y Hughes, 2019).

Las lagartijas pueden presentar dimorfismo sexual en el tamaño corporal total, así como en el tamaño relativo de las partes del cuerpo relacionadas con la reproducción. Estudiar estas partes, que participan en comportamientos como la competencia de pareja, el cortejo y la cópula (p. ej., cabeza, abdomen, cola y extremidades), puede ser muy informativo sobre las presiones selectivas impuestas (Butler y Losos, 2002). En varias familias se observó que los machos presentan mayor tamaño corporal y dimensiones de la cabeza (Cooper y Vitt, 1989; Anderson y Vitt, 1990; Mouton y Van Wyk, 1993; Andersson, 1994; Braña, 1996; Herrel *et al.*, 1996, 1999, 2001a,b; Kratochvíl *et al.*, 2003; Molina-Borja, 2003; Uller y Olsson, 2003; Naretto *et al.*, 2014), directamente relacionadas con la musculatura mandibular y afectan la fuerza mandibular, una estructura implicada no solo en el comportamiento competitivo y la cópula, sino también en la alimentación, el comportamiento antidepredador y el uso de refugios (Herrel *et al.*, 1996, 1999, 2001a,b; Naretto *et al.*, 2014, 2022; De Meyer *et al.*, 2019). Otro aspecto que permite explorar las diferencias entre sexos en lagartijas es el tamaño de las extremidades (Herrel *et al.*, 1996, 2001a, b; Schwarzkopf, 2005). Por ejemplo, en algunos *Anolis* (Butler y Losos, 2002) y *Podarcis muralis* (Ljubisavljević *et al.*, 2017; Head *et al.*, 2024) los machos poseen extremidades más largas, lo cual les daría la ventaja de tener zancadas más largas cuando escapan de sus depredadores o defienden su territorio (Butler y Losos, 2002). Diehl (2007) encontró en una población de *Cercosaura schreibersii* que los machos presentan extremidades más grandes que las hembras. Por otro lado, en varias especies las hembras tienen un tronco más largo (Andersson, 1994; Braña, 1996; Butler y Losos, 2002; Olsson *et al.*, 2002; Schwarzkopf, 2005; Balestrin *et al.*, 2010; Cabrera *et al.*, 2013), y se ha demostrado que la longitud del abdomen se correlaciona positivamente con el tamaño de la puesta.

Muchas lagartijas poseen estructuras epidérmicas en la superficie ventral del muslo (poros femorales) conectadas a glándulas femorales holócrinas que secretan señales químicas. Estas secreciones son especialmente abundantes en los machos durante la época reproductiva (Mason, 1992; Alberts, 1993), y se cree que los compuestos químicos secretados son importantes para la comunicación y la selección sexual (Mason, 1992; Martín y López, 2006). Martín *et al.* (2007) consideran que los machos podrían "invertir" en la señal química (mediante hormonas) para volverse más atractivos, reforzando la idea de que los poros femorales y sus secreciones son un rasgo relacionado con la reproducción (y por ende con la selección sexual); así, los machos transmiten información sobre la calidad de éstos, que las hembras podrían utilizar para seleccionar parejas potenciales (Olsson *et al.*, 2003; Martín y López, 2006). Además, estas señales podrían indicar su presencia en un territorio y/o informar a otros machos sobre su estatus y capacidad competitiva (Aragón *et al.*, 2001; Aragón *et al.*, 2006; Carazo *et al.*, 2007; Martín *et al.*, 2007). Diehl (2007) identificó dimorfismo sexual en el número de poros femorales en *Cercosaura schreibersii*, con hembras entre dos y seis, mientras que en los machos se observaron de seis a diez poros.

Cercosaura es un género de lagartijas pequeñas que pertenecen a la familia Gymnophthalmidae, comprende 18 especies y se distribuye en Sudamérica. *Cercosaura parkeri* se encuentra en las provincias de Catamarca, Jujuy, Salta y Tucumán y recientemente Tedesco *et al.* (2023) la citan para Chaco, Formosa, Santa Fe y Santiago del Estero. Abarca además Brasil, Bolivia y Perú. Además de tener un rango de distribución amplio, en determinados ambientes es una especie común y de hábitos peridomiciliarios. Este es el caso de la provincia de Tucumán (Argentina), donde son lagartijas comúnmente avistadas. Sin embargo, los datos sobre su biología son totalmente desconocidos.

En este estudio analizamos el dimorfismo sexual en tamaño en una población de *Cercosaura parkeri*. En base a lo reportado por Diehl (2007) y Balestrin *et al.* (2010) para *C. schreibersii*, esperamos obtener resultados similares en *C. parkeri*: machos con mayores dimensiones corporales, así como mayores valores en algunas variables cefálicas y de los miembros, además de un número superior de poros femorales. En contraste, en las hembras prevemos encontrar mayores distancias entre los miembros anteriores y posteriores.

Materiales y métodos

Se midió un total de 25 machos y 25 hembras, colectados en Villa Batiruana, al sudoeste de la provincia de Tucumán (27°38’14”S – 65°44’43”O), Depto. La Cocha, Tucumán; el lugar de estudio se caracteriza por ser una zona de una clara confluencia biogeográfica, con presencia de elementos de Yungas y otros propiamente chaqueños (Ayarde, 2018).

Para comparar sólo ejemplares adultos, se determinó el tamaño mínimo sexual, evaluando el estado de las gónadas en todos los ejemplares analizados; las hembras fueron consideradas maduras sexualmente cuando presentaron ovarios con folículos cargados de vitelo u oviductos convolutos y ensanchados, y en el caso de los machos, se consideró maduros sexualmente a aquellos que presentaban el epidídimo enrollado irregularmente y agrandado o los testículos voluminosos y globosos (en contraste con los testículos fusiformes y pequeños de los ejemplares inmaduros) (Fitzgerald *et al.*, 1993; Ibargüengoytía, 2008).

Las variables morfométricas usadas en los análisis (tomadas con calibre Mitutoyo CD-15B; ± 0.01 mm) fueron las siguientes: LHC (longitud hocico-cloaca) (Fig. 1), LCab (longitud de la cabeza, desde el extremo de la escama rostral hasta la abertura auditiva) y AlCab (altura de la cabeza, a la altura de la abertura auditiva) (Fig. 2), AnCab (ancho de la cabeza, a la altura entre las comisuras de la boca), AnCue (ancho del cuello, medido a la mitad de este), LCue (longitud del cuello, tomado desde el borde posterior de abertura auditiva hasta la altura del pliegue antes de la cintura escapular), DM (distancia entre miembros anteriores y posteriores, medida desde axila hasta la ingle), AnCu (ancho del cuerpo, tomado en la mitad del cuerpo), LH (longitud del húmero, desde axila hasta el codo), LRC (longitud radio-cúbito, desde el codo hasta el ángulo interno entre la mano y el brazo), LM (longitud mano, hasta la uña del dedo más largo), LF (longitud del fémur, desde la ingle hasta la rodilla), LTF (longitud de tibia-fíbula, desde la rodilla hasta el ángulo interno con el pie), LP (longitud de la pata, hasta la uña del dedo más largo) y LC (longitud de la cola, desde la cloaca hasta la punta de la cola) (Fig. 1) y NPF (número de poros femorales, Figs. 3 y 4).

Se evaluaron tanto la normalidad (prueba de normalidad de Shapiro-Wilks) y homogeneidad de varianzas (prueba F para igualdad de varianzas) de todas las medidas. Las que no cumplieron con estos supuestos fueron transformadas logarítmicamente para cumplir con la normalidad. Se realizó ANOVA

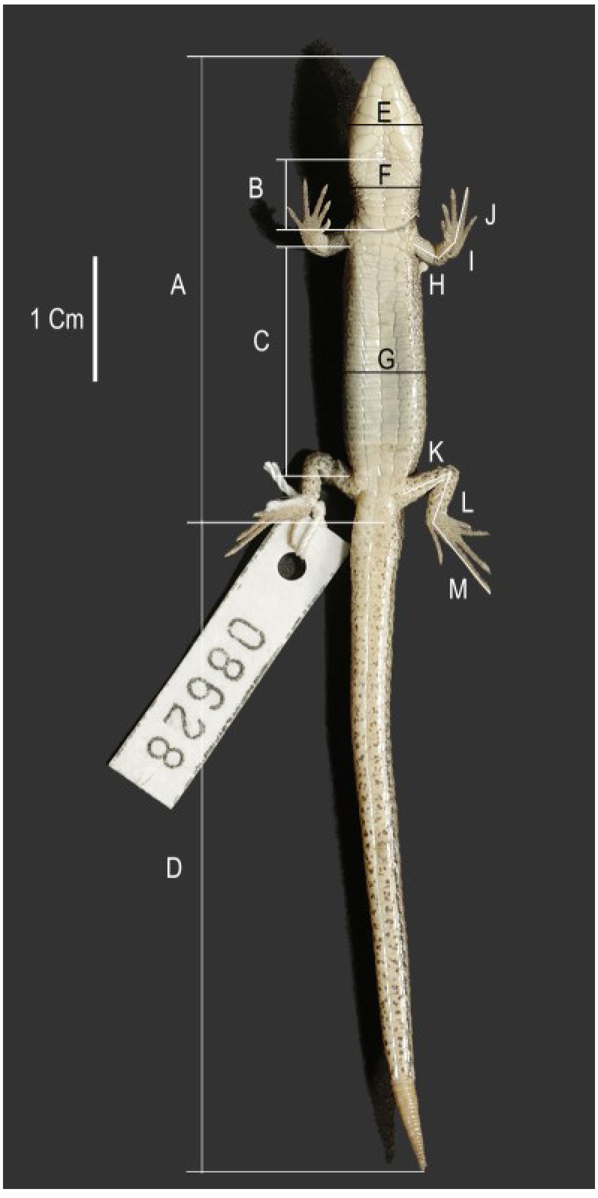

Figura 1. Medidas tomadas en *Cercosaura parkeri*: **A)** longitud hocico-cloaca; **B)** longitud del cuello; **C)** distancia entre miembros anteriores y posteriores; **D)** longitud de la cola; **E)** ancho de la cabeza; **F)** ancho del cuello; **G)** ancho del cuerpo; **H)** longitud del húmero; **I)** longitud radio-cúbito; **J)** longitud de la mano; **K)** longitud del fémur; **L)** longitud tibia-fíbula; **M)** longitud de la pata. Fotografía: H. Folly.

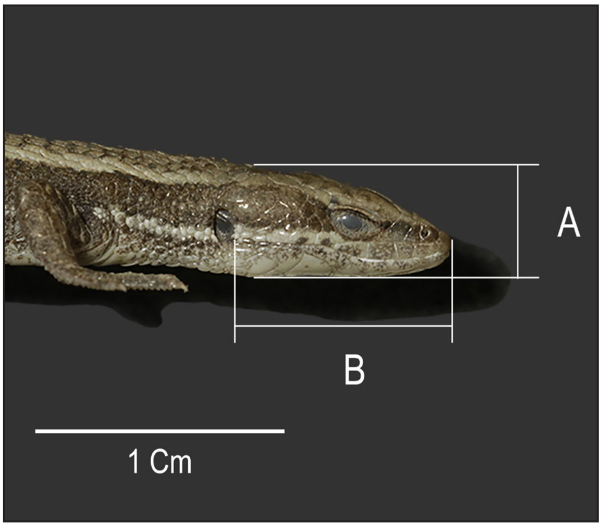

Figura 2. **A)** altura de la cabeza y **B)** longitud de la cabeza de *C. parkeri.* Fotografía: H. Folly.

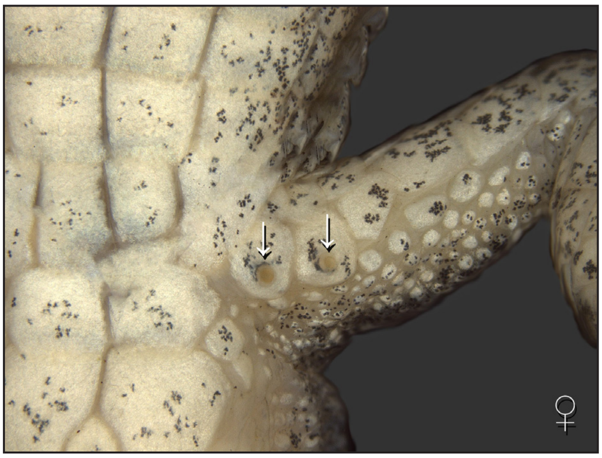

Figura 3. Hembra de *C. parkeri.* Las flechas indican los poros femorales. H. Folly.

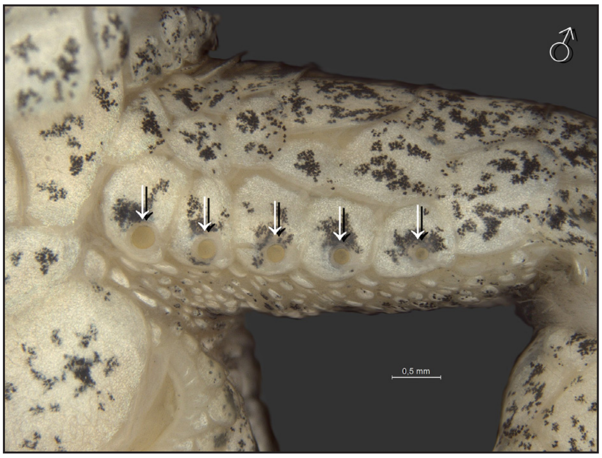

Figura 4. Macho de *C. parkeri.* Las flechas indican los poros femorales. H. Folly.

para comparar la LHC entre los sexos. Para el resto de las variables se realizó un ANCOVA (con la interacción entre sexo y LHC) y en los casos que ésta no fue significativa se llevó a cabo un ANCOVA (con LHC como covariable y sexo como variable categórica) entre cada variable y la LHC, para eliminar el efecto de la longitud hocico-cloaca sobre cada una. El nivel de significación fue de 0.05. Los métodos estadísticos se aplicaron usando Statistica 7.0

Resultados

La LHC promedio de las hembras (38.82 ± 4.5 mm) y machos (38.41 ± 2.57 mm) no presentó diferencia significativa ($F_{1,48}=0.156, p=0.695$). El ANCOVA con la interacción entre el sexo y la LHC sólo arrojó diferencias significativas en la LRC ($F_{1,48}=6.358, p<0.04$) (Fig. 5) y en el LCue ($F_{1,48}=6.225, p<0.04$) (Fig. 6), con los mayores valores en machos.

El ANCOVA (con LHC como covariable y el sexo como variable categórica), no arrojó diferencias significativas en: LH ($F_{1,48}=0.240, p=0.626$), LM ($F_{1,48}=0.015, p=0.901$), LF ($F_{1,48}=0.272, p=0.604$), LTF ($F_{1,48}=0.119, p=0.731$), LP ($F_{1,48}=0.026, p=0.871$), AnCu ($F_{1,39}=2.006, p=0.164$), ni en LC ($F_{1,14}=0.005, p=0.942$). Por otra parte, se registraron diferencias significativas, con valores mayores en los machos en las siguientes variables: Lcab ($F_{1,48}=19.247, p=<0.001$), AlCab ($F_{1,48}=11.828, p=<0.001$), AnCab ($F_{1,48}=26.197, p=<0.001$), AnCue ($F_{1,48}=8.759, p=<0.001$) (Fig. 7) y NPF ($F_{1,48}=379.664, p=<0.001$) que en hembras varió entre dos y tres, mientras que en machos siempre fue mayor a cuatro, llegando hasta seis. Las hembras tuvieron valores estadísticamente mayores que los machos solo en la distancia entre los miembros anteriores y posteriores (DM: $F_{1,48}=39.706, p=<0.001$) (Fig. 8).

Conclusión

Los resultados mostraron que de las 16 variables consideradas en este estudio, se detectó diferencias entre los sexos en ocho de ellas, y sólo las distancia entre miembros anteriores y posteriores (DM) fue significativamente mayor en las hembras que en los machos. Este mayor tamaño del tronco en hembras concuerda con lo esperado, ya que también fue encontrado por Balestrin *et al.* (2010) en *Cercosaura schreibersii;* además, coincide con lo observado para otras lagartijas, como *Cnemidophorus lacertoides* y varias especies del género *Liolaemus* (Verrastro, 2004; Laspiur y Acosta, 2007; Valdecantos y Lobo, 2007; Cabrera *et al.*, 2013). Según varios autores (Andersson, 1994; Braña, 1996; Butler y Losos, 2002; Olsson *et al.*, 2002; Schwarzkopf, 2005), la longitud del abdomen se correlaciona positivamente con el tamaño de la puesta. La familia Gymnophtalmidae presenta como sinapomorfía que la puesta es de un número fijo y reducido de dos huevos (Fitch, 1970; Vitt, 1982; Ávila-Pires, 1995), por lo que el mayor tamaño del abdomen en *C. schreibersii* (Diehl, 2007; Balestrin *et al.*, 2010) y *C. parkeri* (especies cuya puesta tiene un número fijo de dos huevos), podría estar relacionado con un mayor tamaño de los huevos y no con un mayor número de estos. A pesar de que en lo anteriormente expuesto también sería importante una mayor longitud hocico-cloaca en las hembras, esto no fue observado en *C. parkeri*, a diferencia de *C. schreibersii*, donde las hembras presentaron esta variable mayor que en machos (Balestrin *et al.*, 2010).

Los machos presentaron las tres variables cefálicas (ancho, largo y alto de la cabeza), así como el ancho y el largo del cuello, mayor que en las hembras. Las diferencias en el tamaño de la cabeza entre sexos, con valores mayores en machos, también fueron encontradas en otras especies de lagartijas (Feltrin, 2002; McBrayer, 2004; Verrastro, 2004; Diehl, 2007; Balestrin *et al.*, 2010; Cabrera *et al.*, 2013). Esto podría explicarse por dos hipótesis no excluyentes: la primera afirma que los machos con cabezas más grandes son más eficientes en las interacciones agresivas y tienen mayor capacidad para sujetar a las hembras durante la cópula (Anderson y Vitt, 1990; Kratochvíl y Frynta, 2002; Reaney y Whiting, 2002; Naretto y Chiaraviglio, 2020). La otra hipótesis que se admitiría sería que las mayores dimensiones de las cabezas de los machos actuarían para minimizar la competencia intersexual por los recursos alimentarios (segregación ecológica de la dieta) (Schoener, 1971; Camilleri y Shine, 1990; Shine, 1991; Pérez-Mellado y de la Riva, 1993; Van Sluys, 1993). Por otro lado, las mayores dimensiones en el cuello en los machos, podrían brindarle mayor flexibilidad en la sujeción a las hembras al momento de la cópula, pero no hay datos sobre estas diferencias que puedan argumentar lo observado, por lo que se necesitarían más estudios para este fin.

La mayor dimensión en la longitud del radio-cúbito, también fue encontrada por Diehl (2007) para *C. schreibersii*. Otros autores también encontraron dimensiones en los miembros anteriores y/o posteriores mayores en machos que en hembras, como por ejemplo para *Sceloporus variabilis* (Cruz Elizalde *et al.*, 2020) y algunas especies de *Anolis* (Butler y Losos, 2002), dándoles la ventaja de tener zancadas más largas cuando escapan de sus depredadores o defienden su territorio (Butler y Losos, 2002). Diversos estudios han demostrado que en machos las extremidades más largas proporcionan una velocidad de sprint más rápida (Bauwens *et al.*, 1995; Goodman *et al.*, 2008; Winchell *et al.*, 2018), pero la variación en la longitud de las extremidades puede verse influenciada por diversas vías, no solo las que contribuyen a las diferencias sexuales (Cordero *et al.*, 2021). Schuck *et al.* (2021) estudiaron dos poblaciones distintas de *C. schreibersii* de Brasil, y encontraron diferencias en la longitud de distintas variables de los miembros, hipotetizando que el tipo de sustrato utilizado por las lagartijas podría afectar su morfología y a esto podría deberse la diferencia observada entre *C. parkeri* y *C. schreibersii.*

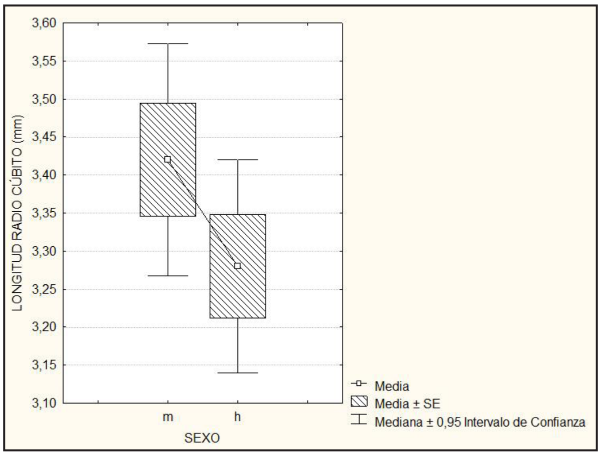

Figura 5. Gráfico de cajas mostrando las diferencias entre los sexos en la longitud radio-cúbito. Sexos (m= machos; h= hembras).

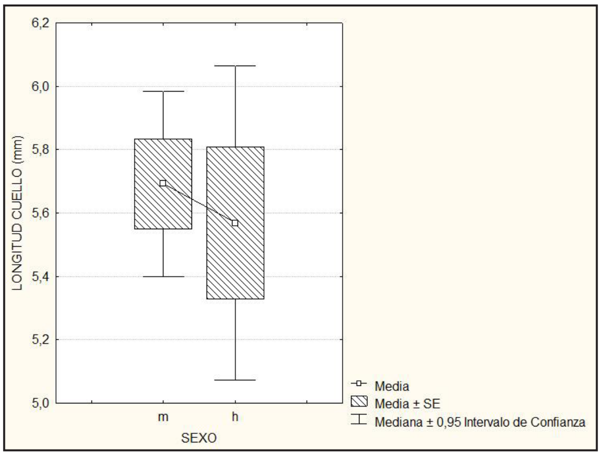

Figura 6. Gráfico de cajas mostrando las diferencias entre los sexos en la longitud del cuello. Sexos (m= machos; h= hembras).

Cercosaura parkeri presentó machos con cuatro a seis poros femorales y hembras con dos a tres, no encontrándose superposición en el número de

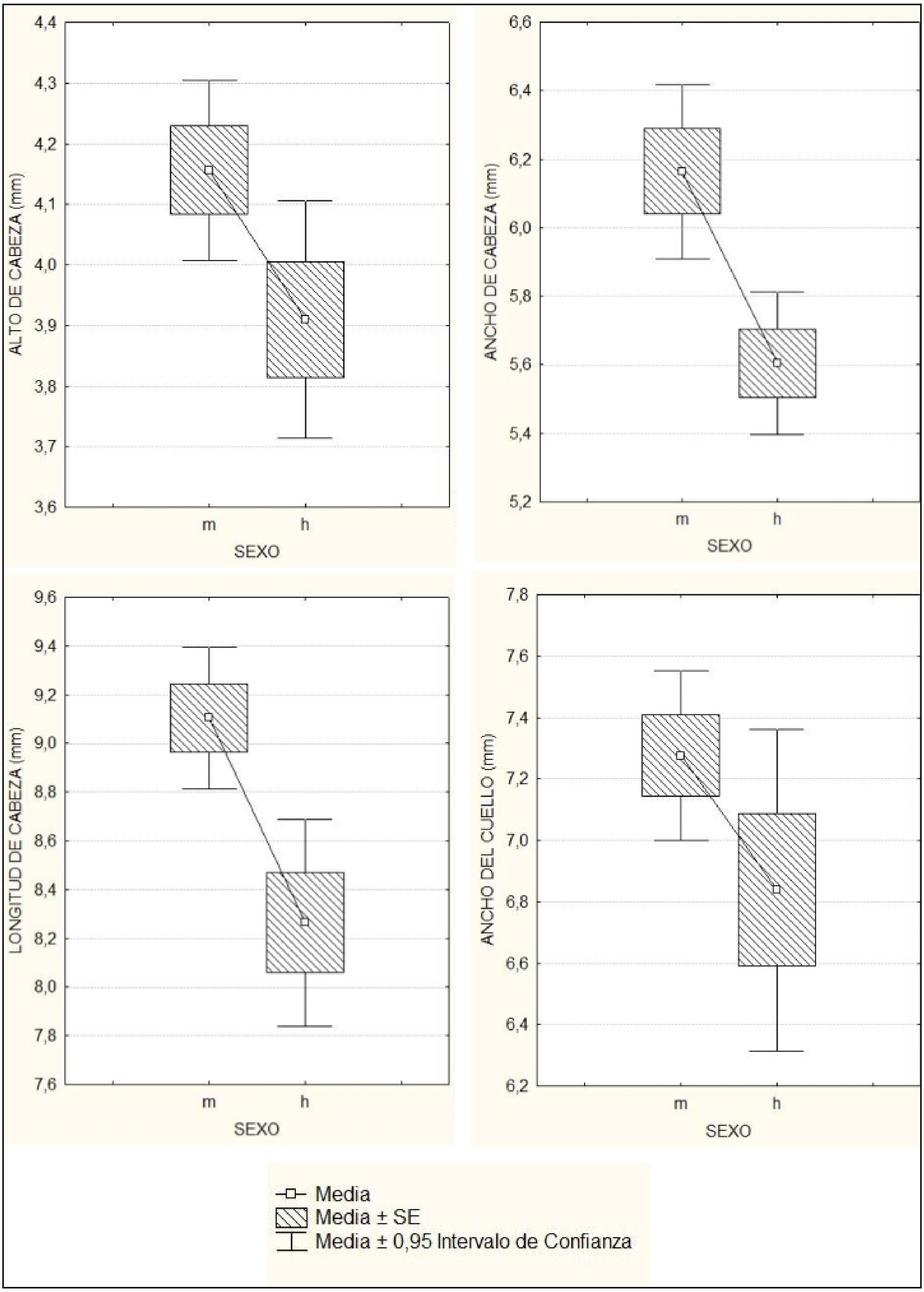

Figura 7. Gráficos de cajas mostrando las diferencias entre los sexos en el alto de la cabeza (arriba izquierda), ancho de la cabeza (arriba derecha), longitud de la cabeza (abajo izquierda) y ancho del cuello (abajo derecha). Sexos (m= machos; h= hembras).

estos, por lo que esta diferencia podría ser utilizada para la determinación del sexo. Por otro lado, Diehl (2007) encontró para *C. schreibersii,* un macho y una hembra con seis poros femorales, mientras que el resto de los machos estudiados tuvo más de seis y las hembras cinco o menos. Algunas lagartijas presentan estos poros a lo largo de la superficie medioventral de cada muslo en ambos sexos (mientras que otras especies están presentes sólo en machos) pero en los machos tienden a ser más grandes y varían en mayor medida (Fergusson *et al.*, 1985), con la finalidad de "invertir" en la señal química para volverse más atractivos hacia las hembras (Martín *et al.*, 2007), o cumplir también funciones competitivas y territoriales entre machos. Se ha encontrado que las variaciones entre individuos en la abundancia de algunos compuestos en las secreciones de los machos se relacionan con las variaciones en las características morfológicas, de condición y estado de salud, y lo que es más importante, otros individuos pueden detectar estas variaciones químicas y ajustar sus comportamientos reproductivos de forma diferencial, lo que indica que algunos compuestos químicos actúan como señales sexuales o feromonas (Martín y López, 2006). Distintos compuestos químicos se relacionan con diferentes características de un individuo, por lo que las secreciones químicas de los machos pueden llevar múltiples mensajes destinados a las hembras o a otros machos, como en *Podarcis hispanica,* donde los machos evitan áreas impregnadas con secreciones de otros machos residentes (Martín & López, 2006). Además, en varios estudios se han encontrado relaciones entre el estado de salud (parásitos, respuesta inmune o condición corporal) de un macho y las proporciones relativas de ciertos compuestos químicos en sus secreciones femorales (López y Martín, 2005).

El estudio del dimorfismo sexual morfométrico de distintas estructuras anatómicas puede requerir investigaciones específicas dentro de varias áreas

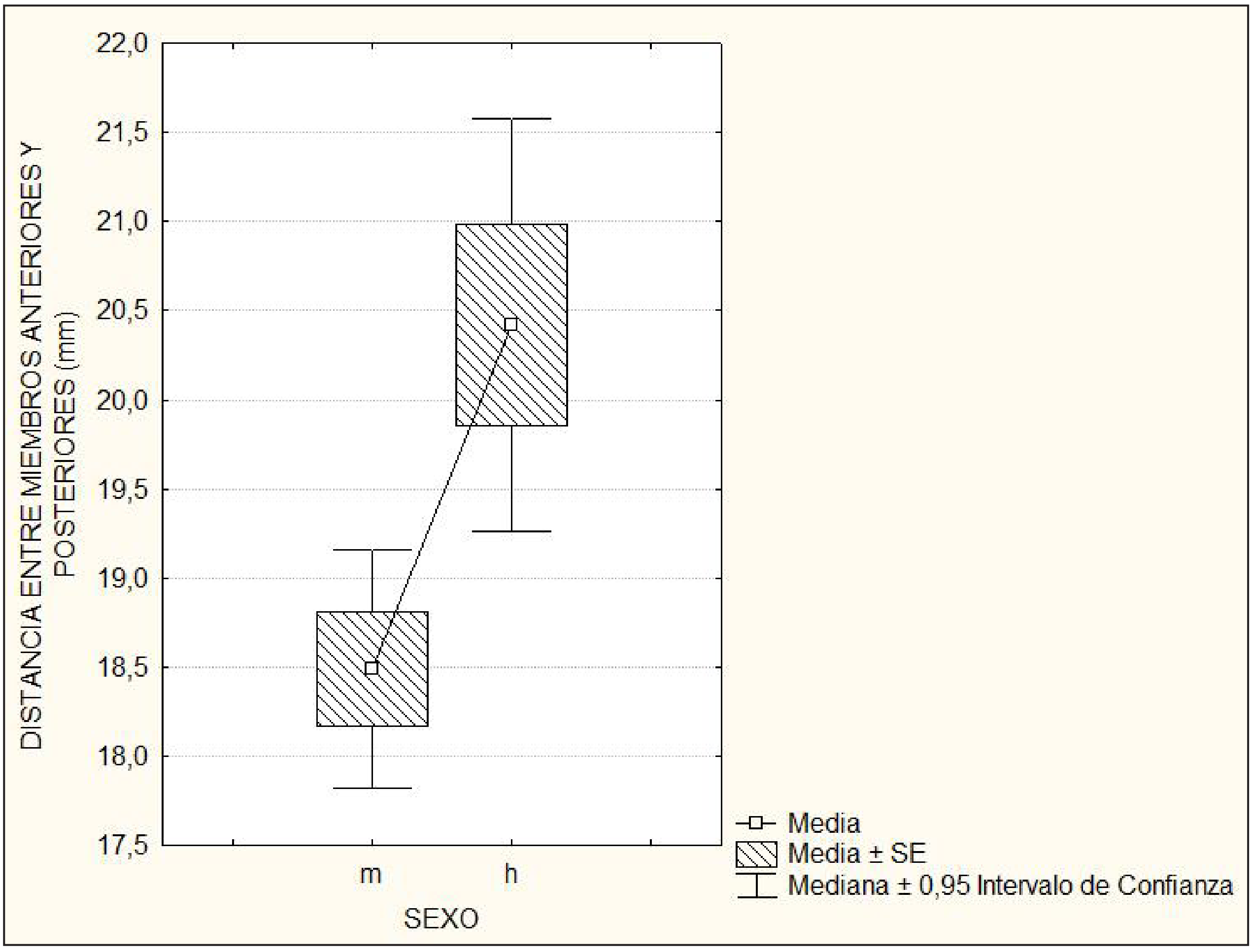

Figura 8. Gráfico de cajas mostrando las diferencias entre los sexos en la longitud en la distancia entre los miembros anteriores y posteriores. Sexos (m= machos; h= hembras).

de la historia natural de un organismo (por ejemplo dieta, reproducción, comportamiento), pudiendo revelar la importancia relativa de la filogenia en la evolución del dimorfismo (Lemos-Espinal *et al.*, 2001). No se conoce nada acerca de la dieta, reproducción o comportamiento de *Cercosaura parkeri,* por lo que futuros estudios en estos aspectos podrían ayudar a explicar en términos ecológicos la falta de diferencias significativas por ejemplo en la LHC y comprender mejor las diferencias encontradas en las otras variables. Por otro lado, sería relevante analizar las secreciones químicas de los poros femorales para comprender por qué los machos presentan un mayor número que las hembras.

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Trabajo

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Scientometric analysis of publications on tadpoles worldwide, with an emphasis on Brazil

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ABSTRACT

Approximately 41% of known amphibian species are at risk of extinction. Amphibians are even more vulnerable during their larval stages, as their skin is more permeable and more susceptible to absorbing environmental contaminants. There has been a significant increase in the number of studies on tadpoles in Brazil in recent years. Despite this increase, the number remains insufficient. Therefore, the objective of this research is to gather information about the current knowledge on tadpoles. To achieve this, a scientometric study was conducted, performing a non-automated systematic review of the available scientific literature. The research used the Web of Science and Google Scholar databases, with the descriptors "tadpoles" or "anuran larvae" covering publications from January 1960 to July 2024. Scientific articles, technical notes, and indexed books were included in this study. The analysis also aimed to identify Brazilian states with the highest number of publications and to analyze keywords using VOSviewer software. A total of 24,971 articles were found, of which 4,845 met the inclusion criteria. The USA had the highest number of publications (1,039), followed by Brazil (962), and China (291). Most worldwide articles mainly focus on specific families, such as Ranidae, Bufonidae, and Hylidae. In Brazil, 843 articles were valid, covering research on 17 families and 541 species, with Hylidae being the most studied (257 species; 46.9%), followed by Leptodactylidae (106 species; 19.3%), and Bufonidae (38 species; 6.9%). The families Alsodidae, Ceratophryidae, and Eleutherodactylidae were the least studied, with only one species each (0.0.1%). Most Brazilian studies are concentrated in the Southeast, especially in São Paulo, Minas Gerais, and Rio de Janeiro, while the North and Northeast regions have fewer publications. The analysis revealed patterns in research distribution, a growth in interest in tadpoles since 2010, and notable gaps in key areas that warrant further investigation.

Key words: Amphibians; Amphibian larvae; Anura; Caatinga; Tadpole ecology.

RESUMO

Aproximadamente 41% das espécies de anfíbios conhecidas estão em risco de extinção. Os anfíbios são ainda mais vulneráveis durante seus estágios larvais, pois sua pele é mais permeável e mais suscetível à absorção de contaminantes ambientais. Nos últimos anos, houve um aumento significativo no número de estudos sobre girinos no Brasil. Apesar desse aumento, o número ainda é insuficiente. Portanto, o objetivo desta pesquisa é reunir informações sobre o conhecimento atual a respeito de girinos. Para tanto, foi realizado um estudo cientométrico, conduzindo-se uma revisão sistemática não automatizada da literatura científica disponível. A pesquisa utilizou as bases de dados Web of Science e Google Scholar, com os descritores "girinos" ou "larvas de anuros", abrangendo publicações de janeiro de 1960 a julho de 2024. Artigos científicos, notas técnicas e livros indexados foram incluídos neste estudo. A análise também visou identificar os estados brasileiros com o maior número de publicações e analisar palavras-chave utilizando o software VOSviewer. Foram encontrados 24.971 artigos, dos quais

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4.845 atenderam aos critérios de inclusão. Os EUA apresentaram o maior número de publicações (1.039), seguidos pelo Brasil (962) e pela China (291). A maioria dos artigos internacionais concentra-se em famílias específicas, como Ranidae, Bufonidae e Hylidae. No Brasil, 843 artigos foram considerados válidos, abrangendo pesquisas sobre 17 famílias e 541 espécies, sendo Hylidae a família mais estudada (257 espécies; 46,9%), seguida por Leptodactylidae (106 espécies; 19,3%) e Bufonidae (38 espécies; 6,9%). As famílias Alsodidae, Ceratophryidae e Eleutherodactylidae foram as menos estudadas, com apenas uma espécie cada (0,1%). A maioria dos estudos brasileiros concentra-se na região Sudeste, principalmente em São Paulo, Minas Gerais e Rio de Janeiro, enquanto as regiões Norte e Nordeste apresentam menor número de publicações. A análise revelou padrões na distribuição da pesquisa, um aumento no interesse por girinos desde 2010 e lacunas notáveis em áreas-chave que justificam uma investigação mais aprofundada.

Palavras-chave: Anfíbios; Anura; Caatinga; Ecologia de girinos; Larvas de anfíbios.

Introduction

Most amphibians have a two-phase life cycle, characterized by distinct larval and adult stages (McDiarmid & Altig, 1999; Pough, 2008). In anuran amphibians, the larval stage is known as a tadpole, and represents one of the main characteristics of the group (McDiarmid & Altig, 1999).

Currently, approximately 41% of known amphibian species worldwide are at risk of extinction (Pimm *et al.*, 2014; Santos *et al.*, 2023), and population declines are associated with high levels of environmental degradation, such as habitat fragmentation, climate change, increased use of chemicals and soil contamination, and pollution of water bodies, all of which have harmful effects on amphibian species (White *et al.*, 1997; Díaz *et al.*, 2000; Driscoll, 2004; Goulart *et al.*, 2012; Deheuvels *et al.*, 2014). The vulnerability of amphibian larvae is even greater because during their metamorphosis, the skin of the individuals becomes more permeable and susceptible to absorbing environmental contaminants (Vitt *et al.*, 1990).

Most tadpoles are adapted to an aquatic life cycle and dependent on water during their development (McDiarmid & Altig, 1999). Tadpoles are found in different microhabitats and present remarkable morphological diversity (McDiarmid & Altig, 1999; Melo *et al.*, 2018; Dubeux *et al.*, 2019, 2020). They play essential ecological roles as primary consumers, being prey for several species, and act as predators that regulate populations of macroinvertebrates (McDiarmid & Altig, 1999; Haddad *et al.*, 2013; Dubeux et al., 2020). Additionally, tadpoles contribute to transferring energy within food webs (Capps *et al.*, 2015), function as environmental bioindicators, and play a role in bioturbation processes (Montaña *et al.*, 2019; Gonçalves *et al.*, 2024). Although research on tadpoles has increased steadily in recent decades, it remains limited to some specific scenarios, regions, and study areas (Provete *et al.*, 2012; Dubeux *et al.*, 2019, 2020; Vera Candioti *et al.*, 2023).

There are currently approximately 8,933 species of amphibians worldwide, including about 230 caecilians (Gymnophiona), 828 salamanders (Urodela), and 7,875 anurans (frogs, treefrogs, and toads), distributed across 80 families (Frost, 2025). Brazil harbors the highest richness of amphibians in the world, with more than 1,188 species, including approximately 1,144 species of anuran distributed among 20 families and 107 genera (Segalla et al., 2021). However, despite this diversity, studies focusing on tadpoles in Brazil remain insufficient when compared to those on other vertebrate groups or even adult anurans (Provete *et al.*, 2012; Dubeux *et al.*, 2019; Vera Candioti *et al.*, 2023). It is estimated that around 40% of Brazilian anuran species still lack descriptions of their larval stages (Provete *et al.*, 2012; Dubeux *et al.*, 2019).

The scarcity of studies focusing on tadpoles has resulted in substantial gaps in knowledge regarding some aspects, such as geographic distribution, diet, and morphology, thereby limiting the development of effective conservation strategies for amphibian populations (Vera Candioti *et al.*, 2023). Given the ecological importance and high diversity of tadpoles, it is essential to assess the current state of knowledge. Accordingly, this study aims to quantify and synthesize available information on tadpoles in Brazil through a scientometric approach, complemented by updated data on the global scenario. Specifically, we aim to: (a) quantify the number of studies on tadpoles published over the last 60 years, corresponding to the period during which detailed studies on tadpoles became more widespread; (b) identify the regions with the highest number of studies; (c) determine which topics and species have been most frequently studied over time; (d) identify potential gaps in knowledge regarding tadpoles; and (e) assess the conservation status of the Brazilian species with described larval stages.

Materials y methods

Study characterization

A scientometric study employs both qualitative and quantitative approaches and aims to examine, in a cumulative and comparative manner, the characteristics and patterns of production, dissemination, and use of scientific information (Silva *et al.*, 2011). This type of study seeks to review the literature in order to identify and discuss possible gaps within a given subject or region (Galvão & Ricarte, 2019). Scientometric studies are also referred to as bibliometric analysis (Bornmann & Mutz, 2015) and can address a wide range of topics, such as citations, authorship, scientific productivity, research trends, publication patterns, and collaborative networks (Bornmann & Mutz, 2015).

Data gathering

A non-automated systematic review of the scientific literature available in the Web of Science (WoS) and Google Scholar (GS) databases was conducted, as these platforms present a large number of both international and national research (Singh *et al.*, 2021; da Costa Neto *et al.*, 2022). Topic searches were performed using the descriptors and Boolean operators "tadpoles" OR "anuran larvae", considering all available fields. Searches were done in English in the WoS database and in Portuguese in the GS database in order to expand the scope of the search (Alves *et al.*, 2021).

The search for documents encompassed all articles available in the aforementioned databases from January 1960 to July 2024, providing a comprehensive overview of approximately 60 years of research on tadpoles. As inclusion criteria, all scientific articles, short communications, and books published in indexed journals that addressed any aspect of tadpole were selected. As exclusion criteria, gray literature (undergraduate theses, master's theses, and doctoral dissertations), paywalled or duplicated papers, conference proceedings, articles presenting only citations, and review articles were excluded. Subsequently, using the same inclusion and exclusion criteria, articles that focused exclusively on Brazil were selected to assess national contributions.

The taxonomic classification and scientific nomenclature of all species recorded during the review were updated following Amphibian Species of the World (Frost, 2025). Conservation status was verified using the Brazilian Red List of Threatened Species (ICMBIO/MMA, 2024) and the Red List of the International Union for Conservation of Nature (IUCN, 2025).

Data analysis

For each article, abstracts and methodologies were initially screened, and those that met the inclusion criteria were read in full. Information on authorship, geographic location of the study (countries and Brazilian states), year of publication, species and families studied, research objectives, and keywords were extracted. All collected information was compiled into a table (see Appendix 1).

Locations of the studies were added to identify the countries with the highest number of publications. The same approach was used to determine the Brazilian states with the highest number of published articles. Articles that did not provide information on study location were excluded from these analyses. Maps were generated using ArcGIS v.10.3 software (Santos *et al.*, 2024).

A correlation of Pearson was performed between the number of articles published in Brazil and the year of publication to assess temporal trends in publications (Mira *et al.*, 2022). To characterize and categorize the studies, both the specific objectives of each article and the thematic scope of the journals in which they were published were considered. Analyses of the number of families and species studied in Brazil was carried out using VOSviewer v.1.6.17 software (Leiden University, The Netherlands) (Bhoomaiah *et al.*, 2020). For species-level analyses, the 20 most representative species were considered, whereas for family-level analyses, the 30 most representative families were included. Based on the results obtained in VOSviewer, clusters were generated and represented by different colors. Within these clusters, the size of the circles corresponds to the number of publications related to a given species or family, and the distance between circles indicates the degree of similarity among them (Zhao *et al.*, 2018).

Results

Worldwide production

A total of 24,971 articles were published worldwide between 1960 and 2024. After applying the inclusion and exclusion criteria, 4,845 articles were considered valid for global analysis. Studies were published in nearly every country worldwide. The United States of America had the highest number of publications (1,039 articles; 21,4%), followed by Brazil (962; 19,8%) and China (291; 6%) (Fig. 1). Most articles focused on specific families, such as Ranidae, Bufonidae, and Hylidae, and their respective genera *Aquarana*, *Rhinella*, and *Scinax*, demonstrating a clear pattern of taxonomic interest among researchers.

Tadpoles in Brazil

In Brazil, an increase in research interest on tadpoles has been evident since 2000, with a continuous growth in the number of publications and no peak moments (Fig. 2). A total of 962 articles were selected, covering 541 species belonging to 17 families. Hylidae was the most represented family, with 257 species studied, which represents 47.5% of the articles. Leptodactylidae and Bufonidae followed, with 106 (19.5%) and 38 (7.0%) species studied, respectively. Other families with notable representation were Odontophrynidae (28 species; 5.2%), Hylodidae (26 species; 4.8%), Aromobatidae (25 species; 4.6%), Microhylidae (18 species; 3.3%), Cycloramphidae (12 species; 2.2%), and Dendrobatidae (15 species; 2.8%). Families with fewer species studied were Centrolenidae (six species; 1.1%), Pipidae (five species; 0.9%), Hemiphractidae (four species; 0.7%),

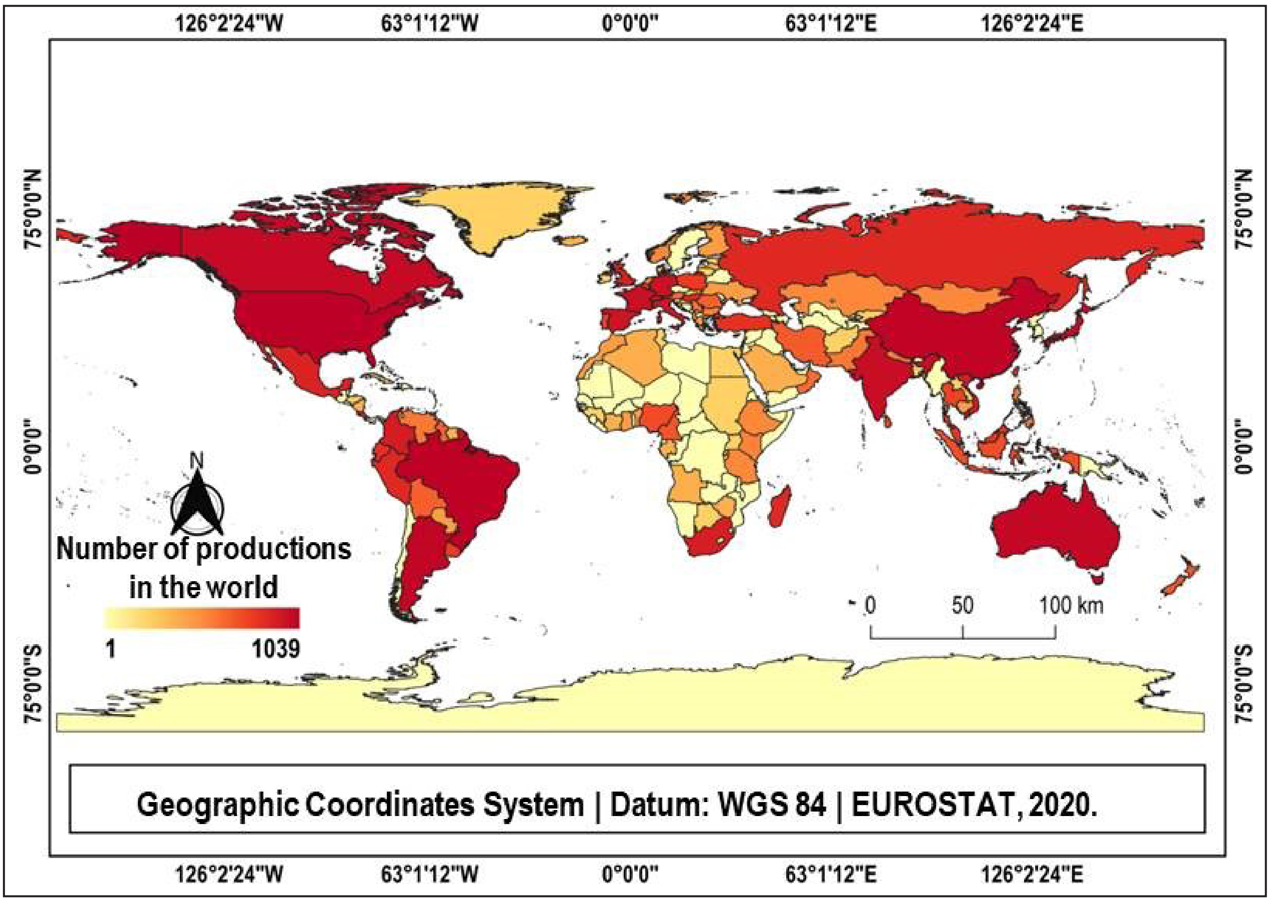

Figure 1. World map showing the distribution of scientific production on tadpoles in all countries over the last 60 years. The intensity of the red color represents the number of studies carried out by the country. Juliana Delfino, 2024.

Ranidae (three species; 0.5%), and Strabomantidae (two species; 0.4%). Alsodidae, Ceratophryidae, and Eleutherodactylidae were each represented by only one species (0.2%).

Hylidae and Leptodactylidae not only consisted of the highest number of studied species, but also showed the highest frequency of occurrence in studies, representing 41% and 27% of the total studies, respectively. Ranidae (23%) and Bufonidae (15%) were also strongly represented, largely due to studies on the genera Aquarana and Rhinella, respectively. The most frequently studied species were Aquarana catesbeiana (Ranidae), Boana faber (Hylidae), Rhinella marina (Bufonidae), Physalaemus cuvieri (Leptodactylidae), and Leptodactylus latrans (Leptodactylidae).

VOSviewer analyses revealed clear patterns of co-occurrence and strong links among the families Leptodactylidae, Hylidae, and Bufonidae, indicating that research focusing on one of these groups often includes the other (Fig. 3). In contrast, families such as Pipidae, Aromobatidae, Dendrobatidae, Eleutherodactylidae, and Hemiphractidae showed fewer publications and weaker associations among them (Fig. 3).

These results demonstrated that Leptodactylidae, Hylidae, and Bufonidae dominate the research output. A distinct pattern was observed for the families Microhylidae, Centrolenidae, Dendrobatidae, and Aromobatidae, which, despite being represented by fewer publications, are often studied in combination. In contrast, Ranidae, although frequently reported, showed limited association with other families, suggesting a more isolated research approach (Fig. 3).

At the species level, analyses included the 45 most frequently reported taxa. Species of Hylidae exhibited higher frequencies and stronger associations with species of Leptodactylidae and Bufonidae (Figure 4). Interestingly, a consistent association with Microhylidae species was also detected, as these groups are often examined together (Figure 4). *Aquarana catesbeiana* (Ranidae) was the most frequently reported species but showed little evidence of co-occurrence with other taxa (Fig. 4).

Based on study locations, 843 out of the 962 selected articles presented well-defined geographic information. The Southeast region accounted for the

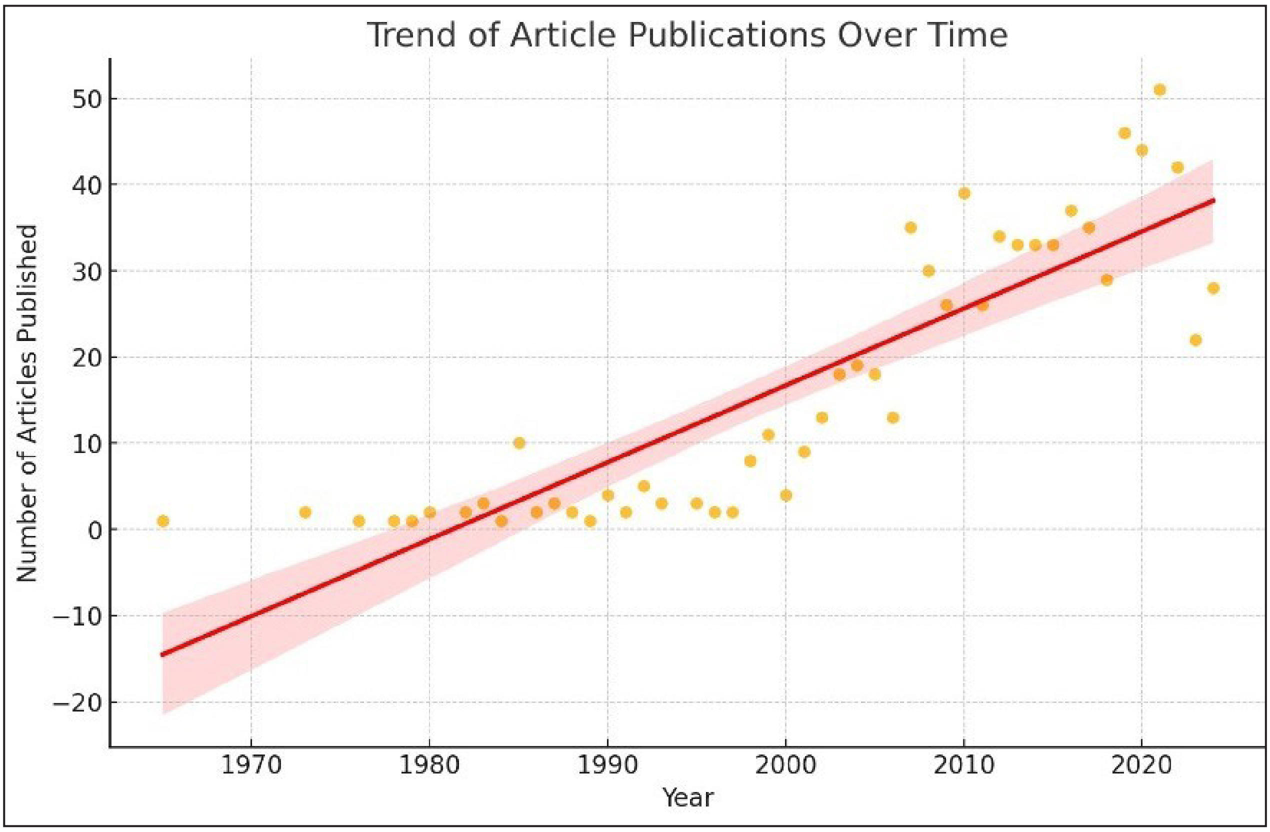

Figure 2. World map showing the distribution of scientific production on tadpoles in all countries over the last 60 years. The intensity of the red color represents the number of studies carried out by the country.

highest number of studies (407 articles), with São Paulo (N = 222), Minas Gerais (N = 94), and Rio de Janeiro (N = 91) being the most represented states. The South region followed with 94 studies, from Rio Grande do Sul (N = 59) and Santa Catarina (N = 35). The Center-West region contributed with 84 articles, including Goiás (N = 63), Mato Grosso (N = 13), and Mato Grosso do Sul (N = 8). The North (63 studies; Amazonas: N = 44 and Pará: N = 19) and Northeast regions (93 studies; Bahia: N = 52, Alagoas: N = 20, Pernambuco: N = 12, and Paraíba: N = 9) represented the lowest number of studies (Fig. 5). In the North region, Tocantins and Rondônia were the least studied states, with two and one publications, respectively.

Trends and knowledge gaps about tadpoles in Brazil

Of the 962 articles analyzed, 789 presented clearly defined objectives and were classified into 13 research categories: systematics and taxonomy (species description and phylogeny; N = 172), population and community ecology (population structure, species richness, and diversity; N = 118), natural history (reproductive strategies, behavior, predation, and diet; N = 96), toxicology (N = 79), physiology (N = 77), morphology (descriptive morphological and anatomical studies; N = 68), frog farming (commercial breeding; N = 55), geographic distribution (occurrence records and spatial distribution; N = 51), ontogeny (developmental studies; N = 23), parasitology (N = 16), microbiology (N = 11), genetics (cytogenetic studies; N = 9), and other areas, including statistics, histology, and pathology (N = 14).

Gaps remain regarding the number of studied species. Despite Brazil harboring more than 1,000 amphibian species, only 541 species from 17 families have been studied, based on 843 national articles analyzed.

Among species assessed, those classified as threatened according to the Brazilian Ministry of the Environment (ME) and the International Union for Conservation of Nature (IUCN) include Critically Endangered species (*Melanophryniscus cambaraensis* and *M. admirabilis* [Bufonidae]; *Phrynomedusa marginata*, *Pithecopus rusticus* [Hylidae]; and *Physalaemus soaresi* [Leptodactylidae]), Vulnerable species (*Cycloramphus faustoi* [Cyclo-

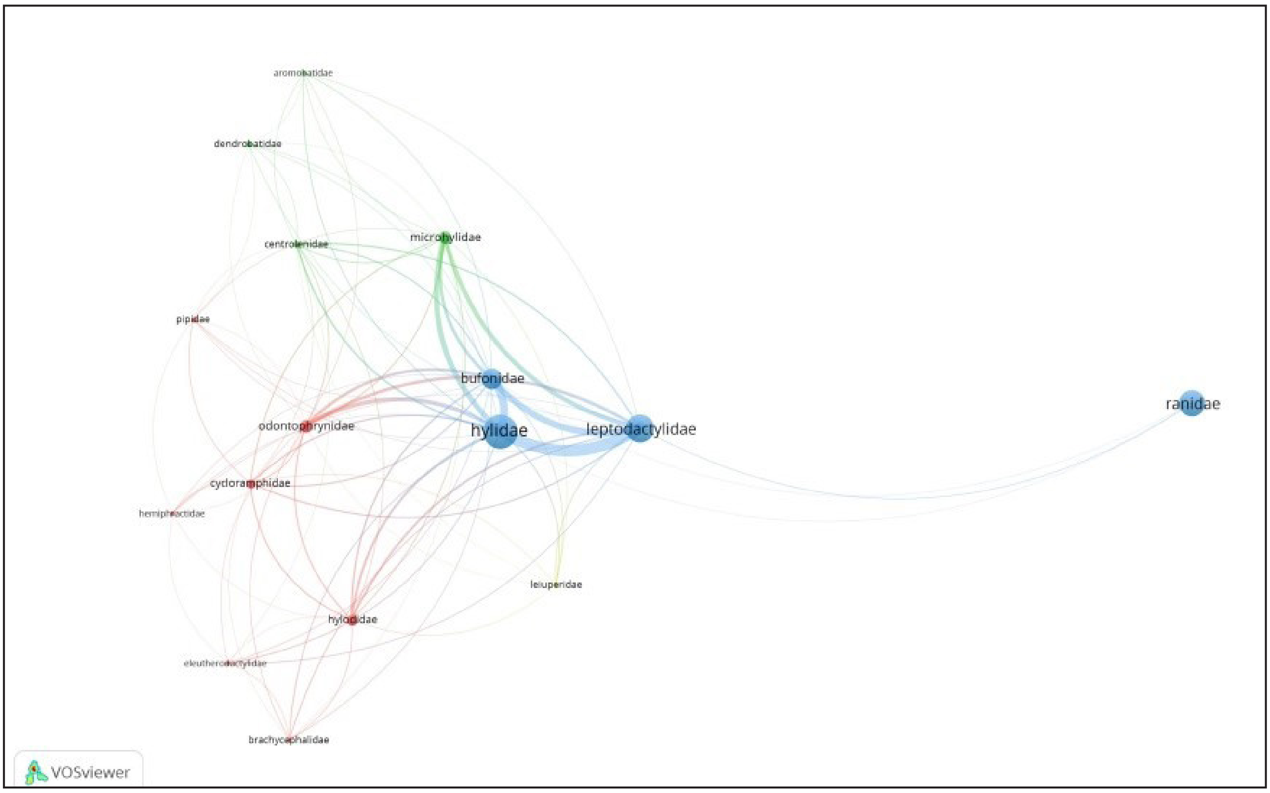

Figure 3. Brazilian trends in the number of scientific publications and tadpole families studied. The size of the circle indicates the number of articles published on each family. The distance between one family and another indicates the extent to which one family is associated with another in studies. The colors indicate groups formed according to the families that were related in the studies found.

ramphidae]), and species listed as Least Concern (*Melanophryniscus dorsalis* [Bufonidae]).

Discussion

Number of articles worldwide

There is a considerably high number of studies related to tadpoles; nevertheless, it is clearly possible to observe that some countries have a substantially higher number of publications compared to others, resulting in a considerable disparity in the scientific knowledge about tadpoles. A clear, visible pattern emerges, with the United States of America, Brazil, and China showing the highest concentrations of scientific studies; a trend that may be related to multiple factors.

The United States and China have large research institutions that invest in herpetology and ecology (De Negri & Squeff, 2014; Segalla *et al.*, 2021; Demartin *et al.*, 2024). In addition, they have more robust infrastructure and funding for field and laboratory research, which facilitates the execution of systematic and long-term studies (Ficetola *et al.*, 2008; Demartin *et al.*, 2024).

In tropical countries such as Brazil, where biodiversity is high and anthropogenic pressures on habitats are intense (e.g. deforestation, urbanization, and water pollution), understanding ecological processes becomes fundamental for conservation strategies (Haddad & Prado, 2005; Rohr *et al.*, 2008). In Brazil, specifically, the high diversity of amphibians (Segalla *et al.*, 2021), especially anurans, makes the country a privileged setting for investigations on tadpoles. Environmental heterogeneity and marked seasonality in tropical regions further expand research opportunities, particularly regarding tadpole ecology and their breeding sites (Haddad & Prado, 2005; Nunes-de-Almeida *et al.*, 2021). On the other hand, in temperate-climate countries or regions with lower amphibian diversity, the reduced availability of suitable aquatic habitats may explain the scarcity of studies. In these contexts, tadpoles may not be considered such relevant models for ecological studies, or herpetological research may focus on other animal groups (Rohr *et al.*, 2008).

The families Hylidae, Leptodactylidae, and Bufonidae exhibit the highest species diversity and the greatest number of published studies. According to Haddad and Prado (2005), the high diversity within these families is explained by their wide range of be-

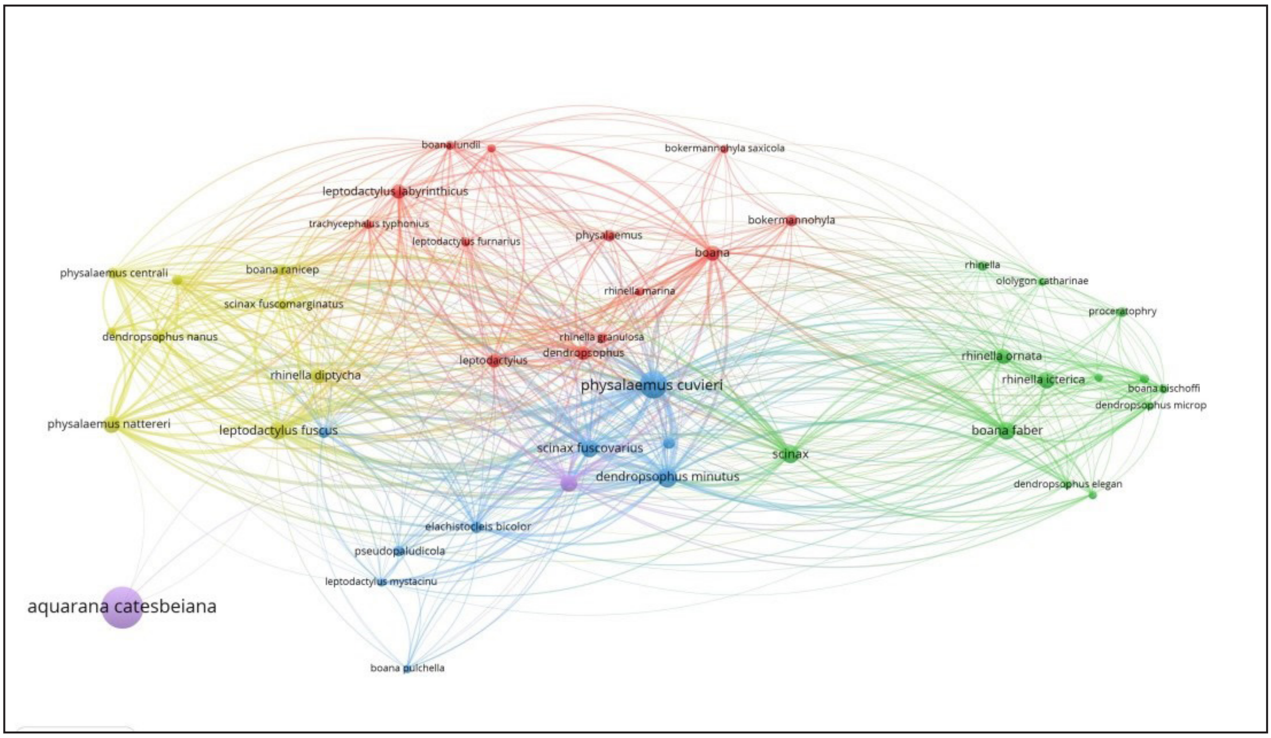

Figure 4. Brazilian trends in the number of scientific publications and tadpole species studied. The size of the circle indicates the number of articles published on each species. The distance between species indicates the extent to which one is associated with another in studies. The colors indicate groups formed according to the species that were related in the studies found.

haviors, habitats, and reproductive strategies, which increase species survival, including their ability to adapt to modified environments. Haddad and Prado (2005) and Nunes-de-Almeida *et al.* (2021) also note that the diversity of reproductive strategies and oviposition site choices within these families increases the occurrence of tadpoles across different aquatic microhabitats, from temporary pools to permanent water bodies, making their study feasible in multiple environmental contexts. The broad ecological plasticity and adaptability of tadpoles from these families facilitate the observation of responses to environmental factors such as resource availability, predators, and seasonal variations (Rossa-Feres *et al.*, 2015). Furthermore, their high species richness enables comparative analyses of reproductive modes and larval development strategies, which are essential for understanding evolutionary patterns and anuran ecology (Rossa-Feres *et al.*, 2015). Therefore, the higher number of studies on tadpoles of Hylidae, Leptodactylidae, and Bufonidae can be attributed both to their abundance in nature and to the diversity of larval life forms within these families.

Tadpoles in Brazil

The analysis of tadpole data in Brazil revealed patterns in research distribution, as well as significant gaps in key areas that deserve future attention. The families Leptodactylidae, Hylidae, and Bufonidae were also those with the highest numerical representation of published articles, whereas Centrolenidae was the least represented family. Centrolenidae is considered poorly studied, especially in relation to its tadpoles, as only about 25% of its diversity has been described (Dias *et al.*, 2020).

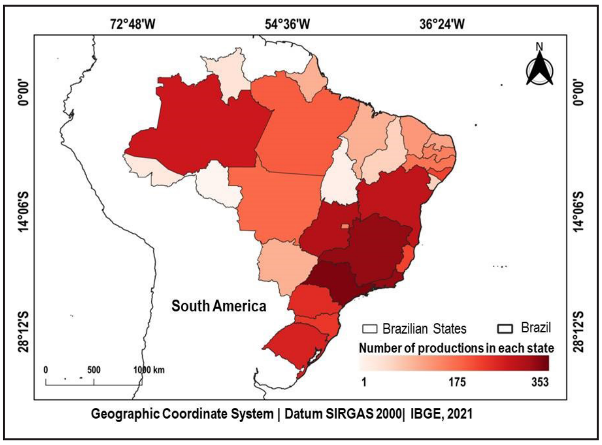

Figure 5. Map of the distribution of scientific production on tadpoles in Brazil showing the distribution of studies published in each state over the last 60 years. The intensity of the red color represents the number of studies carried out per country. Source: Juliana Delfino, 2024.

During the analysis of the articles, it was observed that seven studied species mentioned the family Brachycephalidae in association with the tadpole stage, although this group exhibits direct development, characterized by the absence of a larval stage (Pombal Jr, 1999; Pombal Jr & Izecksohn, 2011). This finding demonstrates the potential for inappropriate and incorrect interpretations of reproductive aspects. Furthermore, inconsistencies in how life history characteristics are reported can hide the compilation of reliable ecological information. Ranidae was an immensely representative family in terms of the number of studies, particularly in the early years of tadpole research (Cruz, 1973; Fontanello *et al.*, 1982; Soares *et al.*, 1983) and during the period when frog farming expanded as a commercial activity (Hayashi *et al.*, 2004; Barbosa *et al.*, 2005; Cribb, 2013; Seixas Filho *et al.*, 2016).

Research on tadpoles has grown exponentially in recent decades, particularly since 2010, as demonstrated in the present study. However, there is a stronger concentration of studies conducted in the Southeastern region of Brazil, a pattern consistent with previous findings (Provete *et al.* 2012; Sidone *et al.* 2016). This region hosts the largest number of studies, likely due to the high density of research institutions and graduate programs in the region (Guerra *et al.*, 2020; Pezzuti *et al.*, 2021; Santos *et al.*, 2023d). In contrast, the Northern and Northeastern regions exhibit the lowest number of studies on tadpoles (Guerra *et al.*, 2020; Santos *et al.*, 2023c). Although research in the Center-West increased, many species remain uninvestigated (Santos *et al.*, 2023b). This scenario is concerning, as it demonstrates that despite the expansion of scientific production over the past six decades, knowledge generation remains geographically concentrated, potentially compromising a comprehensive understanding of tadpole ecology and biogeography in Brazil.

Amphibians are currently the most threatened group of vertebrates (IUCN, 2025), and many species may become extinct before their larvae are even known (Rossa-Feres *et al.*, 2015; Vera Candioti *et al.*, 2023). Knowledge gaps related to tadpoles, such as information on distribution, genetics, and adaptations to environmental factors, further complicate conservation efforts (De Almeida *et al.*, 2015; Almeida *et al.*, 2016; Vera Candioti *et al.*, 2023). Filling these gaps is essential to expand our understanding of the group, particularly for species whose ecology remains undescribed, complementing data on species richness (Silva, 2010; Magalhães *et al.*, 2013; Mascarenhas *et al.*, 2016; Dubeux *et al.*, 2019; Vera Candioti *et al.*, 2023) and biodiversity surveys (Rossa-Feres; Nomura, 2006; Nori & Loyola, 2015; Jordani *et al.*, 2017; Fatorelli *et al.*, 2018; Alves-Ferreira *et al.*, 2021). Additionally, information on tadpoles can contributed to taxonomy and phylogenetic studies (Haas, 2003; Frost et al., 2006; Fouquet et al., 2019), as well ecology and conservation, especially in understanding which environmental factors influence species composition (Marques & Nomura, 2015; Nori & Loyola, 2015; Marques *et al.*, 2018; Annibale *et al.*, 2020), and in ecotoxicological and ecophysiological studies (Simon et al., 2015; Gutiérrez-Pesquera *et al.*, 2016; Macagnan *et al.*, 2017; Da Silva *et al.*, 2021; Malafaia *et al.*, 2022; Dos Santos *et al.*, 2024).

These knowledge gaps hinder identification of other types of threats to tadpole populations beyond environmental changes, complicating the development of effective r conservation strategies. This issue becomes particularly critical for species already considered threatened, such as the eight species recorded in this study.

The Northeastern states are largely located within the Caatinga biome, which is rich in biodiversity but remains undersampled for several groups, including amphibians and especially tadpoles (Marques *et al.*, 2023). Paraíba stands out as one of the states with the lowest number of tadpole-related studies, with only nine publications. Of these, three focused on species descriptions (*Physalaemus cicada*, *Leptodactylus vastus*, and *Phyllodytes brevirostris*; Vieira *et al.*, 2007; Vieira & Arzabe, 2008; Vieira *et al.*, 2009), one pursued to characterize the reproductive modes of Caatinga anurans (Vieira *et al.*, 2009), another described the reproductive behavior of a specific species (Hödl, 1992), and one described an adult specimen, while mentioning some characteristics of tadpoles (Caramaschi, 2006).

The low number of studies in the North and Northeast raises concerns about the underestimation of regional biodiversity in Brazilian research. Although the Caatinga has approximately 15 priority areas for conservation (Camardelli & Napoli, 2012), nearly 40% of the biome remains insufficiently studied (Tabarelli & Silva, 2003; Tabarelli & Vicente, 2004), which is consistent with the low number of studies on tadpoles in this biome.

The Caatinga has been recognized as one of the least known biomes in relation to amphibians, a pattern first noted by Heyer (1988) and later corroborated by other studies (Tabarelli & Silva, 2003; Tabarelli & Vicente, 2004). This suggests that knowledge about amphibian ecology, especially tadpoles, remains limited in this region (Garda *et al.*, 2017). The unique ecological conditions of the Caatinga may influence the behavior, development, and adaptations of tadpoles in ways that are still poorly understood (Garda *et al.*, 2017).

The lack of basic information about the species hampers conservation strategies, such as the scarcity of studies on genetics and tadpole development. Although taxonomy was the category with the highest number of studies, it remains insufficient when considering Brazil's amphibian richness. Another critical gap is the lack of studies directly addressing the impact of climate change on tadpoles (Guerra *et al.*, 2020). While studies on geographic distribution exist, few examine how global warming, altered by changes in precipitation patterns and aquatic habitat degradation, affects the tadpole life cycle and population dynamics (Nori & Loyola, 2015; Guerra *et al.*, 2020). In the context of fast global change, this gap is particularly concerning.

Article categories

Overall, a large number of articles related to the search terms were found in the databases. However, some studies were not freely available, which negatively impacts the global dissemination of information by limiting both the submission of new articles in this format and access to published work. This limitation occurs because the cost of accessing a given article is often unaffordable for many researchers (Gomes *et al.*, 2018), thereby restricting the availability of data on the group. Despite the high proportion of non-open-access publications, the number of studies on tadpoles worldwide has shown continuous growth, especially from 2000 to the present.

The limited attention given to "genetics and microbiology" may indicate a significant gap in our understanding of the evolutionary dynamics and health of tadpoles. Population genetics studies are crucial for assessing genetic variability, gene flow among populations, and the capacity of species to adapt to environmental changes such as pollution and global warming (Allentoft & O'Brien, 2010; Tavares-Junior *et al.*, 2020). The scarcity of genetic data hinders predictions of resilience under increasing selective pressures. Given the crucial role of tadpoles in aquatic ecosystems, especially as bioindicators, expanding studies in these areas is fundamental for evaluating anthropogenic impacts on ecosystems (Thomson *et al*., 2018; Tavares-Junior *et al*., 2020).

Another critical concerns "microbiology". Recent studies have shown that the microbiota of tadpoles can influence health and resistance to pathogens, such as *Batrachochytrium dendrobatidis*, the fungal agent responsible for chytridiomycosis, a disease that has devastated amphibian populations worldwide (Bletz *et al*., 2013; Ujszegi *et al*., 2023). The lack of in-depth research on this topic represents a major gap for amphibian conservation. The diversity of research areas covered also reflects the complexity of tadpole ecology. While studies on physiology and morphology have provided a basic understanding of how these organisms adapt to their environment, fields such as parasitology and microbiology are emerging as important areas for revealing new ecological interactions and challenges for conservation.

Another point worth highlighting is the scarcity of studies that address the impact of climate change on the distribution and ecology of tadpoles. Although 51 studies focused on the geographic distribution of species, few explore how global warming and altered precipitation patterns affect aquatic habitats and, consequently, larval survival (Catenazzi, 2015).

Conclusion

Among the 789 studies analyzed regarding the defined objectives and the thematic scope, "systematics and taxonomy" was the most explored research area. This result is considerably expected, as taxonomy is fundamental to biology and provides the basis for the identification and classification of species (Padial *et al*., 2010). The second most frequently studied area was "population and community ecology", reflecting a strong interest in understanding the structure and dynamics of tadpole populations in natural habitats. Such studies are important because intraspecific and interspecific interactions are naturally present and play an important role in maintaining biodiversity (Parris, 2006). Studies of tadpole community composition are also crucial for assessing the impacts of environmental changes, including habitat loss and forest fragmentation, which threaten the survival of many species (Kopp & Eterovick, 2006).

Overall, the analysis of tadpole-related publications in Brazil reveals a concentration of research in well-established areas such as taxonomy and ecology, with important gaps in emerging fields, such as microbiology and genetics. The pronounced geographic imbalance in research efforts, with an underrepresentation of the North and Northeast regions, highlights the need for greater investment in scientific studies in these areas. Moreover, global issues such as climate change and environmental degradation must be more widely integrated into research on tadpoles, given the vulnerability of amphibians and their importance for the health of aquatic ecosystems.

To address these challenges, it is crucial to increase financial and logistical support for research in underexplored regions, promote interdisciplinary approaches, and prioritize emerging topics such as tadpole health and environmental change. Filling these gaps will make it possible to develop more effective conservation strategies for tadpoles and the ecosystems on which they depend. Furthermore, in light of increasing global threats to aquatic ecosystems, expanding research in toxicology and ontogeny will be essential for predicting how tadpole populations respond to environmental factors.

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Apendice

https://drive.google.com/drive/folders/1kOgA1p8pPe46YyI9rlgchRCk-w4Qb62O?usp=sharing

Trabajo

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Geckos Forasteros: an assessment of the invasion status by exotic geckos in Argentina using citizen science

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ABSTRACT

Geckos are among the most successful reptile invaders and have colonized a wide range of suitable habitats and climates around the world. Outside their native range, they usually show a clear association with urban habitats and human-modified habitats. In Argentina, *Hemidactylus mabouia* and *Tarentola mauritanica* had confirmed records for a few provinces. *Hemidactylus turcicus* was reported for Buenos Aires in 1989 from a single record, but later its presence became dubious as it belonged to a misidentified *H. mabouia.* We started a citizen-science project called Geckos Forasteros, to update the invasion status of gecko species in Argentina. We collected records of geckos from online social networks and the project's online form, where people voluntarily sent pictures and information about their findings. Our results confirm the presence of *H. turcicus* in the country and reveal that the extent of the invasion by *T. mauritanica* and *H. mabouia* in the country is far larger than previously thought, including the southernmost records worldwide for the three species. We explored the environmental variables associated with the presence of exotic gecko species in South America, and discussed global distribution patterns. The updated distribution and list of exotic geckos in Argentina, highlights the need of monitoring these populations, encouraging the study of the biology of these invaders in the different environmental conditions where they are present.

Key words: Alien species; Dispersion; Lizards; Social media; South America.

RESUMEN

Los geckos se encuentran entre los reptiles invasores más exitosos y han colonizado una amplia gama de hábitats y climas adecuados en todo el mundo. Fuera de su área de distribución nativa, suelen mostrar una clara asociación con hábitats urbanos y ambientes modificados por el ser humano. En Argentina, *Hemidactylus mabouia* y *Tarentola mauritanica* contaban con registros confirmados en algunas provincias. *Hemidactylus turcicus* fue registrado en Buenos Aires en 1989 a partir de un único registro, pero posteriormente su presencia se volvió dudosa al comprobarse que se trataba de un ejemplar mal identificado de *H. mabouia.* Iniciamos un proyecto de ciencia

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ciudadana denominado Geckos Forasteros, con el objetivo de actualizar el estado de invasión de las especies de geckos en Argentina. Recopilamos registros de geckos a partir de redes sociales en línea y de un formulario digital del proyecto, en el cual las personas enviaban voluntariamente fotografías e información sobre sus hallazgos. Nuestros resultados confirman la presencia de *H. turcicus* en el país y revelan que la extensión de la invasión por *T. mauritanica* y *H. mabouia* es mucho mayor de lo que se pensaba previamente, incluyendo los registros más australes del mundo para las tres especies. Exploramos las variables ambientales asociadas con la presencia de especies exóticas de geckos en Sudamérica y discutimos los patrones de distribución global. La actualización de la distribución y el listado de geckos exóticos en Argentina, resalta la necesidad de monitorear estas poblaciones y fomenta el estudio de la biología de estos invasores en las diversas condiciones ambientales en las que se encuentran presentes.

Palabras claves: Especies exóticas; Dispersión; Lagartos; Redes sociales; Sudamérica.

Introduction

Alien species are among the main threats to biodiversity and cause major economic losses (Bomford *et al.,* 2009). Gekkota is a highly functionally diverse clade of lizards, with species belonging to several functional groups (Pelegrin *et al*., 2021). Geckos are among the most successful reptile invaders, yet their impact on native species remains debatable (Bomford *et al*., 2009; Winck *et al*., 2017). Gekkonidae is a lizard family with the highest success as invaders (Bomford *et al*., 2009), and specifically, several species of the genus *Hemidactylus* are responsible for such success (Weterings and Vetter 2018). *Hemidactylus mabouia*, native to Central and East Africa, and *H. turcicus*, native to the Middle East and Mediterranean regions (Carranza and Arnold 2006; Locey and Stone 2006) have colonized a wide range of suitable habitats (and climates) around the world (Weterings and Vetter 2018). Similarly, *Tarentola mauritanica* (the Moorish Gecko, Phyllodactylidae) has dispersed from its native distribution in southern Europe and North Africa (Rato *et al*., 2024), successfully establishing populations in countries from both the Old and the New World (Medina *et al*., 2019). Populations of these exotic gecko species outside their native range show a clear association with urban habitats and human-modified habitats (Anjos and Rocha 2008; Weterings and Vetter 2018).

The first reports of *Hemidactylus mabouia* in Argentina date for the end of 1980's and was misidentified as *H. turcicus* by Williams (Williams 1989; Baldo *et al*., 2008), while *Tarentola mauritanica* first arrival to Argentina was apparently in Buenos Aires in the 1970's (Williams and Kacoliris 2012). Even when the first records were from the 80's, the presence of *H. mabouia* could be traced back about 500 years ago, probably related to the slave trade by Europeans (Vanzolini 1978; Carranza and Arnold 2006).

Hemidactylus mabouia is widely distributed in Argentina and has been reported in cities in the provinces of Buenos Aires, Chaco, Corrientes, Formosa, Misiones, Entre Ríos, and Tucumán, and in the wild in the surroundings of the Parque Nacional Iguazú, Misiones (Genise and Montanelli 1991; Federico and Cacivio 2000; Baldo *et al*., 2008; Álvarez *et al*., 2009; Torres *et al*., 2018). *Tarentola mauritanica* has been cited for the provinces of Buenos Aires, CABA, Salta, Tucumán, and Neuquén (Baldo *et al*., 2008; Diaz Fernandez *et al*., 2019; Medina *et al*., 2019; Scrocchi *et al*., 2019). Its presence in Rosario is known from informal records (Scrocchi *et al*., 2019). Reports on the presence of *Hemidactylus turcicus* in Argentina are unclear. After being cited by Williams (1989), no new records for this species were reported, but suggested in some publications (Williams and Kacoliris 2012; Weterings and Vetter 2018).

Records for the three species in Argentina can be easily found on GBIF and websites where contributors voluntarily upload their own records with photographic support. iNaturalist (www.inaturalist.org) and Ecoregistros (www.ecoregistros.org) are the most common sites where people upload records of animals and plants in Argentina. In iNaturalist, contributors would suggest an identification for the photographed specimen, and then iNaturalist community members assess the observation and suggest an identification. When there is a consensus about the identity of a species, the observation is catalogued as "Research grade", making it usable for research purposes through GBIF. In Ecoregistros, contributors assign species names when uploading their photos, and eventually, other community members can request a correction if the specimen is misidentified. Facebook groups about herpetology or general nature topics in Argentina also contain records for introduced geckos, generally from people asking about the identity of a given specimen.

A problem with these record sources is the lack of knowledge about diagnostic characteristics to correctly identify these exotic geckos. *Tarentola mauritanica*, *H. mabouia* and *H. turcicus* can be differentiated by looking at its toes and at the characteristics of its adhesive lamellae, specifically that from the fourth toe. *Tarentola mauritanica* has five full-size toes with an undivided series of toepads (or lamellae) extending along the entire underside surface of the digit. In addition, *Tarentola* has only claws in digits three and four. Unlike *Tarentola*, toe pads of both *Hemidactylus* species are divided and can be differentiated by the extension of the toe pads in the fourth toe. All digits of *Hemidactylus* have claws. *H. mabouia* has 7–9 lamellae, while *H. turcicus* has 9–10 under the fourth toe. Because of the different number of lamellae, toe pads in *H. turcicus* extend from the tip of the toe to its base, whereas in *H. mabouia*, they do not reach the base of the toe (Loveridge 1947; Abdala 1997; Krysko and Daniels 2005). There are also some minor differences in pholidosis and coloration between *Hemidactylus turcicus* and *H. mabouia*, based on the presence of larger and more numerous granular scales and a lighter coloration with light spots in *H. turcicus* (Loveridge 1947), but given the high variability in coloration patterns in both species (specially *H. mabouia*), using these characteristics could lead to misidentification.

Most specimens of *Hemidactylus* and *Tarentola* species published in iNaturalist, Ecoregistros, and Facebook were identified from a single picture, generally from a dorsal perspective, and generally taken in poor conditions (using a cellphone camera, in poor lighting conditions, through a glass, out of focus, from a long distance, etc.), making identification difficult, especially among *Hemidactylus* species. Misidentified specimens can easily reach research grade in iNaturalist and end up in huge databases such as GBIF to be used by scientists in meta-analyses.

Despite the aforementioned problems, free digital platforms with mobile and desktop interfaces (such as iNaturalist) are recommended and very useful in citizen science projects (Encarnação et al., 2021). These have proven to be especially helpful in studies related to alien species, aiding in the detection and tracking of the spread of these species, in the prevention of their dispersal, and in the eradication of localized populations (Spear *et al*., 2017; Encarnação *et al*., 2021; Price-Jones *et al*., 2022). The valuable participation of citizen scientists can be formalized in research projects following some simple criteria, among which stand out: the use of multiple data collection methods, such as digital platforms, websites, personal surveys, forms, among others; mechanisms for data quality control and training provided by the researchers in charge; simplification of information related to the correct identification of taxa (Encarnação *et al*., 2021).

In November 2020 a group of scientists, science teachers, postdoctoral fellows, and graduate and undergraduate students started a citizen science project called "Geckos Forasteros en tu casa: estás seguro?" (Foreign geckos in your home: Are you sure/safe?). This countrywide project intended to update the distribution of the exotic geckos present in Argentina and to confirm the presence of *H. turcicus* in the country through direct interaction with Argentinian citizens.

Materials and methods

On 9 November 2020 the project Geckos Forasteros en tu casa: estás seguro? (hereafter referred to as Geckos Forasteros) began to collect records from several parts of Argentina. We created project profiles on Facebook (https://www.facebook.com/proyecto.geckos.forasteros) and Instagram (https://www.instagram.com/geckosforasteros/), and created a research project in iNaturalist (https://www.argentinat.org/projects/geckos-forasteros-en-tu-casa-estas-seguro), as well as a webpage (https://pelegrinlab.wixsite.com/lecoherp/gecks-forasteros) and an online form to collect records and pictures from observed geckos (https://docs.google.com/forms/d/e/1FAIpQLScyEiLXwW11Du1BNBzDGmu6qCAlcr77GFStMcb1LfWX7qTqBw/viewform), which was shared to every possible observer. Along with these platforms, an email account was also created to answer inquiries by citizens.

To obtain high-quality records, the Geckos Forasteros team created a series of informative materials to assist potential observers in the process of obtaining pictures that allowed the identification of each of the species (*T. mauritanica*, *H. mabouia*, and *H. turcicus*). This was accomplished through a series of videos teaching how to capture, manipulate, take usable pictures, and how to identify exotic geckos in Argentina. In addition, an identification key was created (and a video teaching how to use it), and a series of digital and easily shareable materials showing key features to identify each species (Fig. 1), differences between native and exotic species, basic concepts of invasive species, and some extra information on toe pads of geckos.

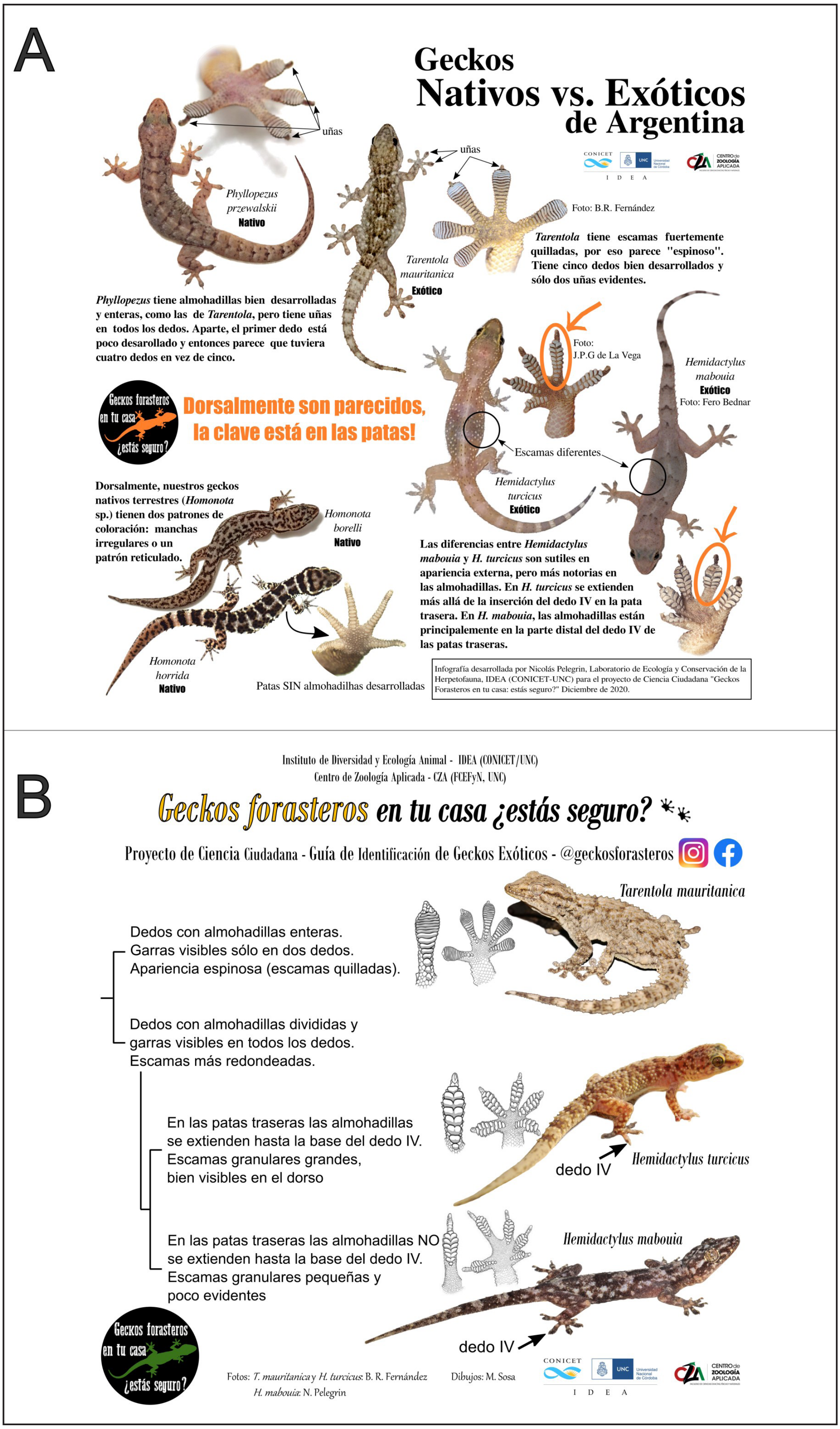
In this form, participants were required to answer a series of questions, such as name, state, city, neighborhood, proximity to warehouses, markets, truck parking lots, and bus stations; characteristics used to identify the observed individual (according to options offered in a plate); and to attach pictures of the specimen, preferably with pictures of forelimb toe pads, to allow the differentiation between *H. mabouia* and *H. turcicus*. We also reviewed observations in iNaturalist and Ecoregistros, contacting contributors if misidentification occurred. In addition, iNaturalist contributors were asked to complete the project form to unify the information available for every observation. Records for each of the studied gecko species were systematically searched on iNaturalist. Each retrieved observation was subsequently revised and validated by checking both the species identification and the associated locality data. An observation was included and cited if the identification was confirmed as correct, the locality represented a novel record, and the observation had achieved "Research Grade" status; these records were cited using their GBIF record number (see GBIF, 2025) and listed in Appendix 1. Furthermore, if an identification was initially incorrect but the organism still belonged to one of the species of interest, and the locality was novel, the authors suggested a corrected identification, and cited the iNaturalist Observation Record number in Appendix 1. None of the records reviewed in Ecoregistros (Ecoregistros, 2024) belonged to new localities for any of the species included.

Observations retrieved from the forms were filtered, and only those corresponding to the focus species were retained. Coordinates for each observation were extracted based on the available information (latitude and longitude for iNaturalist and Ecoregistros, coordinates to the closest locality reported in the forms) and plotted on a map.

We selected easily measurable traits so we could identify gecko species from the pictures sent by project participants or uploaded to iNaturalist or Ecoregistros. *Tarentola mauritanica* was differentiated from *Hemidactylus* species by the form of toe pads (enlarged and undivided in *Tarentola*, divided in *Hemidactylus*) and by the number of claws (only present in toes 3 and 4 in *Tarentola*, all toes with claws in *Hemidactylus*) (Abdala, 1997), and by the presence of large, strongly keeled tubercles in head and back, and the presence of small osteoderms (Levrat-Calviac and Zylberberg, 1986). Pictures obtained generally did not allow counting the number of lamellae in *Hemidactylus* species, so they were identified by the extension of toe pads (reaching the base of the fourth toe in *H. turcicus*, not reaching the base of the toe in *H. mabouia*). Also, as most pictures did not allow to see the lamellae, we used some external characteristics to identify *H. turcicus*, following the descriptions of Loveridge (1947): *Hemidactylus turcicus* has a characteristic dark stripe from the nostril, passing through the eye, to above the ear opening. The back is covered with small granular scales among which are scattered strongly keeled tubercles. These tubercles are dark but many are white or cream. *Hemidactylus mabouia* has no dark stripes in the head, and the back is covered by sparser, smaller and feebly tubercles. Color pattern in this species is highly variable. Also, the snout in *H. mabouia* is longer than in *H. turcicus*.

Results

As of 17 May 2024, 2,680 people followed the project on Facebook and 4,152 on Instagram. After removing duplicated observations and misidentified species, we ended up with 1195 observations, 113 from Ecoregistros (29 *H. mabouia*, 1 *H. turcicus*, and 83 *T. mauritanica*), 225 from the project form (26 *H. mabouia*, 2 *H. turcicus*, 197 *T. mauritanica*) and 857 from iNaturalist (140 *H. mabouia*, 15 *H. turci-*



Tarentola **tiene escamas fuertemente quilladas, por eso parece "espinoso". Tiene cinco dedos bien desarrollados y sólo dos uñas evidentes.**

Phyllopezus **tiene almohadillas bien desarrolladas y enteras, como las de *Tarentola*, pero tiene uñas en todos los dedos. Aparte, el primer dedo está poco desarollado y entonces parece que tuviera cuatro dedos en vez de cinco.**

Dorsalmente son parecidos, la clave está en las patas!

Dorsalmente, nuestros geckos nativos terrestres (*Homonota* sp.) tienen dos patrones de coloración: manchas irregulares o un patrón reticulado.

Las diferencias entre *Hemidactylus mabouia* y *H. turcicus* son sutiles en apariencia externa, pero más notorias en las almohadillas. En *H. turcicus* se extienden más allá de la inserción del dedo IV en la pata trasera. En *H. mabouia*, las almohadillas están principalemente en la parte distal del dedo IV de las patas traseras.

Infografía desarrollada por Nicolás Pelegrin, Laboratorio de Ecología y Conservación de la Herpetofauna, IDEA (CONICET-UNC) para el proyecto de Ciencia Ciudadana "Geckos Forasteros en tu casa: estás seguro?" Diciembre de 2020.

Dedos con almohadillas enteras.
Garras visibles sólo en dos dedos.
Apariencia espinosa (escamas quilladas).

Dedos con almohadillas divididas y garras visibles en todos los dedos.
Escamas más redondeadas.

- En las patas traseras las almohadillas se extienden hasta la base del dedo IV.
  Escamas granulares grandes, bien visibles en el dorso

- En las patas traseras las almohadillas NO se extienden hasta la base del dedo IV.
  Escamas granulares pequeñas y poco evidentes

Figure 1. Example of material used in the citizen-science project showing how to identify exotic gecko species. A) Plate comparing common native gecko species with the three exotic geckos; B) Identification key used to identify exotic gecko species.

cus, and 702 *T. mauritanica*, Fig. 2). Two hundred and thirty eight people from 18 of the 24 states (23 provinces plus Ciudad Autónoma de Buenos Aires - CABA, Federal District) of Argentina completed and sent the online form of the project. None of the records reviewed in Ecoregistros (Ecoregistros, 2024) belonged to new localities for any of the species included.

Ninety new localities from 15 states were reported for the three species (Appendix 1, Fig. 3). *Hemidactylus mabouia* was reported for Buenos Aires, CABA, Santa Fe, Tucumán, Salta, Jujuy, Chaco, Formosa, Entre Ríos, Corrientes, Misiones, and Córdoba. New localities for the species were registered in the provinces of Chaco, Córdoba, Corrientes, Formosa, Jujuy, Misiones and Santa Fe (Appendix 1, Fig. 4 and Fig. 5). *Tarentola mauritanica* was reported for Buenos Aires, CABA, Santa Fe, Entre Ríos, Jujuy, Tucumán, Córdoba, La Pampa, San Luis, Rio Negro, Mendoza, Neuquén, and Tierra del Fuego, with new localities registered for Buenos Aires, Córdoba, Entre Ríos, Jujuy, La Pampa, Mendoza, Río Negro, Santa Fe, San Luis and Tierra del Fuego (Appendix 1, Fig. 4 and Fig. 5). *Hemidactylus turcicus* was reported for Buenos Aires, CABA, and Santa Fe, representing the first confirmed records of the species for Argentina (Appendix 1, Fig. 4 and Fig. 5). The oldest verifiable record for the species in Argentina corresponds to a specimen from Rosario dating January, 2002 (specimen MACN37736).

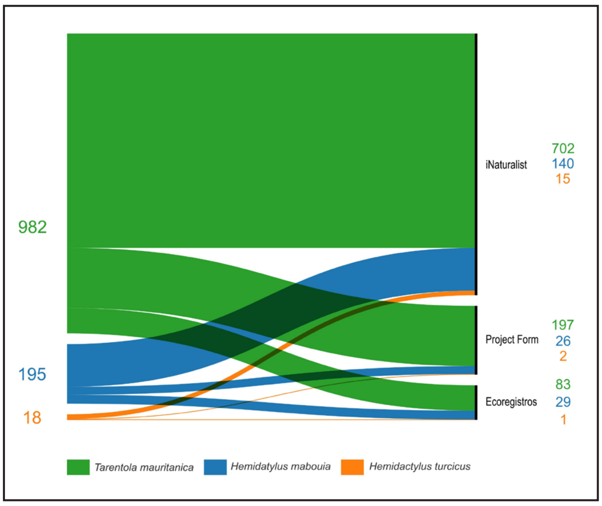


Figure 2. Diagram depicting the importance of each source of information used in this project for each of the studied species. Numbers represent quantity of records. Colors indicate the species identity: green, *T. mauritanica*; blue, *H. mabouia*, orange, *H. turcicus*.

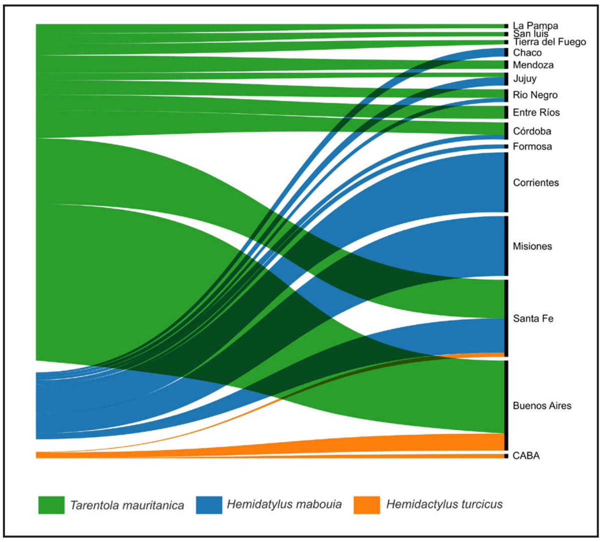


Figure 3. Diagram representing the number of new records for each of the species and for each Argentinean states. The wider the lines, the higher the number of localities where the species was recorded for the specific state. Colors indicate the species identity: green, *T. mauritanica*; blue, *H. mabouia*; orange, *H. turcicus*.

Discussion

This work updates the list and distribution of exotic gecko species in Argentina, confirming the presence of *Hemidactylus turcicus* in the country and revealing that the extent of the invasion by *Tarentola mauritanica* and *H. mabouia* in the country is far larger than previously thought, reporting 90 new localities with presence of at least one exotic gecko species. *T. mauritanica* is present in 13 of the 24 Argentinean districts (23 provinces plus CABA, the Federal District), when previous records only referred to four, being expressively present in numerous localities. *H. mabouia* also had its known distribution extended, from seven to 12 districts and numerous new localities. This study highlights the value of citizen science in projects involving alien species, enabling wider sampling areas and helping to have a more informed and engaged local community on environmental issues.

Until this work, the only published record for *H. turcicus* in South America was that of Williams (1989) which was later revised as being a juvenile *H. mabouia* (Baldo *et al*., 2008) and leaving *H. turcicus* with no records in Argentina and, thus, a dubious presence in South America. Wetering and Vetter (2018) analyzed the worldwide potential distribution of *Hemidactylus* species, using records retrieved from GBIF. These records included four Brazilian specimens from 1988 and 1989 (deposited in the Museum of Comparative Zoology, Harvard

University), iNaturalist records from Argentina, and some specimens deposited in the Argentinian Museum of Natural History (MACN), collected in Rosario (province of Santa Fe), and CABA. We were not able to confirm the identity of *Hemidactylus* specimens collected in Brazil. These records could correspond to misidentified specimens (corresponding to *H. mabouia*) or to isolated individuals and not to established populations of *H. turcicus*, since no other individuals of this species were recorded since then in the whole country. The individuals from Argentina deposited in the MACN were confirmed as *H. turcicus* by the authors, and were collected in 2002 and 2011 in the city of Rosario (MACN 37736, 37820, 37821, 41952, 41953) and 2002 in CABA (MACN 38213). Here we confirm the presence of *H. turcicus* in Argentina, and extending its presence to the cities of Ituzaingó, Lanús, Quilmes, and San Pedro in the Province of Buenos Aires and Santa Fe in the province of Santa Fe, representing the only known records for the species in South America and the southernmost records for the species in the world. The northernmost known established populations of *H. turcicus* corresponds to those found in Nottingham and Hull, UK, at about 53° latitude North (Da Silva *et al*., 2024), showing the extreme adaptability of the species.

The distribution of invasive gecko species in Argentina shows a segregated pattern between *H. mabouia* and *T. mauritanica*, where *H. mabouia* is concentrated mainly in north-east Argentina, with few records in centre and north of the country. According to Vanzolini (1978), the southern limit of the distribution of *H. mabouia* in South America was Porto Alegre (30° latitude South) with a dubious record for Montevideo, Uruguay (~35° latitude South). The first confirmed record for Buenos Aires (~34.5° latitude South; Williams, 1989) dates about ten years after Vanzolini's work. Thirty-five years later, there are no records of established populations for the species south of latitude 35° S. The distribution of *H. mabouia* in continental South America seems to fit the isotherm of 18-20 °C, avoiding mean temperatures below 18 °C (Vanzolini, 1978). The present distribution of the species in Argentina approximates Vanzolini's prediction; the southernmost records for established populations of this species are located between the isotherms of 16-18 °C (CABA) and 18-20 °C (Villa Dolores, Córdoba). The southernmost record for *H. mabouia* in Argentina—at 38.9° latitude South—is also the southernmost record ever reported for the species and refers to an individual found in transit in a cargo truck. Notably, the southernmost published record for *H. mabouia* in its native continent is in South Africa at about 33° South (Agarwal *et al*., 2021); the southernmost African record in iNaturalist is in Bredascorp, at 34.5° latitude South (iNaturalist, 2024a). It is worth mentioning that northernmost records (Ontario, CA and London, UK) for the species are most likely occasional findings associated with plant trade and other commercial activities (iNaturalist, 2024b).

Records for *T. mauritanica* are concentrated in a belt across the central portion of Argentina, mainly in the eastern part, but with extreme records both in northern (Jujuy, this work) and southern (Tierra del Fuego, this work) Argentina. The individual of *T. mauritanica* found in Rio Grande (Tierra del Fuego) is, until now, the southernmost record for the species ever reported. It refers to an individual found in a car traveling from Buenos Aires, and it does not represent an established population. However, it highlights its high capacity of dispersion using human transportation. The species' distribution probability is linked to regions with low to moderate precipitation, moderate to high temperatures, low temperature seasonality, and low to moderate mean diurnal range (Rato *et al*., 2024), and according to future projections, habitat suitability in Argentina was predicted to decrease (Rato *et al*., 2024). However, the progression of records for *T. mauritanica* in the country between late 1970's and the present seem to indicate a rapid dispersion, especially in central Argentina. *T. mauritanica* is a species with high functional diversity and generalist biology (Pelegrin *et al*., 2021), which may allow the adaptation to the variety of climates existing in Argentina. Probably, training the SD models with the records available in this work would end in different predictions for the occupation of the species in the future.

Records for *H. turcicus* in Argentina are scarce and distributed in a very reduced area. The oldest evidence of presence dates from 2002, so it is likely a result of a recent arrival and colonization by the species. *H. turcicus* shows a higher tolerance to cold climates than *H. mabouia*, so, if its populations succeed and disperse, it may segregate spatially from *H. mabouia* (Weterings and Vetter, 2018). The segregated distribution of *H. mabouia* and *T. mauritanica* may indicate different thermal affinities, as both are associated with anthropic environments. However, *T. mauritanica* is not present in Brasil (but it is

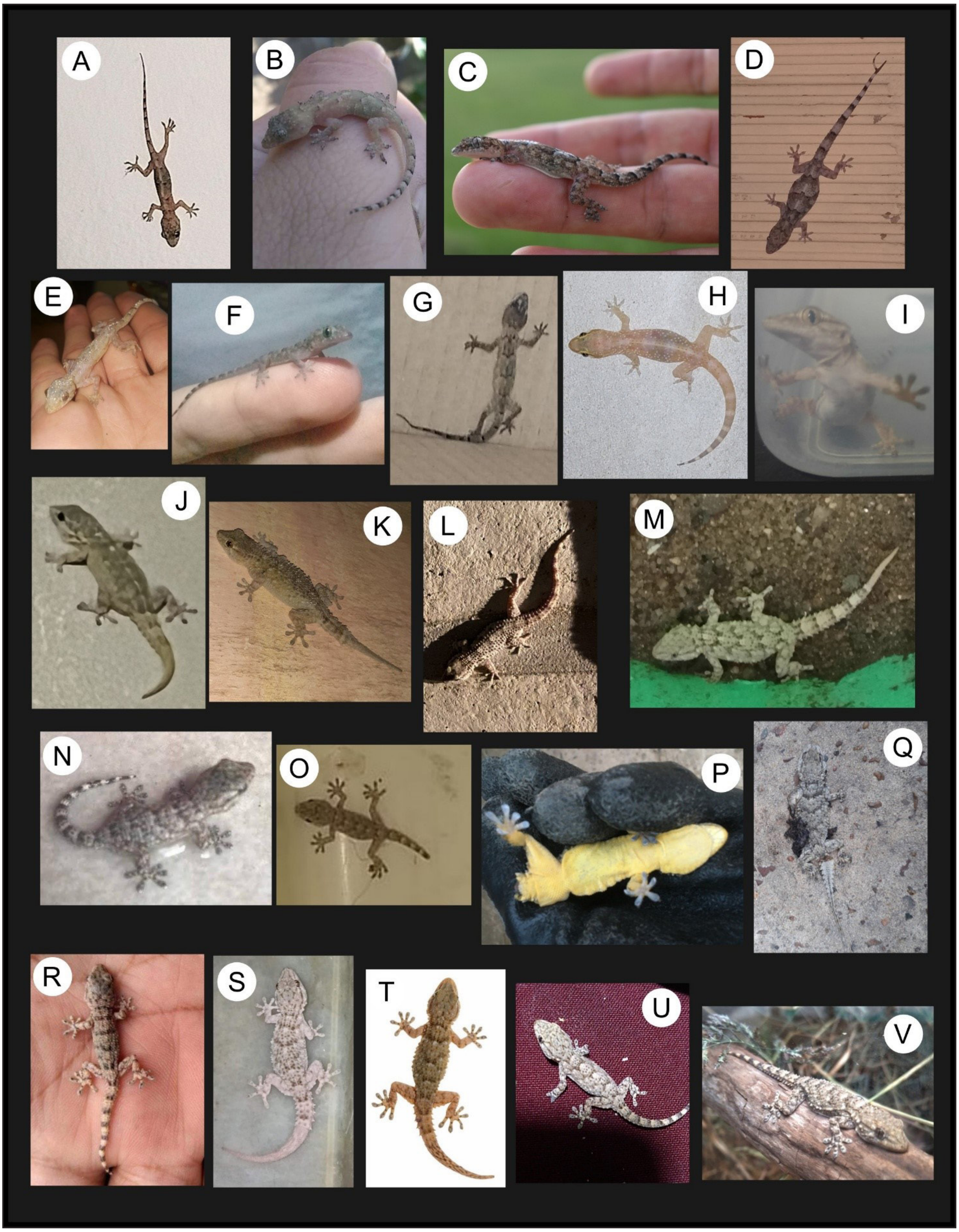


Figure 4. Voucher specimens retrieved from Geckos Forasteros online form, according to the localities listed in Appendix 1. *Hemidactylus mabouia*: Province of Corrientes: A) Mercedes, B) San Cosme, C) Santa Ana, D) Santo Tomé. Province of Jujuy: E) San Salvador de Jujuy. Misiones: F) Puerto Esperanza. Province of Río Negro: G) Cipolletti. *Hemidactylus turcicus*: Province of Buenos Aires: H) Ituzaingó. *Tarentola mauritanica*: Province of Buenos Aires: I) Pilar, J) San Clemente del Tuyú, K) Santa Lucía, L) Tandil. Province of Córdoba: M) Córdoba, N) Villa Las Rosas, O) Villa María. Province of Entre Ríos: P) Colón, Q) Concepción del Uruguay. Province of Jujuy: R) San Salvador de Jujuy; Province of La Pampa: S) Santa Rosa. Province of Río Negro: T) Cipolletti. Province of San Luis: U) Naschel. Province of Tierra del Fuego: V) Río Grande.

present in Uruguay, east from Buenos Aires, in the same latitudinal belt (Achaval and Gudynas, 1983), and *H. mabouia* is not present in Argentina south to latitude 39°.

The study of invasive gecko species received little attention in Argentina, probably because of the strong association of these species with urban environments (Weterings and Vetter, 2018) and scarcity of clear evidence about negative impacts of these invasive geckos on the native fauna (Williams *et al*., 2016; Winck *et al*., 2017; Borroto-Páez and Pérez, 2019). The CABA is invaded by *T. mauritanica*, *H. mabouia* and *H. turcicus*. However, since no native gecko species are present in the city (nor in the province of Buenos Aires; Abdala *et al*., 2012), and the lizard fauna in CABA urban environments is probably reduced to the Gymnophthalmid *Cercosaura schreibersii* (Abdala *et al*., 2012; Williams and Kacoliris, 2012), potential negative effects on native lizard fauna were never a concern. By updating the distribution and list of exotic geckos, here we set a warning about the possible interactions between these exotic species and native lizards and amphibians, encouraging the study of the biology of these invaders in the different environmental conditions where they are present. The results of this project, along with future new records (hopefully with an improved accuracy in the identification) could im-

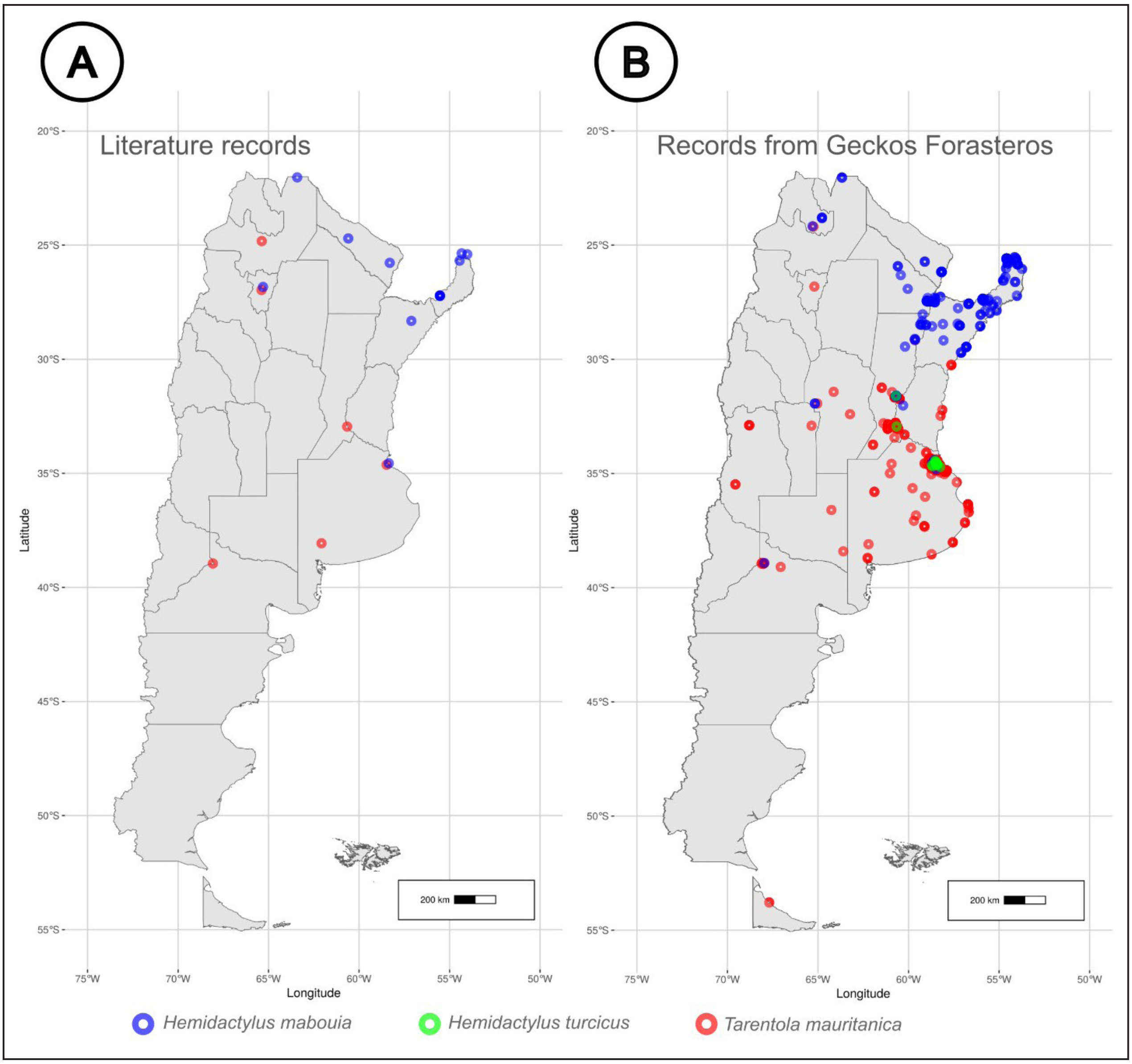


Figure 5. Maps showing the distribution of exotic gecko species in Argentina using A) literature records, and B) records obtained in the project Geckos Forasteros. Blue circles: *H. mabouia*; green circles: *H. turcicus*; red circles: *T. mauritanica*.

prove forecasts of species presence and population tendency. By applying species distribution models to assess the distribution of exotic gecko species for present and future conditions, researchers could be able to address hypotheses regarding interactions with native species in future scenarios of climate change.

The project Geckos Forasteros played an important role, offering information not just about the biology of the gecko species studied, but also about native species, bringing awareness about the problem with alien and invasive species in Argentina. The use of citizen science is a useful tool to sample large areas in a fast way and conduct studies in urban areas (Spear *et al*., 2017). Citizen science stands out as a valuable tool for studying new records, monitoring, distribution, and control measures of invasive species (Encarnação *et al*., 2021). The use of this tool in research projects focused on amphibians and reptiles is rare (Price-Jones *et al*., 2022); however, there are examples of successful application, such as the citizen-science project Reptiles and Amphibians of Southern California (RASCals; see Spear *et al*., 2017). This work notably highlights this tool for urban ecology studies, achieving a much higher number of records compared to those from museum records (Spear *et al*., 2017). Finally, research projects that include or are based on citizen science become highly important as they actively involve local citizens, making them more aware of local ecological aspects and transforming them into part of the solution to environmental issues. We hope that this work serves to encourage the incorporation of citizen science in other research projects and that it remains as a monitoring tool for the distribution of exotic gecko species in Argentina.

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Appendix I

List of new localities were specimens of *Tarentola mauritanica*, *Hemidactylus mabouia* and *H. turcicus* were recorded. Latitude and longitude are expressed in decimal degrees. Voucher specimens are indicated for each locality. GBIF: Gbif record number, iNaturalist: iNaturalist observation number. LECOH: herpetological collection of the Laboratory of Ecology and Conservation of Herpetofauna, Instituto de Diversidad y Ecologia Animal, CONICET. MACN: Museo Argentino de Ciencias Naturales (Argentina). The authors of pictures used as voucher (see Fig. 1) are also included.

Province	Locality	Latitude	Longitude	Voucher
Hemidactylus mabouia				
Chaco	Colonia Benitez	-27.329°	-58.953°	GBIF: 4440790714
Chaco	Juan José Castelli	-25.938°	-60.601°	GBIF: 4846801728
Córdoba	Villa Dolores	-31.949°	-65.188°	LECOH00741
Corrientes	Bella Vista	-28.506°	-59.038°	GBIF: 4440852589
Corrientes	Gobernador Virasoro	-28.054°	-56.014°	iNaturalist: 202888997
Corrientes	Itaí	-27.273°	-58.243°	iNaturalist: 152401125
Corrientes	Ituzaingó	-27.584°	-56.686°	GBIF: 4440614229
Corrientes	Loreto	-27.774°	-57.275°	iNaturalist: 75665970
Corrientes	Mercedes	-29.184°	-58.075°	Fig. 1A – Yamila Parola
Corrientes	Paso de la Patria	-27.314°	-58.562°	GBIF: 4440595389
Corrientes	Paso de los Libres	-29.707°	-57.116°	GBIF: 4519122509
Corrientes	San Cosme	-27.371°	-58.511°	Fig. 1B – Valeria Arraigada
Corrientes	San Luis del Palmar	-27.512°	-58.560°	iNaturalist: 143794320

Corrientes	San Roque	-28.571°	-58.706°	iNaturalist: 77113150
Corrientes	Santa ana	-27.458°	-58.656°	Fig. 1C – Oscar Galli Merino
Corrientes	Santo Tomé	-28.552°	-56.0452°	Fig. 1D – Micaela Romero
Corrientes	Yapeyú	-29.464°	-56.816°	GBIF: 4596892880
Formosa	Pirané	-27.737°	-59.112°	iNaturalist: 37857018
Jujuy	Libertador San Martín	-23.817°	-64.799°	GBIF: 4867732604
Jujuy	San Salvador de Jujuy	-24.186°	-65.319°	Fig. 1E – Lucas Jure
Misiones	Candelaria	-27.447°	-55.585°	GBIF: 4522460132
Misiones	Comandante Andresito	-25.673°	-54.042°	GBIF: 4014866384
Misiones	Concepción de la Sierra	-27.981°	-55.515°	GBIF: 4518973256
Misiones	El Dorado	-26.407°	-54.637°	iNaturalist: 108820055
Misiones	General Manuel Belgrano	-25.534°	-54.134°	GBIF: 4133894347
Misiones	Gobernador Roca	-27.198°	-55.469°	GBIF: 4528381344
Misiones	Guaraní	-27.226°	-54.017°	GBIF: 4440898204
Misiones	Iguazú	-25.828°	-54.537°	iNaturalist: 125906494
Misiones	Leandro N. Além	-27.615°	-55328°	GBIF: 3912259496
Misiones	Montecarlo	-26.559°	-54.776°	iNaturalist: 77128085
Misiones	Oberá	-27.462°	-55.122°	iNaturalist: 122697934
Misiones	Puerto Esperanza	-26.026°	-54.614°	Fig. 1F – Macarena Fernandez
Misiones	San Antonio	-26.057°	-53.735°	GBIF: 3032103916
Misiones	San Pedro	-26.621°	-54.110°	iNaturalist: 180019273
Rio Negro	Cipolletti	-38.933	-67.989°	Fig. 1G – Ignacio Hernández
Santa Fe	Avellaneda	-29.117°	-59.659°	iNaturalist: 74263007
Santa Fe	Florencia	-28.045°	-59.226°	GBIF: 4512191423
Santa Fe	General Obligado	-28.506°	-59.263°	GBIF: 4606745214
Santa Fe	Las Toscas	-28.350°	-59.261°	iNaturalist: 193197211
Santa Fe	Reconquista	-29.169°	-59.651°	iNaturalist: 195128612
Santa Fe	Santa Fe	-31.601°	-60.698°	GBIF: 3881755856
Santa Fe	Vera	-29.457°	-60.203°	GBIF: 4519123196
Santa Fe	Villa Ocampo	-28.484°	-59.354°	GBIF: 4096416791
Hemidactylus turcicus				
Buenos Aires	Ituzaingó	-34.648°	-58.706°	Fig. 1H – Pablo Miranda
Buenos Aires	Lanús	-34.708°	-58.394°	iNaturalist: 217385599
Buenos Aires	Quilmes	-34.721°	-58.255°	GBIF: 4528230293
Buenos Aires	San Pedro	-33.674°	-59.666°	iNaturalist: 101228791
Ciudad Autónoma de Buenos Aires (CABA)	-34.608°	-58.430°	MACN 38213	
Santa Fe	Rosario	-32.950°	-60.682°	MACN 37736, 37820, 37821, 41952, 41953
Tarentola mauritanica				
Buenos Aires	Bahía Blanca	-38.704°	-62.272°	iNaturalist: 202226121
Buenos Aires	Cañuelas	-35.039°	-58.746°	iNaturalist: 192066164
Buenos Aires	Cariló	-37.159°	-56.889°	iNaturalist: 141729805
Buenos Aires	Junín	-34.588°	-60.949°	GBIF: 3858196841
Buenos Aires	La Plata	-34.934°	-57.956°	GBIF: 4606646261

Buenos Aires	Los Toldos	-35.001°	-61.035°	GBIF: 4522726666
Buenos Aires	Luján	-34.563°	-59.121°	iNaturalist: 195419295
Buenos Aires	Mar de Ajó	-36.695°	-56.679°	GBIF: 4430998770
Buenos Aires	Mar del Plata	-38.018°	-57.561°	iNaturalist: 116420398
Buenos Aires	Necochea	-38.542°	-58.735°	iNaturalist: 152400088
Buenos Aires	Pehuajó	-35.811°	-61.898°	iNaturalist: 204791302
Buenos Aires	Pilar	-34.444°	-58.807°	Fig. 1I – Daniel Aguirre
Buenos Aires	Saladillo	-35.652°	-59.788°	GBIF: 4034750030
Buenos Aires	San Clemente del Tuyú	-36.365°	-56.718°	Fig. 1J – Andrea Cabrera
Buenos Aires	Santa Lucía	-33.878°	-59.876°	Fig. 1K – Tomás Bione
Buenos Aires	Tandil	-37.314°	-59.135°	Fig. 1L – Sofía Zurzolo
Buenos Aires	Zárate	-34.094°	-59.022°	GBIF: 4528344537
Córdoba	Córdoba	-31.434°	-64.149°	Fig. 1M – Mariano Romero
Córdoba	Villa Las Rosas	-31.949°	-65.054°	Fig. 1N – Liz Rodríguez
Córdoba	Villa María	-32.414°	-63.243°	Fig. 1O – Jimena Pereyra
Entre Ríos	Colón	-32.224°	-58.144°	Fig. 1P – Claudio Trebaux
Entre Ríos	Concepción del Uruguay	-32.482°	-58.239°	Fig. 1Q – Facundo Cabrera
Entre Ríos	Paraná	-31.710°	-60.563°	GBIF: 4006705068
Jujuy	San Salvador de Jujuy	-24.205°	-65.271°	Fig. 1R – Mariano Benitez
La Pampa	Santa Rosa	-36.607°	-64.274°	Fig. 1S – Lautaro Fernández Artico
Mendoza	Guaymallén	-32.894°	-68.826°	GBIF: 2851323552
Mendoza	Malargue	-35.487°	-69.584°	GBIF: 4111594404
Rio Negro	Cipolletti	-38.933	-67.989°	Fig. 1T – Ignacio Hernández
Rio Negro	Villa Regina	-39.101°	-67.079°	iNaturalist: 193710657
Santa Fe	Carcarañá	-32.855°	-61.155°	GBIF: 2641625312
Santa Fe	Casilda	-33.036°	-61.159°	iNaturalist: 40858266
Santa Fe	Fray Luis Beltrán	-32.791°	-60.729°	GBIF: 3947576114
Santa Fe	Granadero Baigorria	-32.839°	-60.701°	GBIF: 3070626672
Santa Fe	Rafaela	-31.254°	-61.487°	iNaturalist: 45157622
Santa Fe	Rosario	-32.949°	-60.665°	GBIF: 2603417694
Santa Fe	Santa Teresa	-33.441°	-60.789°	iNaturalist: 186855758
Santa Fe	Santa Teresa	-33.441°	-60.789°	iNaturalist: 186855758
Santa Fe	Santo Tomé	-31.671°	-60.767°	GBIF: 4177065048
Santa Fe	Venado Tuerto	-33.749°	-61.975°	GBIF: 4067321101
San luis	Naschel	-32.916°	-65.373°	Fig. 1U – Luis Ginés
Tierra del Fuego	Rio Grande	-53.787°	-67.709°	Fig. 1V – Manuela Gómez

Trabajo

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Habitat loss and climate-induced distributional shifts on the Andean Red-spotted glassfrog (*Nymphargus grandisonae*)

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ABSTRACT

Climate change and habitat loss are two interrelated dimensions of the current global biodiversity crisis. The Red-spotted glassfrog (*Nymphargus grandisonae*) inhabits the northern Andes in Colombia and Ecuador. This study analyses time series of habitat loss within the species' current range, using remote sensing data collected between 1985 and 2022. We also report a new occurrence record in the western foothills of Ecuador. Furthermore, we evaluate potential changes to the climatic suitability of its habitat under a climate change scenario (SSP3-7.0) for the period 2061–2080, using an ecological niche modelling approach. Our results suggest that the species' range could, on average, contract by 45% and shift upwards in elevation by approximately 270 meters. Furthermore, the distribution patterns of the species in the Andean foothills show a high degree of fragmentation. Climate niche analysis shows that the species is highly dependent on humidity and sensitive to temperature fluctuations. In general, models project a decrease in precipitation in the future. Between 1985 and 2022, nearly 32,600 hectares of vegetation cover were lost within the species' range, with the highest rates of loss recorded in Ecuador. These findings highlight the urgent need for conservation strategies that integrate climate change adaptation and habitat protection to reduce the risk of potential extinction.

Key words: Climate change, Biodiversity, Tropical Andes, Amphibians, Habitat loss.

RESUMEN

El cambio climático y la pérdida de hábitat son dos dimensiones estrechamente relacionadas de la actual crisis global de biodiversidad. La rana de cristal de manchas rojas (*Nymphargus grandisonae*) habita en los Andes del norte en Colombia y Ecuador. Este estudio analiza series temporales de pérdida de hábitat dentro del rango actual de la especie, utilizando datos de percepción remota recolectados entre 1985 y 2022. También reportamos un nuevo registro de presencia en las estribaciones occidentales de Ecuador. Además, evaluamos los posibles cambios en la idoneidad climática de su hábitat bajo un escenario de cambio climático (SSP3-7.0) para el periodo 2061–2080, utilizando un enfoque de modelado de nicho ecológico. Nuestros resultados sugieren que el rango de la especie podría, en promedio, contraerse en un 45% y desplazarse hacia arriba en altitud aproximadamente 270 metros. Asimismo, los patrones de distribución de la especie en las estribaciones andinas muestran un alto grado de fragmentación. El análisis del nicho climático indica que la especie depende en gran medida de la humedad y es sensible a las fluctuaciones de temperatura. En general, los modelos proyectan una disminución en la

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precipitación en el futuro. Entre 1985 y 2022, se perdieron cerca de 32,600 hectáreas de cobertura vegetal dentro del rango de la especie, registrándo las tasas más altas de pérdida en Ecuador. Estos hallazgos resaltan la necesidad urgente de estrategias de conservación que integren la adaptación al cambio climático y la protección del hábitat para reducir el riesgo de una posible extinción.

Palabras claves: Cambio climático, Biodiversidad, Andes Tropicales, Anfibios, Pérdida de hábitat.

Introduction

Climate change and biodiversity loss are interlinked issues that humanity faces as part of a planetary crisis (Passarelli *et al.*, 2021). Biodiversity is threatened by habitat loss, fragmentation, overexploitation, invasive species, and climate change (Brook *et al.*, 2008; Bellard *et al.*, 2022). Anthropogenic climate change is already considered one of the most significant threats to biodiversity in the coming decades (Ripple *et al.*, 2025). The acceleration in warming rates has left notable consequences on the marine and terrestrial ecosystems (Burrows *et al.*, 2011). The impacts of climate change on biodiversity have been observed from gene to ecosystem levels (Scheffers *et al.*, 2016), with many species experiencing widespread population collapses (Roman-Palacios & Wiens 2020; Wiens 2016) and extensive distributional shifts (Lenoir *et al.*, 2020; Antão *et al.*, 2020).

Habitat loss and climate change often worsen biodiversity loss by increasing the susceptibility of populations to extinction (Jetz *et al.*, 2007; Mantyka-Pringle *et al.*, 2012). These combined human stressors are exacerbated in taxa with small population sizes and poor dispersal abilities, such as amphibians and reptiles (Newbold 2018). Amphibians are among the most threatened vertebrate groups, with habitat loss and climate change being the most critical extinction drivers (Luedtke *et al.*, 2023). However, it is unknown for many species how these threats act synergistically and can drive population declines across their geographical distribution. Even for many species, there is still a gap in distribution information, the so-called 'Wallacean shortfall', and new geographical records are continually emerging in the literature, mainly for Neotropical species.

In recent years, the Andes of Ecuador and Colombia have seen important rediscoveries of amphibian species, some of which had not been reported for a long time or were considered extinct. Moreover, range extensions have been documented. In the last year alone, several studies have reported these findings (Aponte-Gutiérrez *et al.*, 2024; Copete Mosquera *et al.*, 2024; Sánchez-Nivicela *et al.*, 2024; Vega-Yánez *et al.*, 2024). However, the rediscovery of these species is particularly challenging, given the rapid destruction of their habitats due to anthropogenic activities (Luedtke *et al.*, 2023). For instance, in Ecuador, where between 1990 and 2018, approximately 21,263 km² of forest area was lost, primarily due to its conversion into agricultural land (Rivas *et al.*, 2024). A similar phenomenon was observed in Colombia, where approximately 15,181 km² of tropical forest was lost between 2013 and 2018. The Amazon region was the most affected, followed by the Andean region, and this deforestation trend is projected to continue in the future (González-González *et al.*, 2021). When these effects are combined with the impacts of climate change, it is estimated that between 63.4% and 79.4% of suitable habitat for endemic anurans in the Colombian Andes could be lost (Agudelo-Hz *et al.*, 2019).

Among the group of anurans, the family Centrolenidae (Taylor, 1951) comprises a group of neotropical frogs characterized by their translucent ventral skin, which allows the observation of internal structures, an uncommon feature among amphibians (Guayasamin *et al.*, 2009). These frogs, commonly known as glassfrogs, are found exclusively in Central and South America, particularly in humid and mountainous ecosystems associated with water bodies (Castroviejo-Fisher *et al.*, 2014; Guayasamin *et al.*, 2009). Their evolutionary history shows that they diverged about 30 million years ago and have a diversity peak at intermediate altitudes in the Andes (Hutter *et al.*, 2013a; Castroviejo-Fisher *et al.*, 2014). Similarly, a relationship between rates of climatic niche evolution and altitudinal change has been identified, suggesting that many species maintain their environmental preferences over time (Hutter *et al.*, 2013b).

The Northern Andes house about half of the diversity of glassfrogs, with 83 species documented in this bioregion (Guayasamin *et al.*, 2020). Within this outstanding diversity, one of the most readily recognized species is Red-spotted glassfrog, *Nymphargus grandisonae* (Cochran & Goin, 1970). This taxon is distributed in the Andes of Colombia and Ecuador between 1,140 to 3,200 m (Guayasamin *et al.*, 2020, 2025; Frost, 2025).

The Red-spotted glassfrog is nocturnal, commonly found in primary, secondary forests, grasslands, in vegetation adjacent to streams or marshes (Hutter *et al.*, 2013b; Guayasamin *et al.*, 2020). Although this species is distributed in localities inside and outside private protected areas (Guayasamin *et al.*, 2020), and is tolerable to moderate habitat disturbance, it faces major threats such as deforestation and mining (Roy *et al.*, 2018). We selected this study species for the following reasons: (i) it is easily identifiable, (ii) it has abundant locality records in an area currently facing climate change and deforestation, and (iii) it represents a group of biphasic amphibians that rely on streams with riverine vegetation, thus, the results could be extrapolated to other taxa with similar characteristics.

In this study, we assess the potential impacts of habitat loss and future climate change on the distributional range of *N. grandisonae* in the northern Andes. We conduct a time-series analysis of potential habitat loss within the current distributional range of *N. grandisonae* using remote sensing data from 1985 to 2022. We also assess possible changes in the climatic suitability of *N. grandisonae* under a climate change scenario (SSP3-7.0) for 2061-2080, using an ecological niche modeling approach. These analyses allow us to evaluate potential scenarios for the species, and to guide conservation actions.

Materials and methods

Data collection

Occurrence records of *Nymphargus grandisonae* were compiled from various biodiversity databases, including the Global Biodiversity Information Facility (GBIF), Bioweb-Ecuador (QCAZ), the Base Nacional de Datos de Biodiversidad (BNDB-INABIO), Centro Jambatu, and the Instituto de Ciencias Naturales (ICN) of the Universidad Nacional of Colombia. We also include the new record obtained during field work in the Pululahua Geobotanical Reserve. The specimen was collected by Mateo A. Vega-Yánez and Marco Murminacho (member of the community of Pululahua) on 26 March 2025 at 21h51 in the Pululahua Geobotanical Reserve (0° 3′ 23.65″ N; 78° 30′ 27.21″ W, at 2,120 m. a.s.l.) on a leaf three meters above the ground in a stream next to a rock wall covered with moss and ferns. At the same site, the vocalizations of several males (more than five individuals) were heard more than five meters above the ground. The collection and field research were conducted under the permit MAATE-CMARG-2022-0575, issued by the Ministerio de Ambiente y Energía (MAE) de Ecuador. The specimen of the Pululahua Geobotanical Reserve was deposited at the Centro Jambatu (CJ), Quito, Ecuador. All records were validated, including the verification of geographic coordinates and associated metadata, and then integrated into a standardized database for subsequent analyses, ensuring a minimum distance of approximately 4.6 km between occurrence points.

Species distribution modeling

We downloaded bioclimatic variables from WorldClim v2.1 at a spatial resolution of 2.5 min (Fick & Hijmans, 2017). We selected the variables less autocorrelated using the variance inflation factor (VIF) with the vif function from the R package usdm (Naimi *et al.*, 2014) using a threshold of 0.7. According to this we used the following variables: bio18 = precipitation of the warmest quarter, bio19 = precipitation of the coldest quarter, bio2 = mean diurnal range (mean of monthly (max temp - min temp)), bio4 = temperature seasonality (standard deviation ×100), and bio9 = mean temperature of the driest quarter.

Models were fitted using a calibration area or “M" (Soberon & Peterson, 2005) using a 400 km buffer for each occurrence record of the species (this area encompassed the Andes of Ecuador and Colombia). In addition, the occurrence data were randomly divided into two sets: 70% for calibration and 30% for validation. Using the ecospat package (Broennimann *et al.*, 2014), we generated 1,000 pseudo-absences. We selected three modeling algorithms: support vector machine (SVM), random forest (RF), and boosted regression trees (BRT), and generated 10 replicates per model. Finally, each model was evaluated based on true skill statistics (TSS) and omission rate (Allouche, Tsoar & Kadmon, 2006; Li & Guo, 2013) to build a consensus ensemble model.

Future model projections

For future models, CMIP6 climate projections were used for the period 2061-2080, under the Shared Socio-economic Pathways scenario SSP3-7.0, at the same spatial resolution as the variables for the present models. Four global climate models (GCMs) were randomly selected: EC-Earth3-Veg, IPSL-CM6A-LR, GISS-E2-1-G, and MPI-ESM1-2-HR (Eyring *et al.*, 2016). We generated a series of model transfers for each GCM in a single high-emission climate change scenario (SSP3-7.0) to identify possible changes in distribution patterns throughout the Andean region, where the species is distributed. The previously obtained distribution models were transformed into binary presence/absence models to facilitate the corresponding analyses. A threshold of 0.9 in suitability values at occurrence sites was used to define suitable areas. Based on that, the potential future distribution area of the species was defined, which was subsequently used for the vegetation analysis.

Analysis of climatic variables and the spatio-temporal dynamics of vegetation

We converted the distribution models into binary presence–absence maps to simplify the analysis. Suitable areas were defined using a suitability threshold of 0.9 at the occurrence locations. To explore the similarity patterns between the global climate models (GCMs) as a function of these bioclimatic variables, a non-metric multidimensional scaling analysis was applied using the metaMDS function of the vegan package in R (Oksanen *et al.*, 2022). To ensure the stability of the solution and to avoid local optima, trymax = 1,000 was set, allowing up to 1,000 random optimization trials. Lastly, the surface predicted by the models was calculated, and univariate descriptive statistics were used to analyze the changes. The results were visualised using a series of graphs generated with the ggplot2 package.

The MapBiomas collection (available at https://amazonia.mapbiomas.org/proyecto/), which provides information at a spatial resolution of 30 meters based on supervised classification of satellite imagery, was used to analyze changes in vegetation cover. Land use cover was downloaded for the years 1985, 1990, 1995, 2000, 2005, 2010, 2015, 2020, and 2022. All vegetation covers were transformed to the WGS 1984 UTM Zone 17S (Ecuador) and 18S (Colombia) spatial reference systems to ensure correct overlap and comparison of geographic information. A temporal trend analysis was carried out, estimating the area of vegetation cover for each year, to quantify the loss of vegetation in the potential range of *N. grandisonae* in both space and time. From the values obtained, we estimated the rate of vegetation change and the average annual deforestation for each five-year interval, using the equations proposed by Puyravaud (2003). All analyses were carried out using R software (R Core Team, 2024).

Results

Occurrence and new record

Once the information obtained from biodiversity databases had been validated, 155 occurrence records of *Nymphargus grandisonae* were compiled and used in the distribution models. The new occurrence record (LBE1055) corresponds to a male with a snout-vent length (SVL) of 26.32 mm, which has thirteen distinctive red spots on the body: seven on the dorsum and six on the hind limbs, a diagnostic feature of the species (Fig. 1).

Species distribution model.

All the algorithms evaluated showed high prediction performance in estimating the distribution of *Nymphargus grandisonae*, especially Random Forest, which achieved the best overall score. This algorithm obtained the highest AUC value (0.99), indicating an adequate discriminative ability. In addition, it obtained the highest correlation (0.87), the highest TSS value (0.90), and the lowest Deviance (0.21), reflecting a lower prediction error. In contrast, both Boosted Regression Trees (BRT) and SVM also showed robust performance, with AUC values above 0.95 and TSS values above 0.85, suggesting that all the applied models were effective. The consensus ensemble model for the current distribution indicates that the species is primarily concentrated in the Andean foothills of northern Ecuador and Colombia, between 589 and 3,328 m elevation. A few scattered pixels also appear along the Colombia–Venezuela border, corresponding to marginal areas of the Eastern Cordillera. In Ecuador, the most suitable areas are located in the western foothills of the north, particularly in montane and piedmont forests, which narrow towards the south. Whereas in Colombia, the distribution is wider, with high

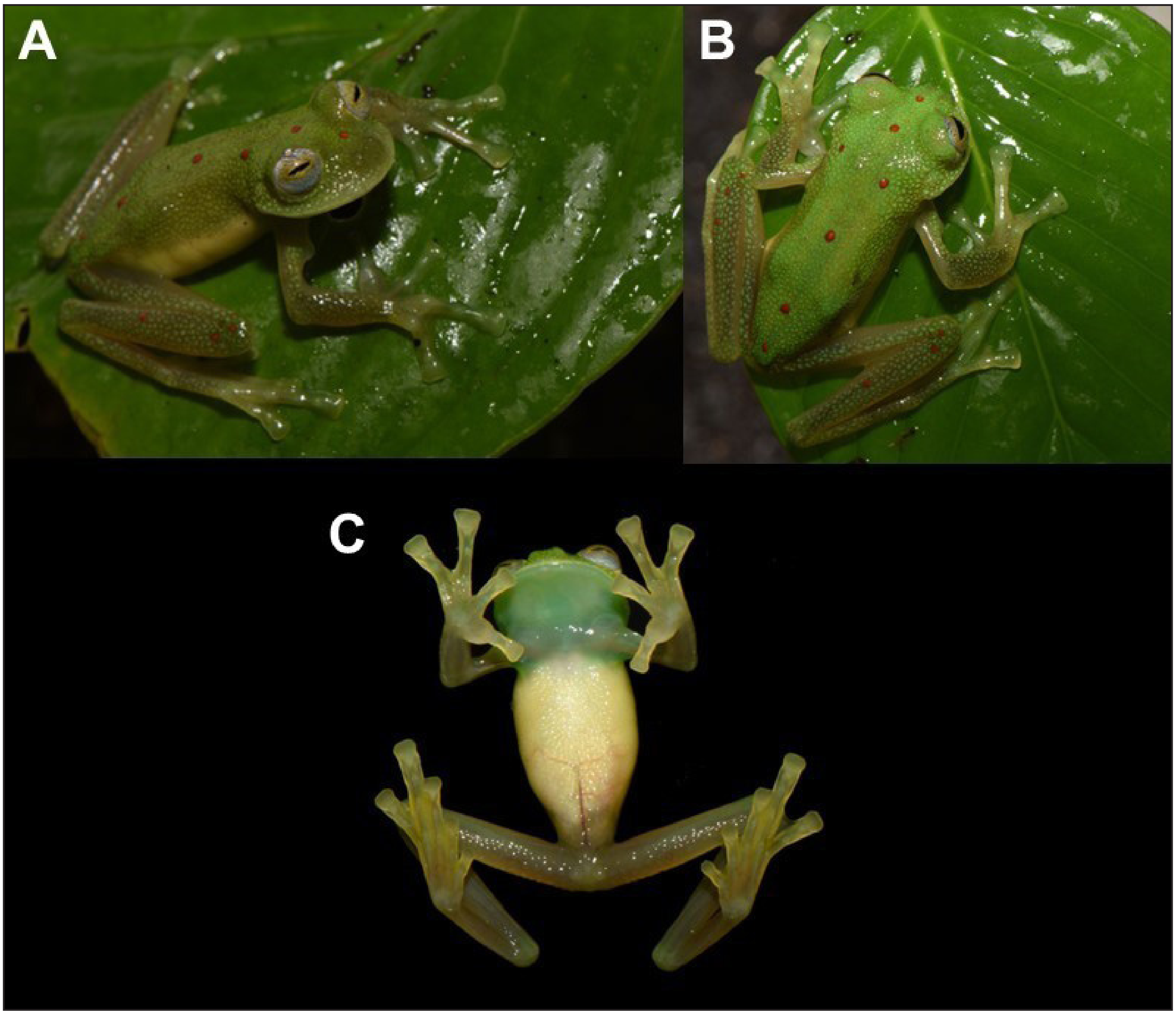

Figure 1. Photographs of the new occurrence record of *Nymphargus grandisonae* in Pululahua Geobotanical Reserve. **A.** lateral view, **B.** dorsal view, and **C.** ventral view. Photographs by: Mateo A. Vega-Yánez

suitability in the Central and Western cordillera, and important areas also in the Eastern cordillera.

Future model projections.

Distribution projections for the period 2061-2080 under the SSP370 scenario, based on four global climate models (EC-Earth3-Veg, GISS-E2-1-G, IPSL-CM6A-LR, and MPI-ESM1-2-HR), show heterogeneous patterns with areas of convergence (Fig. 2). The models project a fragmented distribution of the species in certain areas of the foothills of the Andes in Ecuador and Colombia. In addition, an average elevational shift of 270 m is projected throughout the range, with a higher increase of 312 m in Ecuador.

On the other hand, a significant reduction in the area projected by the different global climate models (GCMs) is observed in Colombia, Ecuador and throughout the full range of *N. grandisonae* (Table 1). The EC-Earth3-Veg model projects the highest total area loss (33,420 km^2), which is concentrated primarily in Colombia, and demonstrates the most significant contraction of the full range (57%). In contrast, the GISS-E2-1-G model projects the highest area gain (16,438 km^2), particularly in Colombia, and shows the lowest contraction in this country (23%). However, in Ecuador, this model estimates a significant loss of 6,667 km^2, the highest among all models for that country, with a contraction of 51%. The IPSL-CM6A-LR model is an intermediate projection, with a total loss of 31,069 km^2 and an overall contraction of 37%. In Colombia, the loss extends

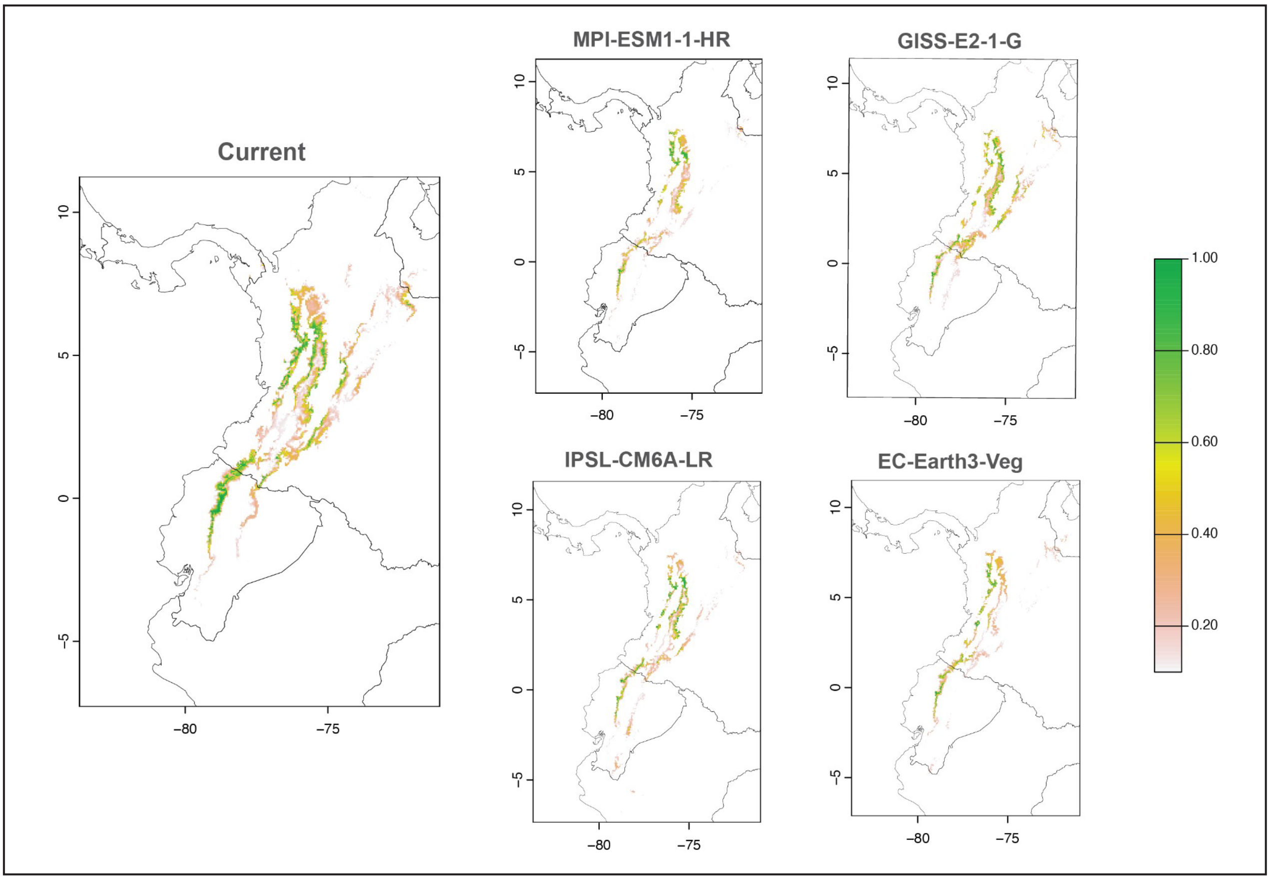

Figure 2. Geographical patterns of suitable habitat for *Nymphargus grandisonae* in the Northern Andes of South America and future models under four global climate models (GCMs) for the SSP3-7.0 scenario for the time-horizon 2061 - 2080.

to 26,583 km^2 (indicating a 50% contraction), while in Ecuador, the projected reduction is 47%. The MPI-ESM-2-HR model also projects a considerable loss (31,169 km^2) and a total range contraction of 52%. Despite Colombia maintaining its status as the most affected country in absolute terms (29,739 km^2 lost), Ecuador demonstrates the most significant percentage contraction (54%) among all models analyzed (Fig. 3).

Analysis of climatic variables.
The results of the Variance Inflation Factor (VIF) analysis indicate that five bioclimatic variables (bio2, bio4, bio9, bio18, and bio19) do not exhibit significant autocorrelation, so they can be considered independent of each other. The correlation coefficients between them vary from a minimum of -0.0418 (between bio9 and bio2) to a maximum of 0.4347 (between bio9 and bio19), indicating a low correlation. These variables help to explain, to a certain extent, the climatic niche of *N. grandisonae*. The species avoids areas of excessive heat and drought, and requires moisture even in winter. Its thermal tolerance varies according to the environment: in hot, dry climates it is adapted to water stress, while in regions with more stable temperatures it depends on permanently humid environments. It is particularly sensitive to variations in rainfall and temperature, with a strong dependence on rainfall in the warm season and humidity in the winter.

Analyzing the changes of these variables in the future (2061-2080) under Shared Socio-economic Pathways SSP3-7.0 as a function of the four global climate models (GCMs), it is observed that they have different climate projections (Fig. 4). However, there is a general trend towards an increase in the variables bio4 and bio9, while the variables bio2, bio18, and bio19 tend to decrease. In particular, the variables bio18 and bio19 (precipitation) show an increase only in the IPSL-CM6A-LR model compared to current conditions (Fig. 4A). The temperature variables, especially bio4, show a decrease in all models, with the GISS-E2-1-G model projecting the highest decrease compared to current conditions. An increase is projected for bio2 and bio9, although the IPSL-CM6A-LR model indicates a decrease for bio9 (Fig.

Table 1. Values of total area, loss, and potential area gain of *N. grandisonae* based on global climate models for Ecuador and its entire range. Negative values show loss of surface

		Full Range (km2)	**Colombia (km2)**	**Ecuador (km2)**
Current	Total area	49,466	40,512	8,953
EC-Earth3-Veg	Projected total area	21,137	16,203	4,934
	Gain Area	5,176	4,407	684
	Loss Area	33,420	29,596	5,363
	Absolute change	28,329	24,309	4,020
	Contraction area %	57	60	45
GISS-E2-1-G	Projected total area	37,366	32,952	4,413
	Gain Area	16,438	15,563	1,133
	Loss Area	28,495	25,441	6,667
	Absolute change	12,100	7,560	4,540
	Contraction area %	32	23	51
IPSL-CM6A-LR	Projected total area	24,815	20,055	4,760
	Gain Area	6,418	5,201	1,217
	Loss Area	31,069	26,583	6,966
	Absolute change	18,397	20,457	4,194
	Contraction area %	37	50	47
MPI-ESM-2-HR	Projected total area	23,923	19,782	4,141
	Gain Area	5,749	5,215	534
	Loss Area	31,169	29,739	7,051
	Absolute change	25,543	20,730	4,813
	Contraction area %	52	51	54

4B). Non-metric multidimensional scaling (NMDS) analysis showed that the Procrustes analysis showed a good fit between the configurations, with a low root mean square error (RMSE) (0.0453) and a moderate maximum residual (0.0819), indicating a high similarity between the compared structures. Moreover, the algorithm sufficiently complied with the convergence criteria and stopped at a sufficiently low stress level. In the reduced space (dimensions MDS1 and MDS2), clear patterns of similarity and difference between the climate models and the current conditions are observed (Fig. 4B). The EC-Earth3-Veg model is the closest to the present, suggesting a high structural similarity according to the variables analysed. In contrast, IPSL-CM6A-LR is the most distant model from the present model, indicating a higher divergence in terms of climate structure. Among the models, GISS-E2-1-G and MPI-ESM1-2-HR show the highest mutual proximity, that they share common features in multivariate space, although both are relatively far from the current. The IPSL-CM6A-LR model is not only far from the present, but also maintains a considerable distance from the other models, which positions it as the most isolated in terms of structural similarity.

Spatio-temporal dynamics of vegetation.

It is estimated that between 1985 and 2022, there was a net loss of approximately 32,600 hectares of vegetation cover within the potential range of *N. grandisonae* in the northern Andes of South America (Fig. 5). In Colombia, the loss is predominantly concentrated in the foothills of the Western, Central and Eastern Cordilleras. In Ecuador, deforestation is most severe along the western slopes of the Andes, including areas in close proximity to the new site where the species has been recorded (Pululahua Geobotanical Reserve). The analysis of rates of change and average deforestation values between 1985 and 2020 shows variations both at the full range level and in national contexts (Colombia and Ecuador) (Fig. 6; Table 2). Within the full range, the dynamics of vegetation cover loss have been marked by fluctuations, with negative deforestation rates observed in the majority of the periods analyzed. The 1995-2000 and 2015-2020 periods registered the highest average deforestation rates, with estimated losses of 13,060 ha/year (2.0%) and 9,800 ha/year (1.5%), respectively. In Colombia, the period 1985-1990 evidenced a net increase in forest cover, with an annual gain of 9,880 ha. However, between 1990 and 1995, there was a sharp decrease, with a nega-

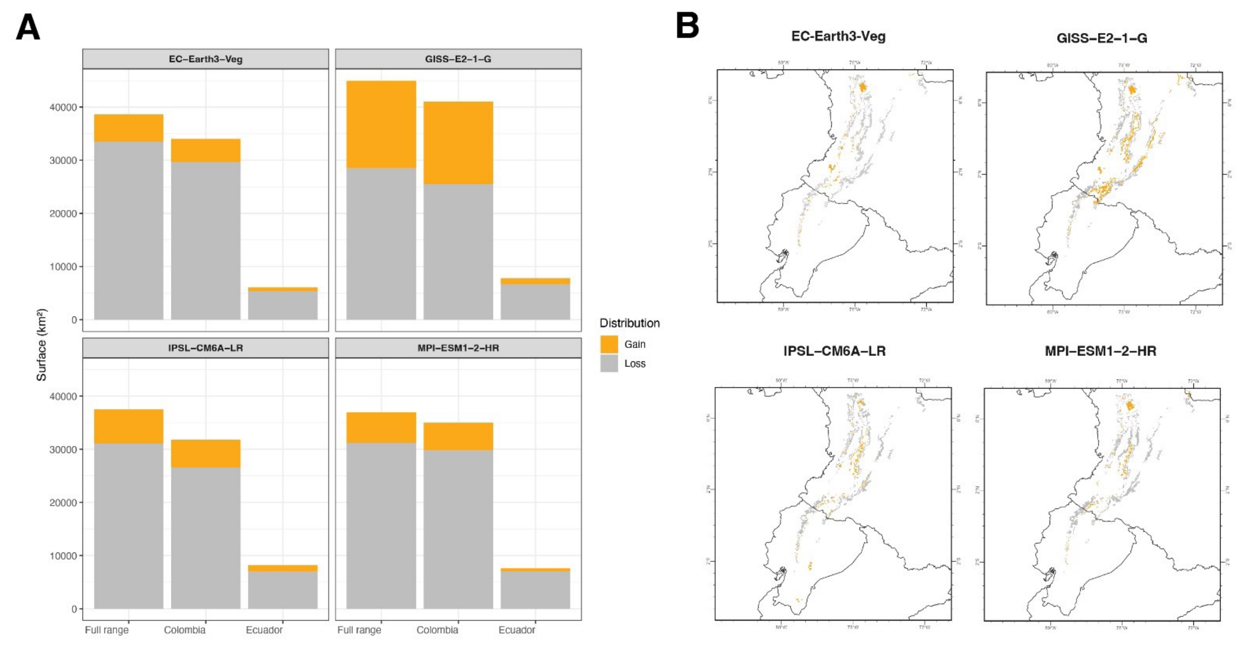

Figure 3. A. Surface area in square kilometers of gain and loss in the distribution of *Nymphargus grandisonae* according to the four global climate models (GCMs), compared to its current distribution. **B.** Maps of gain and loss in distribution according to the different models.

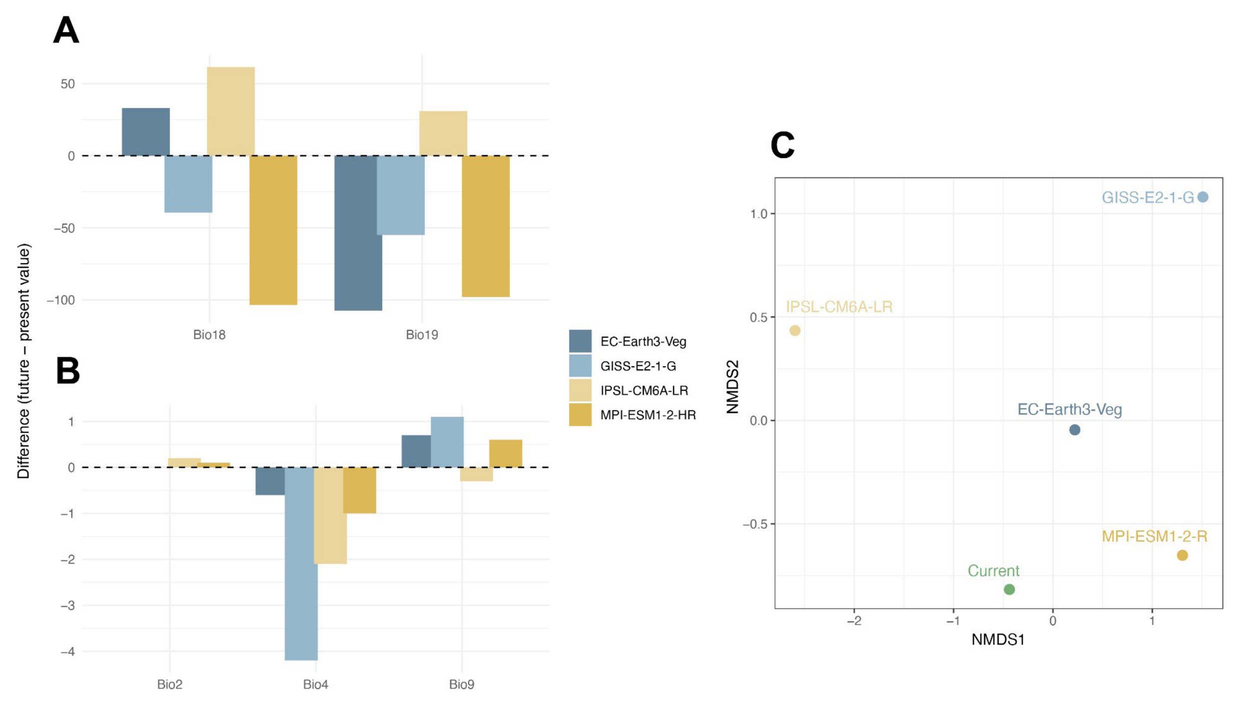

Figure 4. A. Difference between future and present values of precipitation variables (bio18 = Precipitation of Warmest Quarter and bio19 = Precipitation of Coldest Quarter) according to the four global climate models for the distribution of *N. grandisonae* in Ecuador. ***B***. Difference between future and present values of temperature variables (bio2 = Mean Diurnal Range, bio4 = Temperature Seasonality, and bio9 = Mean Temperature of Driest Quarter). **C**. Non-metric multidimensional scaling (NMDS) of temperature and precipitation variables grouped according to the four global climate models (GCMs) and current conditions.

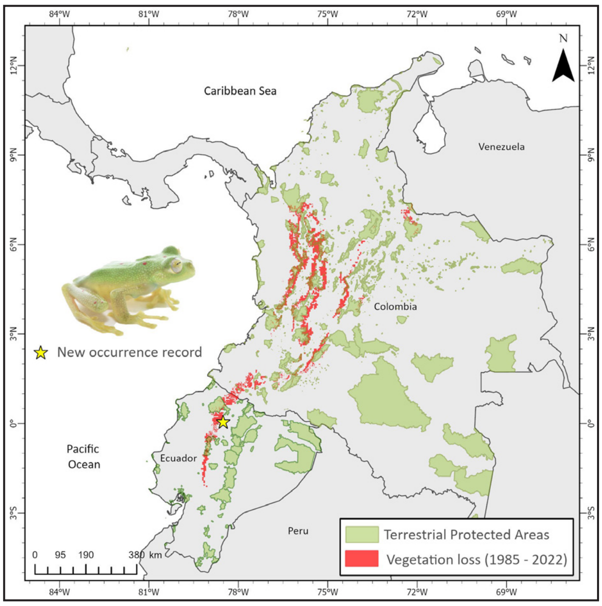

Figure 5. Map of gross vegetation loss in the distribution range of *N. grandisonae* and its new record in the Pululahua Geobotanical Reserve, Ecuador.

tive rate of change (-0.1436), a net loss of 3,720 ha/year and a percentage rate of deforestation of 0.72%. Subsequently, between 1995 and 2000, there was a considerable increase (15,140 ha/year), followed by a slight growth trend until reaching a significant loss again between 2015 and 2020 (8,980 ha/year). While in Ecuador exhibits a more persistent pattern of forest loss over time. The highest recorded rates were observed between 1995-2000 and 2000-2005, with averages of 2,080 ha/year (1.62%) and 1,880 ha/year (1.48%), correspondingly. In contrast to the Colombian case, Ecuador experienced a temporary recovery between 2005 and 2015, with net increases in vegetation cover during two consecutive periods. However, this trend underwent a reversal between 2015 and 2020, during which a loss of 820 ha/year was recorded (Table 2). Currently, across its entire range, the species covers approximately 49,466 km^2, of which 19,515 km^2 are within protected areas, equivalent to only 39.4% of its potential habitat under formal protection. Representation differs significantly between countries. In Ecuador, the species occupies 8,953 km^2, but only 2,833 km^2 are included in protected areas (31.6%). In Colombia, which has the largest proportion of the distribution (40,512 km^2), around 16,681 km^2 are under protection (41.1%).

Table 2. Rate of vegetation change and average deforestation in the potential habitat of the *Nymphargus grandisonae*. Negative (-) values are related to deforestation, while positive (+) values represent gain in forest cover.

Period	**Rate of change**	**Average deforestation ha/year**	**Average deforestation rate (%)**
	Full range		
1985 - 1990	-0.0029	-9,300	1.46
1990 - 1995	0.0010	+3,360	-
1995 - 2000	-0.0040	-13,060	2.0
2000 - 2005	0.0005	+1,620	-
2005 - 2010	-0.001	-3,340	0.5
2010 - 2015	-0.0008	-2,500	0.38
2015 - 2020	-0.003	-9,800	1.50
	Colombia		
1985 - 1990	0.0038	+9,880	-
1990 - 1995	-0.1436	-3,720	0.72
1995 - 2000	0.0058	+15,140	-
2000 - 2005	0.0001	+240	-
2005 - 2010	0.0005	+1,240	-
2010 - 2015	0.0007	+1,900	-
2015 - 2020	-0.0034	-8,980	1.68
	Ecuador		
1985 - 1990	-0.0009	-580	0.45
1990 - 1995	0.0006	+360	-
1995 - 2000	-0.0033	-2,080	1.62

2000 - 2005	-0.0030	-1,880	1.48
2005 - 2010	0.0034	+2,140	-
2010 - 2015	0.0009	+580	-
2015 - 2020	-0.0013	820	0.64

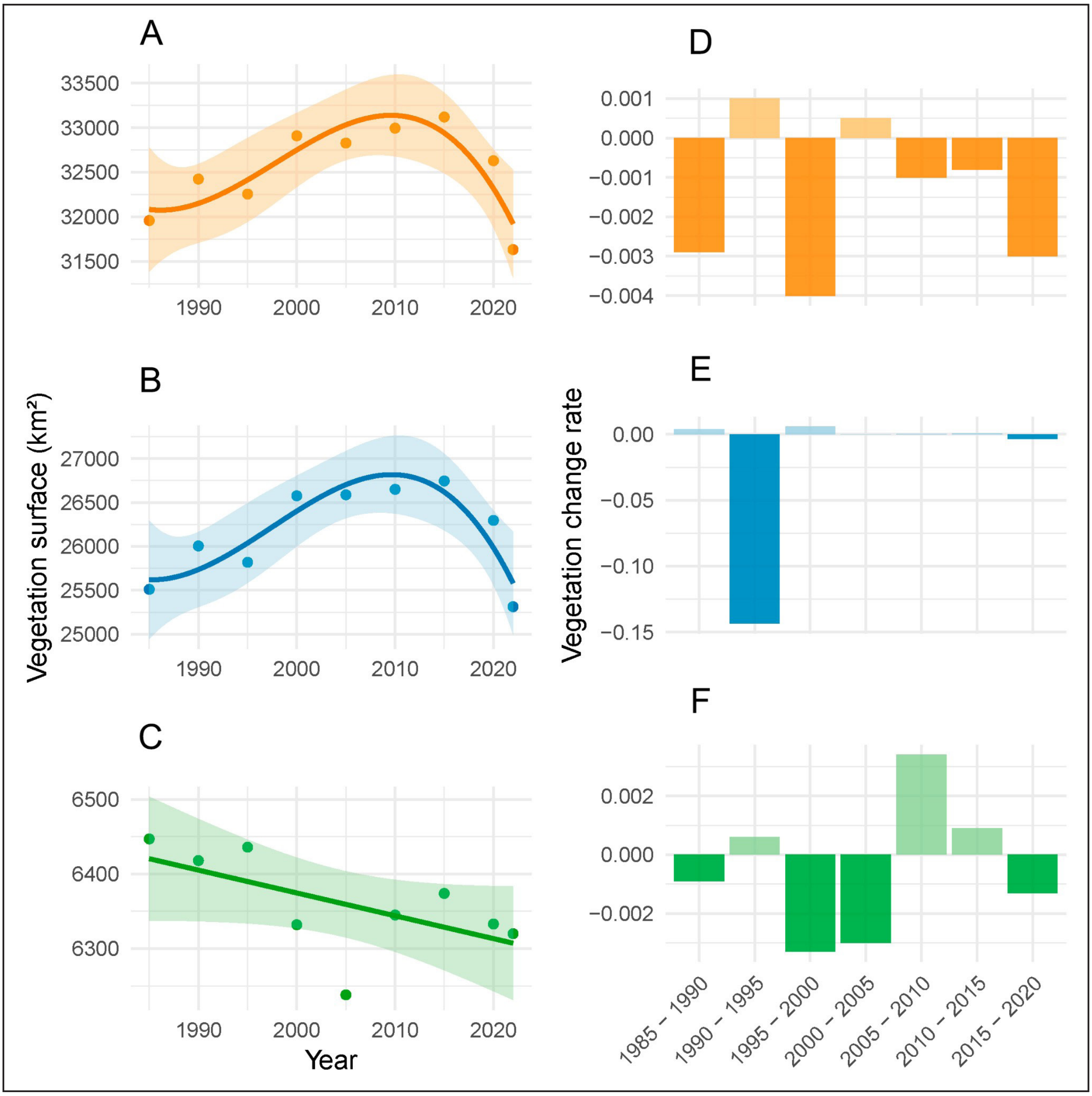

Figure 6. Changes in vegetation cover within the range of *N. grandisonae* between 1985 and 2022. **A**-**C**. Vegetation surface area (km²): **A**. full range, **B**. Colombia, and **C**. Ecuador. **D**-**F**. Rate of change vegetation cover: **D**. full range, **E**. Colombia, and F. Ecuador.

Discussion

Our study underscores the value of integrating ecological, climatic, and spatial evidence to refine the conservation status of *Nymphargus grandisonae*. Beyond documenting a new record for the species, our results show that accelerated habitat loss combined with projected climate change could reduce its suitable range by nearly half by the end of the century. Although currently listed as Least Concern (LC), the species shows marked sensitivity to declining humidity, temperature shifts, and increasing fragmentation. Because climate alone rarely captures the full extent of future pressures on amphibians, incorporating land-use dynamics is essential. Studies integrating climate and land-use scenarios have shown that while climate drives broad distributional trends, land-use trajectories can modulate or even redirect range shifts (Blank & Blaustein, 2012). Likewise, presence-only modeling in threatened amphibians demonstrates that accounting for fine-scale habitat attributes substantially improves the identification of priority conservation areas (Préau *et al.* 2019). Together, these insights highlight the importance of combining multiple modeling approaches and reinforce the urgency of conservation strategies that link habitat protection, land-use planning, and climate-change adaptation for the long-term persistence of *N. grandisonae*.

Regularly updating geographic distribution data remains fundamental for effective biodiversity assessment (Meyer *et al.*, 2015), particularly because species occurrence accuracy directly influences model performance. Likewise, future projections under climate change demand the incorporation of multiple global climate models (GCMs) to better capture the uncertainty surrounding potential species distributions. Although CMIP6 models share core physical foundations, they differ in methodological structure, component interactions, and the representation of processes such as carbon cycling, aerosols, and volcanic activity (Eyring *et al.*, 2016; Kim *et al.*, 2020). These differences can lead to contrasting outcomes, even under comparable emission scenarios. Our analyses indicate that IPSL-CM6A-LR is the only model projecting increases in wet-season (bio18) and dry-season (bio9) precipitation within the climatic niche of *N. grandisonae*, likely reflecting shifts or intensification of regional convergence zones and wind systems (Boucher *et al.*, 2020). Across scenarios, climate models predict an average 45% reduction in suitable range by 2061–2080, effectively erasing nearly half of the species range. Such contraction is expected to amplify fragmentation, elevate the risk of demographic bottlenecks, and erode genetic diversity (Beebee, 2005; Guan *et al.*, 2021). Restricted gene flow among isolated populations would further increase drift and inbreeding, reduce the capacity of the species to respond to environmental change, and raise the risk of local and even global extirpation.

Projections also indicate an upward shift in the species altitudinal distribution, emphasizing the need to safeguard potential refuge areas and limit human activities within them to ensure long term persistence. In Ecuador, *N. grandisonae* occupies a relatively small range and continues to experience vegetation loss, with degradation occurring even inside protected areas. This pattern shows that protected areas remain vulnerable to deforestation, degradation, fragmentation and fire. Between 1990 and 2018, about four percent of national cumulative deforestation took place within the Sistema Nacional de Áreas Protegidas (Kleeman *et al.*, 2022). These trends raise concerns about the effectiveness of protected area management and the broader capacity to conserve vegetation in Ecuador. Given the projected upslope shift of *N. grandisonae*, conservation strategies should prioritize maintaining elevational connectivity by protecting the remaining forest along altitudinal gradients and restoring degraded high elevation habitats. This continuity is essential for enabling populations to track suitable climatic conditions through time (Hannah *et al.*, 2007). In addition, streams and rivers, together with their riparian vegetation, should be recognized as key ecological corridors because they connect breeding sites, facilitate dispersal and provide stable microclimatic refuges for biphasic amphibians. Strengthening enforcement within protected areas is essential to curb illegal logging and limit further fragmentation. Restoring riparian buffers and safeguarding the integrity of headwater streams would improve habitat quality and connectivity while reducing sedimentation and hydrological disruption (Thieme *et al.*, 2023). Establishing ecological corridors between isolated populations would help maintain gene flow and reduce the risk of inbreeding. Implementing long term monitoring programmes that combine field surveys with remote sensing would support adaptive management and allow early detection of habitat change.

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Nota

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Corrigendum to "Nomenclature and taxonomic status of the lizards listed by Philippi (1860) (Squamata: Liolaemidae, Teiidae and Tropiduridae)" to comply with the International Code of Zoological Nomenclature (ICZN)

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ABSTRACT
Troncoso-Palacios and Marambio-Alfaro (2021) published in Cuadernos de Herpetología, Supl. 1, 2021, the proposal of several nomenclatural act, including the establishment of a secondary homonym, and the designation of lectotypes and paralectotypes for several lizard species. However, the LSID (Life Science Identifier) registration in Zoobank was not provided. In order to fulfill the Art. 8.5.3 of the International Code of Zoological Nomenclature, here we provide a corrigendum to validate and make these nomenclatural acts available.

Key Words: Homonym; Lectotype; Paralectotype; *Proctotretus*; *Liolaemus*.

RESUMEN
Troncoso-Palacios y Marambio-Alfaro (2021), publicaron en *Cuadernos de Herpetología*, Supl. 1, 2021, la propuesta de varios actos nomenclaturales, incluyendo el establecimiento de un homónimo secundario y la designación de lectotipos y paralectotipos de diversas especies de lagartos. Sin embargo, no se proporcionó el registro LSID (Life Science Identifier) en ZooBank. Con el fin de cumplir con el Artículo 8.5.3 del Código Internacional de Nomenclatura Zoológica, aquí presentamos una corrigenda para validar y poner a disposición dichos actos nomenclaturales.

Palabras claves: Homónimo; Lectotipo; Paralectotipo; *Proctotretus*; *Liolaemus*.

Nomenclatural acts

Troncoso-Palacios and Marambio-Alfaro (2021) carried out the following nomenclatural acts, which are here made validated through Zoobank registration. Zoobank LSID: urn:lsid:zoobank.org:pub:2B550AB5-A1EA-47D7-88E6-260511107C35.

a) *Proctotretus marmoratus* Philippi, 1860, is declared a secondary homonym. Its type locality is unknown. Philippi´s *P. marmoratus* was regarded as a questionable junior synonym of *Liolaemus nitidus* (Wiegmann, 1834) by Boulenger (1885). Therefore, the combination *Liolaemus marmoratus* (Philippi, 1860) (Troncoso-Palacios and Marambio-Alfaro, 2021) becomes a secondary homonym of *Liolaemus marmoratus* (Gravenhorst, 1838) according to ICZN (1999, Art. 53.3). Since the taxonomic identity of Philippi´s species remains uncertain, the proposal of a replacement name is discouraged.

b) *Proctotretus modestus* Philippi, 1860— lectotype and paralectotype designation. In the origi-

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nal description (Philippi 1860) no type specimens were listed. The type locality was stated as Atacama Desert and the mountains of the Santiago Province, but restricted by Troncoso-Palacios and Marambio-Alfaro (2021) to mountains of the Santiago Province. Müller and Hellmich (1933) reported three specimens housed in the Zoologisches Museum Berlin (currently Museum für Naturkunde Berlin), referring to the largest one as the "type". Troncoso-Palacios and Marambio-Alfaro (2021) designated the largest specimen (ZMB 5350) as the lectotype, and the specimens ZMB 70546–47 as paralectotypes. In the Regarding taxonomy, Troncoso-Palacios and Marambio-Alfaro (2021) agree with Müller and Hellmich (1933) that this species is a junior synonym of *L. bellii* Gray, 1945.

c) *Proctotretus melanopleurus* Philippi, 1860— lectotype and paralectorype designation. In the original description (Philippi 1860) no type specimen was designated. Type locality is unknown. Quijada (1916) assumed that the type locality is Atacama, Chile, and reported three syntypes housed in the Museo de Historia Natural de Chile (MNHNCL). Ortiz and Núñez (1986) indicated that two syntypes are placed in MNHNCL (1549 and 1550), and the third in the Field Museum of Natural History, Chicago (FMNH 9969). Pincheira-Donoso and Núñez (2005, p. 455) provide different catalog number for the syntypes (MNHNCL 1646, two specimens). According to Troncoso-Palacios and Marambio-Alfaro (2021), when JTP examined the syntypes (May 2011 and November 2016), both still shared the catalog number MNHNCL 1646, without distinction between specimens. However, they are easily distinguishable, since one is much larger (snout-vent length= 70.6 mm) than the other (SVL= 46.7 mm). Troncoso-Palacios and Marambio-Alfaro (2021) designed the largest specimen (MNHNCL 1646) as the lectotype, and the smaller specimen (MNHNCL 1646) together with FMNH 9969 as paralectotypes. Morphologic features are detailed in Troncoso-Palacios and Marambio-Alfaro (2021). Regarding the taxonomy, although undoubtedly *P. melanopleurus* belongs to *Liolaemus* (*sensu stricto*), the exact type locality remains unknown, and its morphology does not allow assignment to any know population of *Liolaemus*. It is possible that these specimens represent aberrant individuals or an extinct species, or that their conservation status will make it impossible assigned them to a particular species.

d) *Proctotretus pallidus* Philippi, 1860— lectotype and paralectotype designation. In the original description (Philippi 1860) no type specimens were listed; the type locality is Paposo, Atacama Region, Chile. Tiedemann and Häupl (1980) listed two syntypes of *P. pallidus* housed in the Naturhistorisches Museum Wien, Austria (NMW 18914: 1, 2). Troncoso-Palacios and Marambio-Alfaro (2021) reported on the morphology and diagnostic characters of both specimens, concluding that their belongs to different species. One specimen (NMW 18914: 2) was designated as the lectotype of *P. pallidus*. The other (NMW 18914: 1) was designated as a paralectotype; however, it cannot serve as a name-bearing type of *P. pallidus* following ICZN (Art. 73.2.2), because it belongs to unidentified species of the *Liolaemus platei* group. Regarding taxonomy, Troncoso-Palacios and Marambio-Alfaro (2021) considered *P. pallidus* a junior synonym of *L. nigromaculatus*.

Taxonomic or data changes

Troncoso-Palacios and Marambio-Alfaro (2021) also proposed or commented the following taxonomic and data changes. Although these changes do not require a LSID registration in Zoobank, they are summarized here to facilitate understanding of the current valid names.

a) *Proctotretus bisignatus* Philippi, 1860, is a junior synonym of *P. nigromaculatus* Wiegmann, 1834. Troncoso-Palacios and Marambio-Alfaro (2021) did not performed any new nomenclatural act or taxonomic change regarding this species, but commented on this synonymy, which was already stablished and published earlier by Troncoso-Palacios and Garín (2013). The currently valid combination is *Liolaemus nigromaculatus*.

b) *Microlophus* species clarification. Philippi (1860) reported *Microlophus lessoni* Duméril and Bibron, 1837, for Chile. However, Troncoso-Palacios and Marambio-Alfaro (2021) concluded that these specimens actually belong to *M. marianus* (Donoso-Barros, 1966). Regarding taxonomy, I emphasize that the valid name for the *Microlophus* species inhabiting most of the coastal area of the Atacama Desert is *M. marianus*, as already corrected by Núñez and Jaksic (1992) and Troncoso-Palacios (2018), since it is the first available name with a valid description of this taxon. This follows the Principle of Priority (ICZN, 1999, Art. 23.1). Nevertheless, several publications (e.g. Mella-Ávila, 2020) have used *M. atacamensis* (Donoso-Barros, 1966) as a valid name, which is in fact the second available name for this taxon, following Ortiz (1980) who argued that the epithet "*atacamensis*" better reflect the distribution of the species. This, however, openly contradict the Code.

c) *Helocephalus nigriceps* Philippi, 1860. The currently valid name of this species is *Liolaemus nigriceps*. Troncoso-Palacios and Marambio-Alfaro (2021) corrected the collection date of type specimens to 1855, instead of 1860, which is the year of Philippi´s publication.

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Nota

Cuad. herpetol. 40 (1): 165-168 (*2026)*

Predation of the frog *Physalaemus biligonigerus* (Anura: Leptodactylidae) by a giant water bug (Hemiptera: Belostomatidae) in the Brazilian Pantanal

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ABSTRACT

Amphibians play a fundamental role in aquatic and terrestrial food chains. They are frequently preyed upon by vertebrates and, less commonly, by invertebrates. Among invertebrate predators, aquatic insects of the family Belostomatidae stand out for their predatory efficiency and wide geographic distribution. Here we report a predation event of an adult male *Physalaemus biligonigerus* by an aquatic insect of the genus *Lethocerus*, observed in a temporary pond during an explosive breeding event in the municipality of Aquidauana, Mato Grosso do Sul, Brazil. This kind of records, still poorly documented for anurans in the Pantanal, reinforces the importance of belostomatids as predators influencing the dynamics of anuran populations in temporary aquatic environments.

Key Words: Amphibians; Predator-Prey; Natural History.

Amphibians play a crucial role in both aquatic and terrestrial food webs, acting as predators and prey at multiple trophic levels. Several vertebrate groups, including birds, snakes, mammals, and crocodilians, include amphibians in their diets, particularly adults, which are more visible and accessible (Toledo *et al.*, 2007; González-Maya *et al.*, 2019; Landgref Filho *et al.*, 2019; Hernández-Ruz *et al.*, 2022; Mori *et al.*, 2023). Previous studies have shown that anurans can be preyed upon by a wide variety of invertebrates, including spiders, odonates, and aquatic bugs, which may attack both tadpoles and adults (Toledo, 2005; Nenda *et al.*, 2008; Taffarel *et al.*, 2019; Hernández-Ruz *et al.*, 2022; Howard *et al.*, 2024). Although underreported than predation by vertebrates, attacks by predatory invertebrates can significantly influence amphibian population dynamics, in freshwater environments (especially lentic systems) where these taxa coexist (González-Maya *et al.*, 2019; de Luna *et al.*, 2022).

Among invertebrate predators, aquatic bugs (Belostomatidae) are notable for their efficiency in prey capture and their wide distribution across freshwater habitats (Toledo, 2003; Hernández-Ruz *et al.*, 2022; Mori *et al.*, 2023). These insects use their raptorial forelegs to immobilize prey and a piercing proboscis to inject digestive saliva, enabling a suction-based feeding mechanism (Toledo, 2005;

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Ohba *et al.*, 2008; Maffei *et al.*, 2014). Belostomatids are known to prey upon both tadpoles and adult anurans, with records involving species of the several genera including *Dendropsophus*, *Scinax*, *Leptodactylus*, *Physalaemus*, *Pseudis*, *Atelopus*, and *Boana* (Nenda *et al.*, 2008; González-Maya *et al.*, 2019; Landgref Filho *et al.*, 2019; Taffarel *et al.*, 2019; Hernández-Ruz *et al.*, 2022; Howard *et al.*, 2024; Ceron *et al.*, 2017; Gambale *et al.*, 2014). Records of *Physalaemus* predation by aquatic insects of the family Belostomatidae have been increasing across South America. Nenda et al. (2008) reported *Belostoma* sp. preying upon an adult *P. cuvieri* in Argentina, while Schalk (2010) documented the predation of *P. biligonigerus* by a belostomatid in Bolivia. Subsequently, Taffarel et al. (2019) recorded species of *Lethocerus* preying upon *P. biligonigerus* and *P. cristinae* in Argentina, and Sousa-Félix et al. (2025) reported *Belostoma* sp. preying upon *P. cuvieri* in the Brazilian Cerrado.

Moreover, direct competition for prey between Belostomatids and vertebrates has been documented, with simultaneous predation events involving snakes and birds (Toledo, 2003; de Luna *et al.*, 2022). Despite several studies on the predatory behavior of belostomatids, records involving vertebrate prey remain scarce, especially in natural environments. Reports of attacks on adult anurans are even rarer, highlighting the importance of new records. In this context, we present a predation event involving a belostomatid and an adult individual of *Physalaemus biligonigerus* in the Brazilian Pantanal, contributing novel data on interactions between aquatic insects and anurans.

On January 17, 2025, at approximately 21:44 p.m., we observed an immature giant water bug (*Lethocerus* sp.) preying upon an adult male *Physalaemus biligonigerus* (Fig. 1) in a temporary pond during a breeding explosion event at Fazenda Aguapé, municipality of Aquidauana, Mato Grosso do Sul, Brazil (20°06’46.8”S, 55°58’01.7”W, WGS84, 130 m. a.s.l.).

At the moment of observation, the giant water bug had already captured the anuran. We assumed that the anuran was vocalizing at the time of capture, as its vocal sac appeared flaccid and other individuals of the same species were calling nearby. When we observed the scene, the anuran was still alive and struggling to escape; this active behavior lasted for approximately five minutes. Subsequently, both individuals remained motionless for about three minutes. After this period, we collected both specimens. Throughout the collection and transport process, the water bug did not release its prey at any point. We estimate that the insect held the anuran under control for approximately one hour. It is important to emphasize that at no time was any attempt made to forcibly remove the anuran.

The *P. biligonigerus* individual measured 31.7 mm in total length (Snout-vent length), and the water bug measured 44.1 mm in total length. Both specimens were collected under the appropriate authorization (SISBIO: 89284-2) and are deposited in the zoological collection of the Federal University of Mato Grosso do Sul (ZUFMS), catalogued as ZUFMS-AMP20779 (*P. biligonigerus*) and ZUFMS-HEM00944 (*Lethocerus* sp).

Such records are essential for understanding the ecological role of belostomatids as relevant predators in aquatic ecosystems, particularly in temporary water bodies where explosive breeding events of anurans occur (Toledo, 2003; Ceron *et al.*, 2017; de Luna *et al.*, 2022; Hernández-Ruz *et al.*, 2022). Although invertebrate predation has historically received less attention than predation by vertebrates, it is increasingly recognized as an important ecological factor in structuring amphibian communities (Toledo, 2005; Toledo *et al.*, 2007). Belostomatids, especially those of the genus *Lethocerus*, are efficient predators of both tadpoles and adult frogs, with records involving species such as *Dendropsophus minutus*, *Dendropsophus nanu*s, *Scinax fuscovarius*, *Rhinella crucifer*, *Physalaemus cristinae*, *Physalaemus biligonigerus*, *Physalaemus cuvieri*, *Physalaemus nattereri*, *Pseudopaludicola mystacalis* and *Nyctimantis siemersi* (Nenda *et al.*, 2008; Schalk, 2010; Batista *et al.*, 2013; Landgref Filho *et al.*, 2019; Taffarel *et al.*, 2019; Macedo *et al.*, 2021; Mori *et al.*, 2023; Howard *et al.*, 2024; Souza-Felix *et al.*, 2025). These studies demonstrate that belostomatids are recurrent predators of *Physalaemus* species across different Neotropical environments and reinforce their role in trophic interactions involving anurans.

Moreover, less typical interactions, such as egg predation by cockroaches (Toledo, 2005) and cannibalistic behavior or carnivory among tadpoles (Escalante *et al.*, 2022), highlight the complexity of trophic relationships involving anurans. Tadpole predation on eggs or conspecifics has been documented in species such as *Leptodactylus savagei* and *Dendrobates* spp. (Toledo *et al.*, 2007), showing that predation among amphibians themselves may

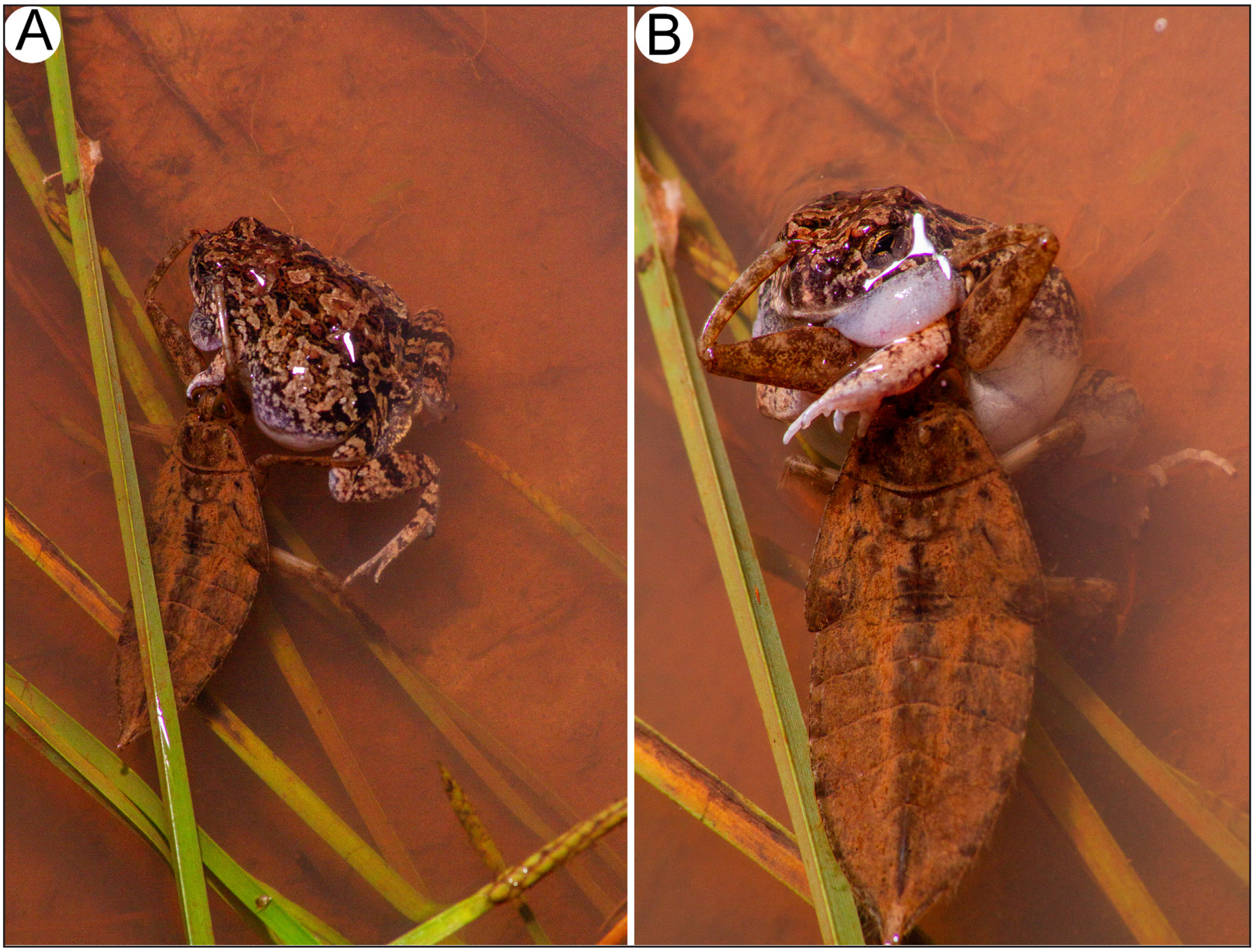

Figure 1. (A and B) Predation by an immature giant water bug (*Lethocerus* sp.) on *Physalaemus biligonigerus* (ZUFMS-AMP20779). Specimens collected at Fazenda Aguapé, Pantanal region, municipality of Aquidauana, Mato Grosso do Sul, Brazil.

also be ecologically relevant. Other invertebrates, including spiders (e.g., *Ancylometes*), dragonfly larvae, and scorpions, have been reported preying upon juvenile or adult frogs in various environmental contexts (Toledo, 2005; Maffei *et al*., 2014; Hernández-Ruz *et al*., 2022).

Thus, our record from the Brazilian Pantanal broadens the current understanding of interactions between anurans and invertebrate predators. Although the region harbors a high abundance of amphibians (Strüssmann et al., 2011), reports involving the genus *Physalaemus* remain scarce. This observation represents the first documented evidence of *Lethocerus* preying upon *P. biligonigerus* in the Pantanal, providing data that may help elucidate local trophic interactions. Together with previous observations, this study highlights the importance of natural history records as fundamental tools for advancing our knowledge of amphibian–invertebrate relationships in the Neotropical region.

Acknowledgments

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Nota

Cuad. herpetol. 40 (1): 169-173 (*2026*)

Reevaluación de la distribución de *Leptodactylus savagei* (Heyer, 2005) en Colombia, con un nuevo registro en Puerto Salgar, Cundinamarca

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ABSTRACT
We report the first record of *Leptodactylus savagei* in the Distrito de Manejo Integrado Cuchilla de San Antonio, Municipality of Puerto Salgar, Cundinamarca, Colombia. The individual was found in the rural area of La Risaralda, associated with a small pond in a shrub-dominated habitat under conditions of moderate humidity and high temperatures. The specimen was an adult male with a minor internasal wound and no other apparent morphological abnormalities. This finding allows us to discuss discrepancies with the species current distribution model as reported by the IUCN.

Key Words: Distribution; Cundinamarca; Anura; Leptodactylidae; IUCN.

RESUMEN
Reportamos el primer registro de *Leptodactylus savagei* en el Distrito de Manejo Integrado Cuchilla de San Antonio en el municipio de Puerto Salgar, Cundinamarca, Colombia. El individuo fue encontrado en la vereda La Risaralda asociado a un pequeño estanque en una zona con vegetación arbustiva en condiciones de humedad moderada y temperaturas elevadas. El macho presentaba una leve herida internasal, sin otras anomalías morfológicas aparentes. Este hallazgo nos permite discutir las diferencias de las ocurrencias con el modelo de distribución actualmente reportado por la UICN para la especie.

Palabras claves: Distribución; Cundinamarca; Anura; Leptodactylidae; IUCN.

La rana de dedos delgados de Savage, *Leptodactylus savagei* (Heyer, 2005) es una especie de rana de gran tamaño de la familia Leptodactylidae que se encuentra en bosques primarios y secundarios, zonas de borde o áreas deforestadas, distribuyéndose en Costa Rica, Colombia, Honduras, Nicaragua y Panamá, entre los 0 y los 1385 msnm (Heyer, Heyer & de Sá, 2010; IUCN SSC Amphibian Specialist Group, 2020). En Colombia la especie se ha reportado en los departamentos de Antioquia, Bolívar, Boyacá, Córdoba, Cundinamarca, Guajira, Huila, Magdalena, Santander y Valle del Cauca (Ruthven, 1922; Cochran y Goin, 1970; Renjifo y Lundberg, 1999; Cuentas et al., 2002; Heyer, 2005; Acosta, Huertas & Rada, 2006; Romero, Vidal & Lynch, 2008; Romero y Lynch, 2012; Rodríguez, Cortez & Osorno-Muñoz 2014; Ovalle-Pacheco, Camacho-Rozo & Arroyo, 2019; Mogrovejo et al., 2025). La distribución de *L. savagei* en Colombia se ha actualizado con nuevos registros en el Valle del Río Magdalena, Depar-

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tamento de Cundinamarca y en el Pacifico en el Departamento del Valle del Cauca (Mogrovejo et al., 2025); estos reportes mejoran el conocimiento de la distribución de la especie en el país y amplían la distribución sugerida por la IUCN (IUCN SSC Amphibian Specialist Group, 2020). El presente trabajo describe el primer registro de *Leptodactylus savagei* en el Distrito de Manejo Integrado Cuchilla de San Antonio, Municipio de Puerto Salgar, Cundinamarca, y en inmediaciones del Valle del Río Magdalena, aportando al conocimiento sobre la distribución de la especie.

El registro se realizó durante una salida de campo a la vereda La Risaralda, Municipio de Puerto Salgar, en inmediaciones del Distrito de Manejo Integrado Cuchilla de San Antonio (coordenadas: 5.5319961, –74.5597836; WGS84; Fig. 1). El 10 de mayo de 2025 se observó un individuo adulto de *Leptodactylus savagei* el cual fue capturado en un estanque permanente (Fig. 2). Posteriormente, el ejemplar fue colectado siguiendo los lineamientos establecidos para estos protocolos (HACC 2004). El ejemplar se sacrificó utilizando clorhidrato de lidocaína al 5%; luego fue fijado en formalina al 10% y conservado en etanol al 70%. El ejemplar está depositado en la Colección de Zoología "José Ricardo Cure Hakim" de la Universidad Militar Nueva Granada, bajo el consecutivo CZCH-UMNG-A-248. El estanque donde se encontraba el individuo se ubicaba dentro de un área de vegetación arbustiva (Fig. 3). Durante el día de la captura, las condiciones climáticas presentaban 97% de humedad debido a lluvias recientes, con temperaturas que oscilaban entre los 26 y 32°C.

Realizamos un mapa de distribución para *Leptodactylus savagei* usando datos disponibles (Mogrovejo et al. 2025), los datos georreferenciados para la especie en GBIF (2025), el modelado de distribución de la especie propuesto por la IUCN (2025) y el registro reportado en este estudio (Fig. 1).

El individuo fue identificado como *Leptodactylus savagei* siguiendo el diagnóstico realizado por Heyer (2005). El ejemplar presenta una coloración de fondo café claro a grisáceo, con manchas irregulares de tonalidades más claras en la superficie dorsal, y un patrón ventral compuesto por manchas irregulares en distintos tonos de café. Las extremidades muestran bandas horizontales que las rodean: de color marrón oscuro a negruzco en las patas traseras, y marrón tenue en las delanteras. En la región labial, superior e inferior, se observan manchas intergulares de color marrón oscuro. Asimismo, se destaca una franja marrón oscura a negruzca comenzando detrás de las fosas nasales, se interrumpe antes de alcanzar el ojo, lo rodea parcialmente, y continúa por encima del tímpano hasta el final de la cabeza, extendiéndose luego en segmentos irregulares a lo largo de la línea lateral del cuerpo (Fig. 2). El individuo es de constitución robusta y la longitud Hocico-Cloaca (LHC) es de 153 mm. Es un ejemplar macho que presenta hipertrofia muscular en los antebrazos, sus pulgares están fuertemente queratinizados y presenta hendiduras vocales; presenta una herida a 0.09 mm de la fosa nasal (Fig. 2).

El registro de *Leptodactylus savagei* en el bosque húmedo tropical (Bh-T) de la Cuchilla de San Antonio amplía su nicho ecológico conocido. La especie fue considerada típica de bosque seco tropical (Bs-T) del Caribe y los valles interandinos colombianos (Heyer, 2005; Ovalle-Pacheco, Camacho-Rozo & Arroyo, 2019), por lo que su presencia en el Bh-T del valle medio del río Magdalena junto con registros recientes en el Valle del Cauca (Mogrovejo et al., 2025), sugieren plasticidad ecológica. Los individuos observados se encontraban asociados a cuerpos de agua al borde del estanque permanente, rodeado de vegetación riparia densa, estos fueron localizados por vocalizaciones que realizaban en los bordes de los estanques, lo que podría indicar fidelidad a ciertos microhábitats más allá del bioma.

Desde una perspectiva biogeográfica, este hallazgo plantea dos hipótesis relevantes: 1. el rango real de *L. savagei* podría ser más amplio y continuo a lo largo del corredor del Magdalena, conectando Bs-T y Bh-T como hábitats funcionales; 2. los modelos de distribución actuales, incluido el de la IUCN (IUCN SSC Amphibian Specialist Group, 2020), podrían estar subestimando su área potencial. La distribución reportada por la IUCN se concentra en regiones como Santa Marta, Chocó, Córdoba y Antioquia y no incluye registros intermedios como Norcasia, Yacopí o Puerto Salgar. Esta omisión limita la precisión de los modelos predictivos. La tolerancia de *L. savagei* a ambientes fragmentados y húmedos sugiere adaptaciones como ser mecanismos de regulación hídrica cutánea o estrategias reproductivas flexibles, que podrían explicar su éxito en hábitats contrastantes (Prado, Uetanabaro & Haddad, 2005).

Confirmamos la presencia de *Leptodactylus savagei* en el municipio de Puerto Salgar, ampliando los municipios de Cundinamarca donde se ha confirmado la presencia de la especie en Colombia. Este

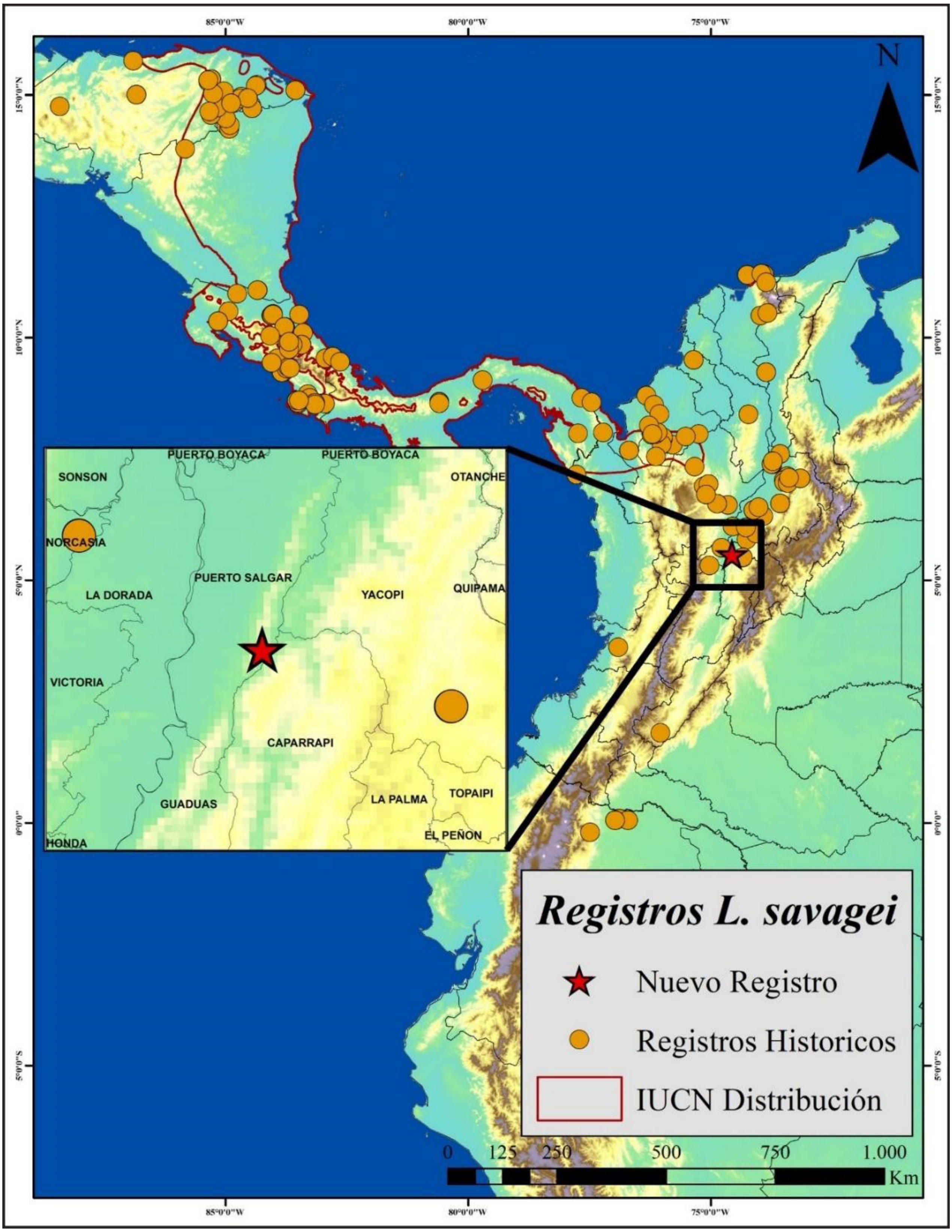

Figura 1. Mapa de distribución de *Leptodactylus savagei*. Los círculos naranjas indican registros históricos provenientes GBIF y Mogrovejo et al. (2025), el contorno rojo representa el área de distribución estimada por la UICN. La estrella roja señala el nuevo registro documentado en este estudio. El recuadro ampliado muestra con mayor detalle la ubicación del nuevo registro en el contexto regional del Magdalena Medio.

hallazgo resalta la necesidad de actualizar los modelos de distribución vigentes, como los propuestos por la IUCN (2020). Además, registros históricos y recientes evidencian una ocupación más extensa, posiblemente estructurada a lo largo de gradientes altitudinales y climáticos. Comprender esta expansión no solo redefine los límites geográficos de la especie, sino que también tiene implicaciones clave

Figura 2. Ejemplar macho adulto de *Leptodactylus savagei* registrado en la vereda La Risaralda, municipio de Puerto Salgar, Cundinamarca, Colombia. (**A**) Vista lateral izquierda. (**B**) Vista dorsal. (**C**) Detalle de la región cefálica.

Figura 3. Hábitat de *Leptodactylus savagei* en la vereda La Risaralda, municipio de Puerto Salgar, Cundinamarca, Colombia. (**A**) y (**B**) Estanque permanente rodeado de vegetación riparia densa, donde se realizó la colecta del ejemplar. (**C**) Vista general del paisaje de bosque húmedo tropical en la Cuchilla de San Antonio.

para su evaluación en términos de conservación, conectividad de hábitat y resiliencia ecológica.

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Nota

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New record of leg-interweaving behavior in *Boana polytaenia* (Cope, 1870) (Anura: Hylidae): an expansion of the antipredator repertoire in Neotropical anurans

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ABSTRACT
Amphibians exhibit a wide range of antipredator behaviors, such as thanatosis, alarm vocalizations, and distraction displays, aimed at reducing predation risk. Leg-interweaving is a rare antipredator behavior, characterized by crossing the hind limbs over the body. Here, we report the first record of this behavior for *Boana polytaenia*, which represents the first documented occurrence within the genus. It is thought to represent a displaced behavior in an out-of-context response to stress rather than a true defense mechanism, although it is discussed to have a potential role in enhancing aposematic displays, reproductive signals, chemical defenses, physical obstruction against predation, or body pattern distortion, favoring camouflage. The inconsistent occurrence and scarce reports of leg interweaving emphasize the importance of further experimental studies to determine its functional role and ecological relevance, thereby enriching our understanding of the evolution and functional diversity of defensive strategies in anurans.

Key words: Legs-interweaving; Anuran behavior; Defensive strategies.

RESUMEN
Los anfibios exhiben una amplia gama de comportamientos antidepredadores, como la tanatosis, las vocalizaciones de alarma y las exhibiciones de distracción, destinados a reducir el riesgo de depredación. El entrelazamiento de las piernas es un comportamiento antidepredador poco común, caracterizado por el cruce de las extremidades posteriores sobre el cuerpo. Aquí, reportamos el primer registro de este comportamiento para *Boana polytaenia*, lo que representa la primera ocurrencia documentada dentro del género. Se cree que representa un comportamiento desplazado en una respuesta de estrés fuera de contexto, en lugar de un mecanismo de defensa real, aunque se discute su papel potencial en la mejora de las exhibiciones aposemáticas, las señales reproductivas, las defensas químicas, la obstrucción física contra la depredación o la distorsión del patrón corporal, favoreciendo el camuflaje. La ocurrencia inconsistente y los escasos reportes de entrelazamiento de piernas enfatizan la importancia de realizar más estudios experimentales para determinar su papel funcional y relevancia ecológica, enriqueciendo así nuestra comprensión de la evolución y la diversidad funcional de las estrategias defensivas en los anuros.

Palabras claves: Entrelazamiento de piernas; Comportamiento de anuros; Estrategias defensivas.

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Animal behavior encompasses the observable responses of an organism to internal or external stimuli, representing a direct product of natural selection that reflects adaptations enhancing survival and reproductive success (Tinbergen, 1963; Alcock, 2013). These responses variate from simple motor responses to complex behavior patterns, such as communication, parental care, and predator avoidance. As a central component of biology, behavior is particularly diverse in vertebrates, where it is shaped by multiple selective pressures, among which predation represents one of the most intense (Lima & Dill, 1990). Among anurans, behavioral diversity is exceptionally pronounced. Extensive research has documented intricate strategies in reproductive behavior (Wells, 2007), territorial defense (Toledo *et al.*, 2015), acoustic communication (Gerhardt & Huber, 2002), and, notably, antipredator behavior (Toledo & Haddad, 2009; Caro, 2014; Ferreira *et al.*, 2019). Given their heightened vulnerability to predators across life stages, anurans have evolved a wide array of defensive mechanisms, including morphological, physiological, and behavioral traits (Duellman & Trueb, 1994; Toledo *et al.*, 2011; Mukherjee & Heithaus 2013).

In the context of antipredator behavioral, strategies that reduce the likelihood of detection, capture, or consumption by predators are particularly significant (Feder & Lauder, 1986). Many of these behaviors have evolved under long-term selective pressures, favoring individuals with effective responses to threat (Edmunds, 1974; Ruxton *et al.*, 2004). Documented antipredator strategies include thanatosis (feigning death), body inflation, alarm vocalizations, legs-interweaving, distraction display, among others (Toledo *et al.*, 2010; Toledo *et al.*, 2011). These behaviors often function synergistically with morphological adaptations, such as aposematic coloration or mimicry, enhancing their overall defensive efficacy (Skelhorn & Rowe, 2006). For instance, thanatosis, widely reported in amphibians, involve complete immobility to deceive predators, proving especially effective against visual predators or those that rely on movement cues (Toledo *et al.*, 2010; Ramalho *et al.*, 2019). Body inflation, a common trait in many Bufonidae species, increases the animal apparent body volume, making it harder for predator to grasp or ingest (Moroti *et al.*, 2018; Ferreira *et al.*, 2019). In contrast, legs-interweaving is a rare and less-studied behavior, documented in only few families of frogs (e.g., Bufonidae, Craugastoridae, Hylidae, Hyperolidae, and Leptodactylidae). Its function remains debated: it may serve as an active defense mechanism or represent displaced behavior, an out of-context response to stress (Velasco *et al.*, 2025).

Leg-interweaving behavioral was observed in an adult male of *Boana polytaenia* at the Instituto Alto Montana da Serra Fina, Itamonte municipality, Minas Gerais state, Brazil. The specimen was collected on April 12 2025 at 20:20 by the senior author (SISBIO Permit # 66852-7) while vocalizing 20 cm above water in grasses, in the Pinhão Assado waterfall (-22.358591, -44.797457). During photographic documentation prior to euthanasia, the individual jumped from a surface, falling approximately 10–15 cm. Immediately after impact, it exhibited leg-interweaving behavior, characterized by crossing its hind limbs over the body and exposing the orange-colored inner thigh surfaces. This posture was maintained for approximately two minutes without any additional stimulus before the animal spontaneously resumed normal movement. The euthanasia was conducted using specimen lethal dose of sodium thiopental. Subsequently, the specimen was fixed in 4% formalin solution for 24 h and, later, transferred to 70% ethanol for long-term preservation. The specimen was deposited in Coleção Teresa Cristina Sauer de Avila-Pires (CHTC 1591), Universidade Federal de São Paulo, campus Diadema, São Paulo, Brazil.

This record represents the first documented occurrence of leg-interweaving behavior in the genus *Boana*, representing the thirteenth recorded anuran species to exhibit this rare antipredator strategy (Velasco *et al.*, 2025). Beyond expanding the known taxonomic distribution of this behavior, this finding holds particular significance in understanding origins and functional diversity of defensive mechanisms in Neotropical anurans. The presence of leg-interweaving in *B. polytaenia* suggests either convergent evolution of this strategy or a potentially wider phylogenetic distribution among hylids than previously recognized.

Aposematic coloration consists of conspicuous visual patterns that typically signal cutaneous toxins in amphibians, warning predators of an individual's unpalatability or danger (Toledo *et al.*, 2010; Ferreira *et al.*, 2019). These displays commonly employ high-contrast hues (e.g. red, orange, yellow, or blue) that enhance predator recognition and memory (Toledo & Haddad, 2009; Protti, 2019). Many anurans exhibit such coloration only on normally concealed

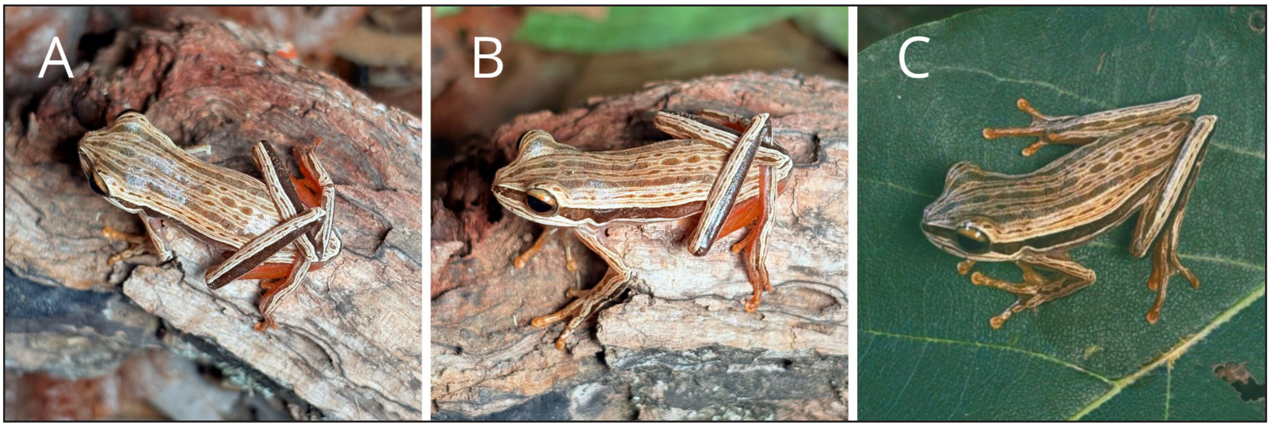

Figure 1. Male *Boana polytaenia* exhibiting leg-intertwining behavior. Dorsal and lateral views of the behavior observed on a wooden substrate, highlighting the display of bright orange inner coloration on the hind limbs (A–B). Same individual at rest, with hind limbs in a natural position and inner coloration not visible (C).

body regions (e.g., posterior thighs, belly, or limb surfaces), revealing them through specific defensive postures like body elevation or leg-interweaving (Mallet & Joron, 1999; Toledo & Haddad, 2005). In *B. polytaenia*, the bright orange inner thighs and tibiae remain hidden at rest but become highly visible during leg-interweaving behavior (Fig. 1A–B). This dynamic display likely enhances aposematic signaling while minimizing continuous exposure to predators (Rößler *et al.*, 2019; Barnett *et al.*, 2023). However, conspicuous coloration may also increase detection risk, creating an evolutionary trade-off between warning efficacy and predator attraction (Hall *et al.*, 2013; Rößler *et al.*, 2019). This paradox explains why many species combine aposematic with cryptic resting posture, a strategy that optimizes the balance between concealment and warning (Toledo & Haddad, 2009; Ferreira *et al.*, 2019; Pedroso-Santos *et al.*, 2022).

Bright coloration on the internal regions of anuran hind limbs has been interpreted as serving (1) a distraction mechanism during escape behaviors (e.g. rapid jumping), in which sudden flashes of color may disorient predators (Toledo *et al.*, 2010; Ramalho *et al.*, 2019), and (2) a potential visual signal in reproductive contexts. Alternatively, these color patterns may specifically enhance the efficacy of leg-interweaving behavior. When the limbs are crossed over the body in this distinctive posture, colors exposure create maximal visual contrast, potentially amplifying the aposematic signal or startling effects (Toledo *et al.*, 2011).

Beyond its potential role in enhancing aposematic displays and reproductive signal, leg-interweaving behavior may serve additional, yet understudied, defensive function. One proposed mechanism involves physical obstruction: by crossing its limbs over the body, the frog increases its effective volume and interference with predator jaws mechanisms, especially for predator that employ rapid gape-limited attacks (Wells, 2007; Ruxton *et al.*, 2019). This strategy parallels other anurans defenses, including thanatosis (death feigning) and body inflation, which similarly complicate the prey handling. (Toledo *et al.*, 2011; Gally *et al.*, 2014). A second hypothesis suggests disruption of predator search images through visual pattern distortion (Toledo & Haddad, 2009; Ramos *et al.*, 2021). Visual predators often rely on prey silhouettes for recognition (Wells, 2007; Zlotnik *et al.*, 2018), and the anomalous posture by leg-interweaving may break the frog's characteristic outline. In species like *B. polytaenia*, which exhibits longitudinal dorsal stripes, this effect could be intensified, as the behavior disrupts these linear patterns into discontinuous segments (Velasco *et al.*, 2025), potentially delaying predator identification. A third, chemically mediated function may involve the release of defensive skin secretions (Dreher *et al.*, 2015). Although undocumented in *B. polytaenia*, Velasco *et al.* (2025) demonstrated that some anurans release bioactive peptides through the skin during stress responses. Limb movements during interweaving may mechanically stimulate dermal glands, facilitating secretion release while simultaneously exposing warning coloration, thus forming a synergistic defensive strategy (Amézquita *et al.*, 2017; Velasco *et al.*, 2025). These peptides, stored in granular glands, function as both as antipredator and antimicrobial agents, offering protection during vulnerable defensive postures.

This observation represents the first documented case of leg-interweaving behavior in the genus *Boana*, significantly expanding our knowledge of this poorly documented antipredator strategy in anurans. The behavior's close association with sudden display of otherwise vibrant coloration reinforces its function as a complex defensive mechanism. The context-dependent nature of this color exposure - occurring exclusively during leg-interweaving - suggests an adaptive specialization for maximizing visual deterrence during predator encounters. The coordinated presentation of postural modification, dynamic color display, and potential chemical secretion release indicates an integrated defensive response. This finding highlights important questions requiring experimental investigation, particularly regarding the behavior's effectiveness against different predator types, its associated biochemical components, and the potential evolutionary trade-offs involved.

With only twelve previously documented species exhibiting this behavior, this record of *B. polytaenia* provides valuable comparative data for understanding the evolution and functional diversity of defensive strategies in anurans. The scarcity of field observations of leg-interweaving emphasizes the need for further research to clarify its adaptive significance and ecological context. This discovery not only adds to the known taxonomic distribution of this behavior but also enhances our understanding of the sophisticated antipredator adaptations employed by anurans under predation pressure.

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Novedad zoogeográfica

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New record and update on the geographical distribution of the snake *Atractus pantostictus* Fernandes & Puorto, 1993, for Northeast Brazil

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Locality. – Brazil, state of Bahia, municipality of São Desidério (12,4422°S, 45,1811°W, WGS 84, 607m above sea level). The specimen was captured in a pitfall trap in a transitional environment between cerrado and vereda team working in Wildlife Monitoring Program, on November 25th, 2017, around 07:31 am. The specimen was fixed whole in 10% formalin and deposited to the Zoological Collection of the Federal University of Goiás, Brazil (ZUFG1437). Identification of the specimens was based on Fernandes and Puorto (1993) and Passos *et al.* (2010). The specimen presents 2 postoculars; temporals 1+2; 7 supralabials, with the third and fourth contacting the orbit; 7 infralabials, with the first four contacting the chinshields; 3 gulars; 3 preventrals; 17 dorsal scale rows at midbody; 146 ventrals; cloacal plate single; and 36 divided subcaudals. A Collecting permit (# No 3979) was granted by the Instituto do Meio Ambiente e Recursos Hídricos (INEMA), Bahia, Brazil.

Comment. – The Dipsadine genus *Atractus* is endemic to the Neotropical region (Passos, 2008). This genus of semi-fossorial or cryptozoic snakes currently comprises about 149 species, most of them exhibiting restricted distributions (Passos *et al.*, 2010; Uetz, 2024). In Brazil, 45 species of the genus *Atractus* have been recorded (Guedes *et al.*, 2022), including *Atractus pantostictus* Fernandes and Puorto 1993, which is considered an endemic species to Brazil (Nogueira *et al.*, 2019; Guedes *et al.*, 2022), and the type locality is for the Municipality of Franco da Rocha, State of São Paulo. The species occurs in the central and southeastern regions of Brazil, in the states of Goiás, Distrito Federal, Tocantins, Minas Gerais, São Paulo and Mato Grosso (Guedes *et al.,* 2022). The species inhabits areas of Cerrado and Cerrado/Submontane to Lower Montane Semi-deciduous forest transition zones (Passos *et al.*, 2010).

We collected an adult snake (snout-vent length 223 mm, tail length 37 mm; total length 260 mm; Fig. 1) on Nov 25th, 2017, in the country of Brazil, state of Bahia, municipality of São Desidério. The species was captured in a pitfall trap in a transitional environment between cerrado and vereda. The area is in the drainage basin of the Fêmeas river, predominantly characterized by cerrado *sensu stricto*, semi-deciduous, and deciduous forest vegetation, gallery forest and "veredas" (Mendonça *et al.,* 2008; Oliveira *et al.*, 2015).

Although the distribution of *Atractus pantostictus* is widely recognized, there is currently no confirmed record of the occurrence of this species in the state of Bahia. According to Haddan and Lira-da-Silva (2012), who documented the presence of 129 snake species in the State, *Atractus pantostictus* was not documented. Subsequent studies conducted by Lima *et al.* (2016) in Cerrado localities in the western region of the State also did not record the presence of this species. Additionally, in the list of reptiles in Brazil compiled by Guedes *et al.* (2022), there is no record of the species for the state of Bahia. Based on

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Figure 1. *Atractus pantostictus* from São Desidério Municipality, Bahia State, Brazil.

these pieces of evidence, we present the first documented record of *Atractus pantostictus* for the state of Bahia and the Northeast region of Brazil.

To update the current geographic distribution map of *A. pantostictus*, we considered literature records from Nogueira *et al.* (2019) and the data available from the SpeciesLink network (2024). Our record extends the known distribution area to approximately 257 km from the municipality of Mateiros, in the State of Tocantins, 288 km from the Municipality of Cavalcante, in the State of Goiás, and 375 km from the Municipality of João Pinheiro, in the State of Minas Gerais. These are the closest points to our distribution extension. The new record reported in this study fills a distributional gap of the poorly known on *A. pantostictus* in northeastern Brazil.

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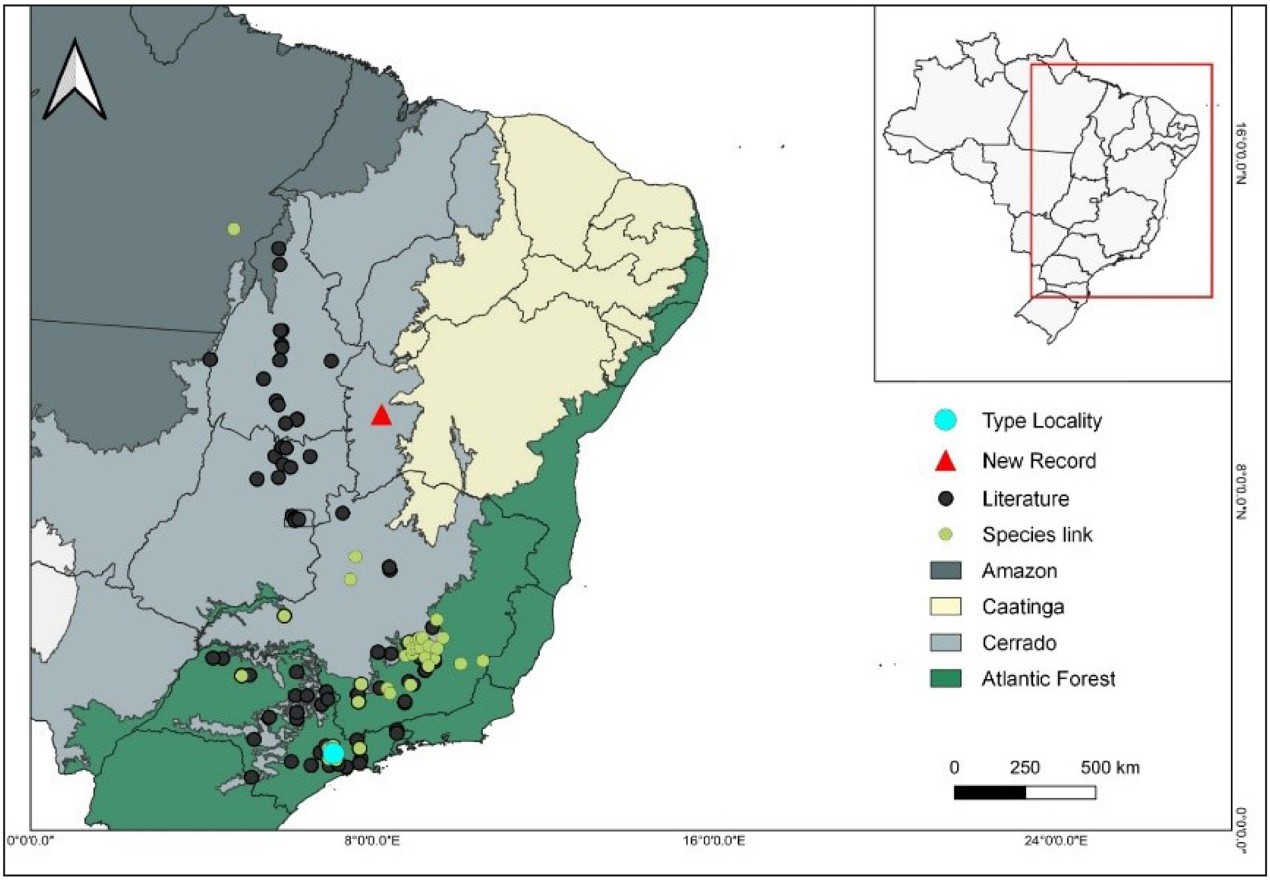

Figure 2. Map showing the known localities in Brazil for *Atractus pantostictus.*

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Novedad zoogeográfica

Cuad. herpetol. 40 (1): 185-189 (*2026*)

Primer registro de la salamandra gusano *Oedipina berlini* (Caudata: Plethodontidae) en Panamá

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Localidad.— Panamá, Provincia de Colón, Área Recreativa Lago Gatún (9° 19’ 48”N, -79° 50’ 24”O, 45 m s.n.m; Fig. 1 A-B). Entre el 19 de noviembre y el 5 de diciembre de 2021, se observaron dos individuos de la salamandra gusano, *Oedipina berlini* en el sendero El Búho, entre las 19:00 y las 21:00 h, dentro del bosque y cerca de una corriente de agua temporal. El bosque es intervenido, incluyendo áreas de bosque secundario joven y maduro (ANAM, 2013). El dosel está compuesto por especies como *Luehea seemannii*, *Cordia alliodora*, *Handroanthus guayacan*, *Anacardium excelsum*, entre otras (ANAM, 2013). La zona de vida corresponde al bosque húmedo tropical (ANAM, 2010). El primer espécimen fue fotografiado por el primer autor y liberado inmediatamente en el sitio (Fig. 2 A-C). El segundo espécimen, fue recolectado por el primer autor (Fig. 3A) y depositado en el Museo de Vertebrados de la Universidad de Panamá bajo el número de colección MVUP 2739.

Posteriormente, el 16 de junio de 2022, el primer autor observó tres ejemplares más, de los cuales se colectó el segundo ejemplar en la misma localidad (Fig. 3 B-E). Este espécimen se depositó en la Colección Zoológica Dr. Eustorgio Méndez del Instituto Conmemorativo Gorgas de Estudios de la Salud (COZEM-ANF 0713). La observación se hizo dentro del sendero El Búho, entre las 19:00 y las 21:00 h, después de fuertes lluvias. Durante la

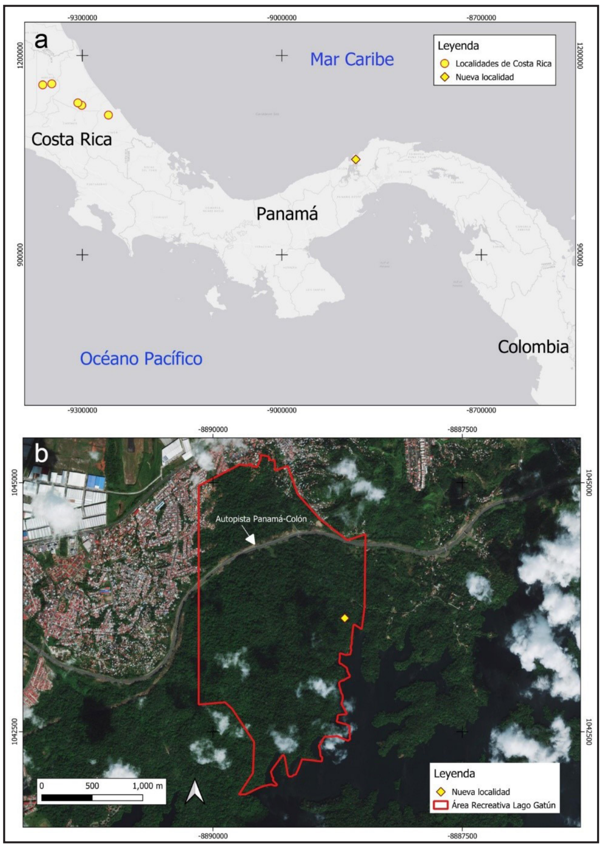

Figura 1. Mapa con localidades conocidas (círculos amarillos) de *Oedipina berlini* en Costa Rica y la nueva localidad (rombo amarillo) en Panamá (a). Sitio de observación (rombo Amarillo) en el Área Recreativa Lago Gatún, la flecha señala la Autopista Panamá-Colón que fragmenta el área protegida (b).

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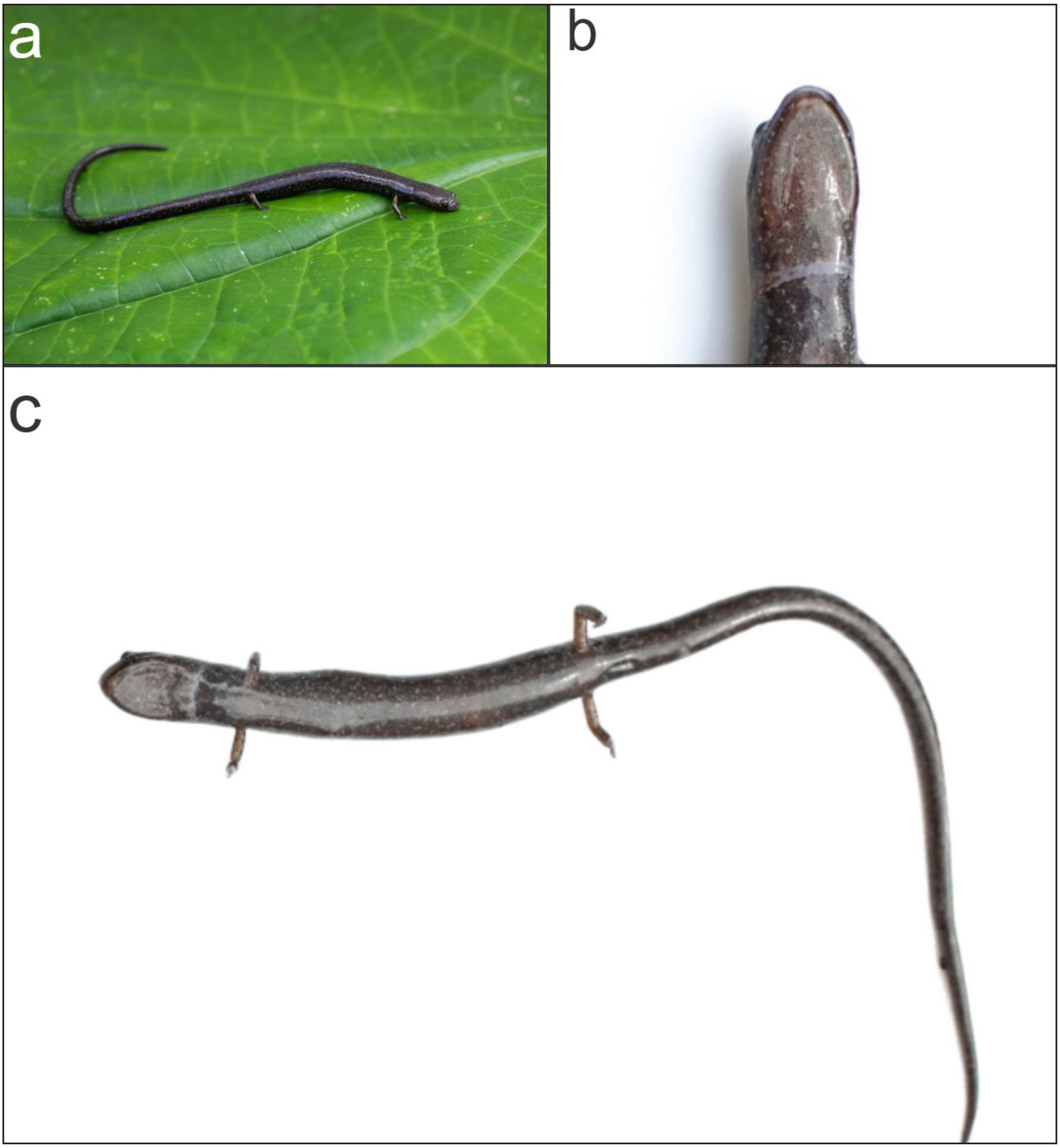

Figura 2. Vista dorsal completa (a), ventral de la cabeza (b) y ventral completa (c) de un especimen no colectado de *Oedipina berlini* fotografiado en el Área Recreativa Lago Gatún, Panamá.

sesión fotográfica, se observó el mismo comportamiento defensivo registrado por Gómez-Campos *et al.* (2024). Las medidas morfométricas de los dos ejemplares capturados fueron tomadas con un calibre de precisión de 0.1 mm. Las fotografías y medidas de los especímenes fueron revisadas por Brian Kubicki, autor de la descripción original de la especie e investigador del Costa Rican Amphibian Research Center, quien confirmó su identidad.

Comentarios.— El Área Recreativa Lago Gatún (ARLG), con una extensión de casi 360 hectáreas, brinda protección al Lago Gatún, un cuerpo de agua estratégico para el abastecimiento de la ciudad de Panamá y las operaciones del Canal Interoceánico (Navarro, 2001; Jaramillo *et al.*, 2010). Adicionalmente, posee un alto valor ecoturístico debido a su

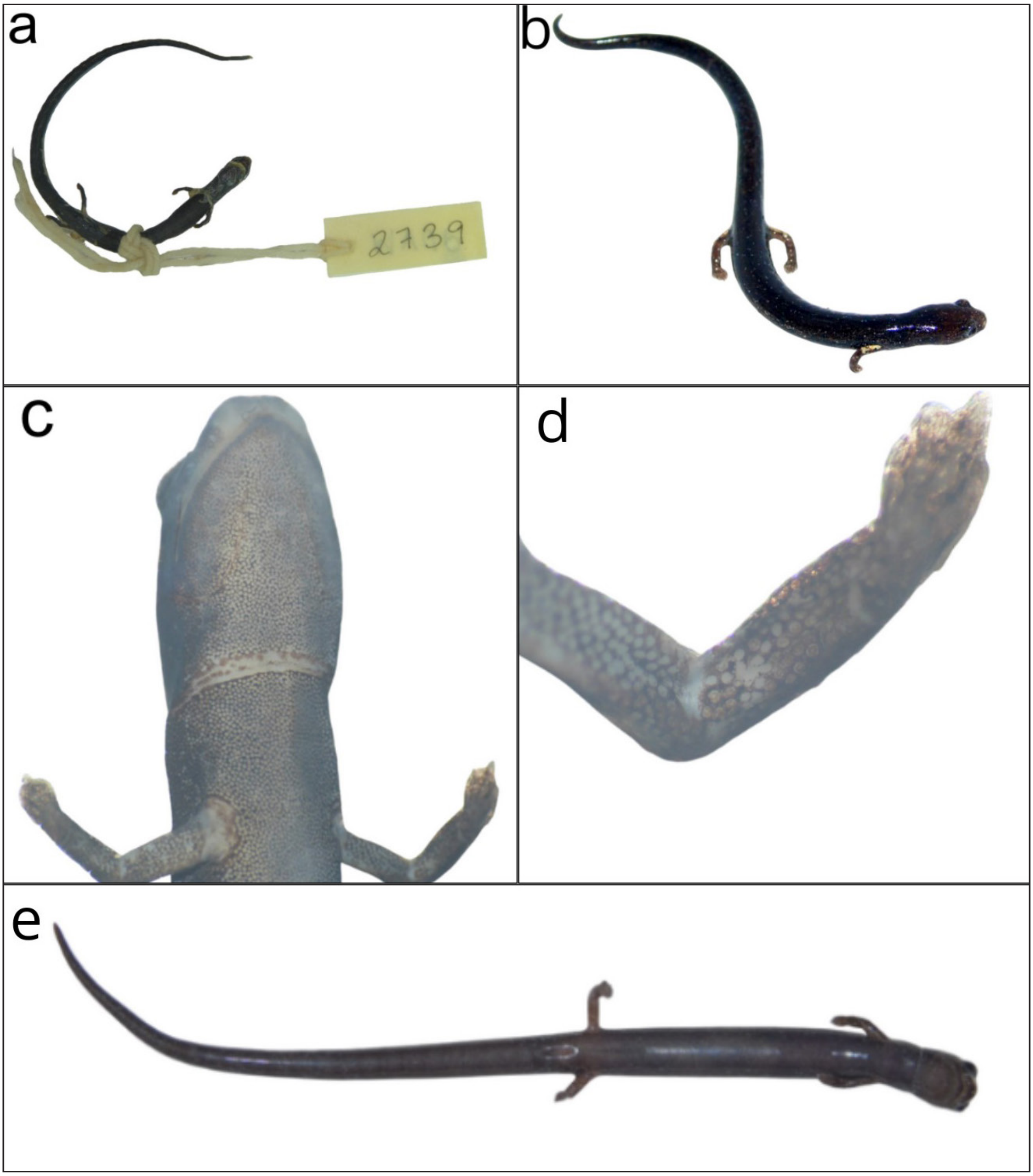

Figura 3. Fotografías de los especímenes MVUP 2739 (a. vista ventral completa) y COZEM-ANF 0713 (b. vista dorsal, c. vista ventral de la cabeza, d. vista ventral de la mano izquierda, e. vista ventral completa) colectados en el Área Recreativa Lago Gatún, Panamá.

biodiversidad y paisajes naturales (Navarro, 2001; Contreras *et al.*, 2023). Sin embargo, el ARLG representa un vacío significativo en el conocimiento científico de las áreas protegidas de la provincia de Colón. Según Ortiz *et al.* (2020), menos del 5% de las investigaciones en áreas protegidas de la provincia se han llevado a cabo en esta área. Estas investigaciones están conformadas por inventarios de macrohongos (Farnum Castro & Burgos Andreve, 2012), mariposas nocturnas (Lanuza Garay *et al.*, 2022) y anuros (Contreras *et al.*, 2023), así como observaciones de interacciones depredador-presa entre artrópodos y herpetofauna (Walter-Conrado *et al.*, 2023). Esto evidencia que se requiere más investigación en el

ARLG para documentar y proteger su biodiversidad.

La especie *Oedipina berlini*, Kubicki, 2016, se encontraba registrada hasta este estudio solamente en cinco localidades en la vertiente caribe de Costa Rica (Fig. 1A). Se describió originalmente de la Reserva de Bosque Tropical Guayacán y la cara noreste del volcán Turrialba (Kubicki, 2016), y se han registrado ejemplares en la Reserva Rara Avis (Leenders, 2016) y la Reserva Privada Veragua Rainforest (IUCN, 2020). Recientemente se reportó una nueva localidad en la región El Ceibo, dentro del Parque Nacional Braulio Carrillo (Gómez-Campos *et al.*, 2024). La identificación de los nuevos ejemplares reportados en este trabajo se realizó mediante una revisión bibliográfica (Savage, 2002; Köhler, 2011; Raffaëlli, 2013; Kubicki, 2016; Leenders, 2016) y la corroboración por parte del autor de la descripción de la especie.

Los dos especímenes panameños colectados de *Oedipina berlini* tienen medidas morfométricas dentro de los rangos de los ejemplares costarricenses descritos para la localidad tipo (Kubicki, 2016), con una mayor longitud de la cola del ejemplar MVUP 2739 (Tabla 1). Existen pocos individuos colectados en cada una de las localidades de registro, por lo que futuras investigaciones podrían enfocarse en describir su variabilidad morfológica intra e interpoblacional.

El registro de esta salamandra en el ARLG, que se encuentra fragmentada por la autopista Panamá-Colón y amenazada por la expansión urbana y asentamientos informales (Fig. 1B), refuerza la necesidad de impulsar los estudios de diversidad en áreas protegidas poco exploradas de Panamá. Ortiz *et al.* (2020) identificaron seis amenazas principales para la conservación del ARLG: extracción selectiva de recursos, invasión de tierras, falta de personal capacitado, escasez de equipos y gestión deficiente del área protegida, conflictos de tenencia de tierras y ausencia de programas de vigilancia y control. Estas presiones, combinadas con la fragmentación del hábitat, seguramente ponen bajo amenaza a *O. berlini* y toda la biodiversidad en esta área protegida por lo que sería recomendable desarrollar planes de mitigación de impactos antropogénicos que mitiguen o eliminen las actuales amenazas sobre el ARLG dado que constituye el único punto de registro de la especie en este país.

Esta nota representa una extensión de la distribución conocida para la especie en unos 371 km en línea recta hacia el suroeste y el primer registro en Panamá. El patrón de distribución disyunta es similar al observado en *Ecnomiohyla bailarina* (Kubicki y Salazar, 2015). Esto destaca la necesidad de incrementar muestreos más intensivos y extensos en toda la región. La distancia entre las localidades de registro en Costa Rica y Panamá abre la posibilidad de la existencia de poblaciones intermedias de *O. berlini* aún no descubiertas.

Tabla 1. Características morfológicas y medidas morfométricas de dos ejemplares de *Oedipina berlini* del Área Recreativa Lago Gatún en Panamá y los especímenes tipo de Costa Rica. Las medidas y rangos se expresan en mm (n = 3).

	MVUP 2739	COZEM-ANF 0713	Holotipo UCR 22845	Paratipos UCR 22843, UCR 22844 y CRAC 0241
Surcos costales	No visible	15	15	15
Ancho de la cabeza	4.9	5.1	4.9	4.1 – 5.1
Ancho del cuello	4.0	3.5	4.1	3.8 – 4.1
Ancho de los hombros	4.4	4.4	4.6	3.5 – 4.3
Ancho del tronco	4.6	4.7	4.5	3.8 – 4.2
Longitud del cuerpo	38.0	36.0	38.7	30.1 – 38.0
Longitud de la cola	65.0	44.0	56.1	40.9 – 45.9
Longitud de la abertura cloacal	2.0	2.1	2.6	2.2 – 2.5

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Este estudio fue realizado gracias al fondo de investigación CUFI-2021-EG-CNET-003, financiado por la Universidad de Panamá. A B. Kubicki por la corroboración en la identificación de los ejemplares. A los profesores de la Universidad de Panamá (CRUC) A. Lanuza Garay y V. Murillo, por su apoyo en la revisión de una versión preliminar del manuscrito. A los asistentes de campo J. Clement, V. Castañeda, J. Peralta y V. Smith miembros de la Asociación Biológica de Panamá (ABIOPA, OBC). A J. Pascale y A. Valderrama, M. Santos y E. Pérez del Instituto Conmemorativo Gorgas de Estudios de la Salud por permitir el acceso a la Colección Zoológica Dr. Eustorgio Méndez. Al Ministerio de Ambiente de Panamá por facilitar el permiso de colecta ARB-055-2021.

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Novedad zoogeográfica

Cuad. herpetol. 40 (1): 191-194 (*2026*)

After four decades, a new record of the rare *Ceratophrys aurita* (Raddi, 1823) (Anura, Ceratophryidae) for the state of Rio de Janeiro, Brazil

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Locality.— Brazil: Rio de Janeiro state, municipality of Cambuci, area of rural properties near secondary forest fragment (21°29'32.7"S, 41°53'56.7"W; WGS84, 865.37 m above sea level). Collected on 8 January 2024 by D. M. Silva and H. A. P. B. Lima. Voucher specimen deposited in the Coleção Herpetológica do Norte Fluminense, at the Universidade Estadual do Norte Fluminense Darcy Ribeiro (CHNF 1326).

Comments.— The global decline of amphibians is a well-documented and alarming phenomenon, driven by the synergistic effects of habitat degradation, emerging diseases, climate change, and invasive species (Stuart *et al.*, 2004; Wake & Vredenburg, 2008; Scheele *et al.*, 2019). In the Brazilian Atlantic Forest, considered one of the most biodiverse and threatened biomes in the world, amphibians have experienced severe declines, frequently associated with the chytrid fungus (*Batrachochytrium dendrobatidis*), in addition to historical and recent environmental changes (Becker and Zamudio, 2011; Toledo *et al.*, 2023). Despite the extensive documentation of these threats, sampling gaps hinder the accurate assessment of declining populations and species considered rare, especially in poorly explored areas (Augusto-Alves *et al.*, 2023).

Similar to other horned frogs (Ceratophryidae), *Ceratophrys aurita* is emblematic due to its rarity and cryptic habits (Jorge *et al.*, 2015). The species typically inhabits well-conserved forest fragments, burying itself in the leaf litter on the forest floor (Heyer *et al.*, 1990; Izecksohn and Carvalho-e-Silva, 2001). Its distribution spans coastal rainforest from Rio Grande do Sul to southern Bahia, with a few records extending into eastern Minas Gerais (Faivovich *et al.*, 2014; Vieira *et al.*, 2018; Augusto-Alves *et al.*, 2023).

Although *C. aurita* is the only species of the genus occurring in the Atlantic Forest (Faivovich *et al.*, 2014), the geographically closest congener to our record is *C. joazeirensis*, and distinguishing both species may be relevant in transitional areas of eastern Minas Gerais. *C. aurita* can be readily differentiated by its markedly larger body size, a well-developed digitiform palpebral crest, and a non-cornified inner metatarsal tubercle (Lynch, 1982; Mercadal, 1986). In contrast, *C. joazeirensis* is considerably smaller, exhibits a less pronounced triangular palpebral crest, and possesses an inner metatarsal tubercle with a distinctly darkened cornified and keratinized margin (Mercadal, 1986).

Despite this wide distribution, *C. aurita* faces a dramatic decline in confirmed records during recent decades, particularly within the state of Rio de Janeiro (Augusto-Alves *et al.*, 2023). According to Toledo *et al.* (2023), the last voucher-collected specimen of *C. aurita* from the state of Rio de Janeiro dates from 1984 (voucher ZUFRJ 3168). The same voucher is listed by Augusto-Alves *et al.* (2023) but assigned to 1982. Despite this discrepancy, all available records indicate that no additional occurrences have been documented in the state after a field visual and auditory observation made in 1989 (see supplementary material of Toledo *et al.*, 2023).

The new record from Cambuci extends the species' known range by approximately 150 km northwards from historical localities in Rio de Ja-

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Figure 1. Adult male *Ceratophrys aurita* (CHNF 1326) photographed *in situ* in Cambuci, Rio de Janeiro, Brazil. Photo by Diego Moura da Silva.

neiro state and represents its northernmost known occurrence to date. The region is considered undersampled for amphibians (Augusto-Alves *et al.*, 2023), reinforcing the significance of this finding. Other nearby locality records include the municipalities of Araponga, Minas Gerais, and Santa Leopoldina, Espírito Santo, at about 110 km and 211 km, respectively.

On 7 January 2024, a local resident informed the authors about a large frog observed during a motorcycle trail ride and provided photographs and videos of the encounter. The following day, we located an adult male *C. aurita* (snout–vent length 185 mm) ~20 m from the originally reported site. The frog was found alive but appeared lethargic, emaciated, and presented multiple cream-white, oval subcutaneous cysts, especially visible along the hind limbs. It died within 24 hours, was necropsied, and subsequently deposited in CHNF. Necropsy findings included cachexia and widespread parasitic cysts in skeletal muscle, liver, and gastrointestinal tissues, indicating prolonged starvation and severe parasite load.

The site of collection corresponds to a disturbed landscape near banana plantations, pastures, and human settlements, at the edge of a secondary Atlantic Forest fragment. The record was made in the rainy season, and no calling males or additional individuals were observed. Although the precise cause of death remains uncertain, the deteriorated condition of the specimen may reflect weakening associated with a high parasitic load, maybe related to environmental pollution (Toledo *et al.*, 2023).

This rediscovery of *C. aurita* in Rio de Janeiro state highlights the value of citizen involvement in detecting rare species, an approach that has proven effective for other *Ceratophrys* species such as *C. ornata* in Argentina (Deutsch *et al.*, 2017). It underscores the urgent need for conservation strategies beyond protected areas, especially in historically overlooked regions of the Atlantic Forest. Targeted surveys and monitoring efforts in Cambuci and surrounding areas may yield further insights into the species actual distribution and conservation status.

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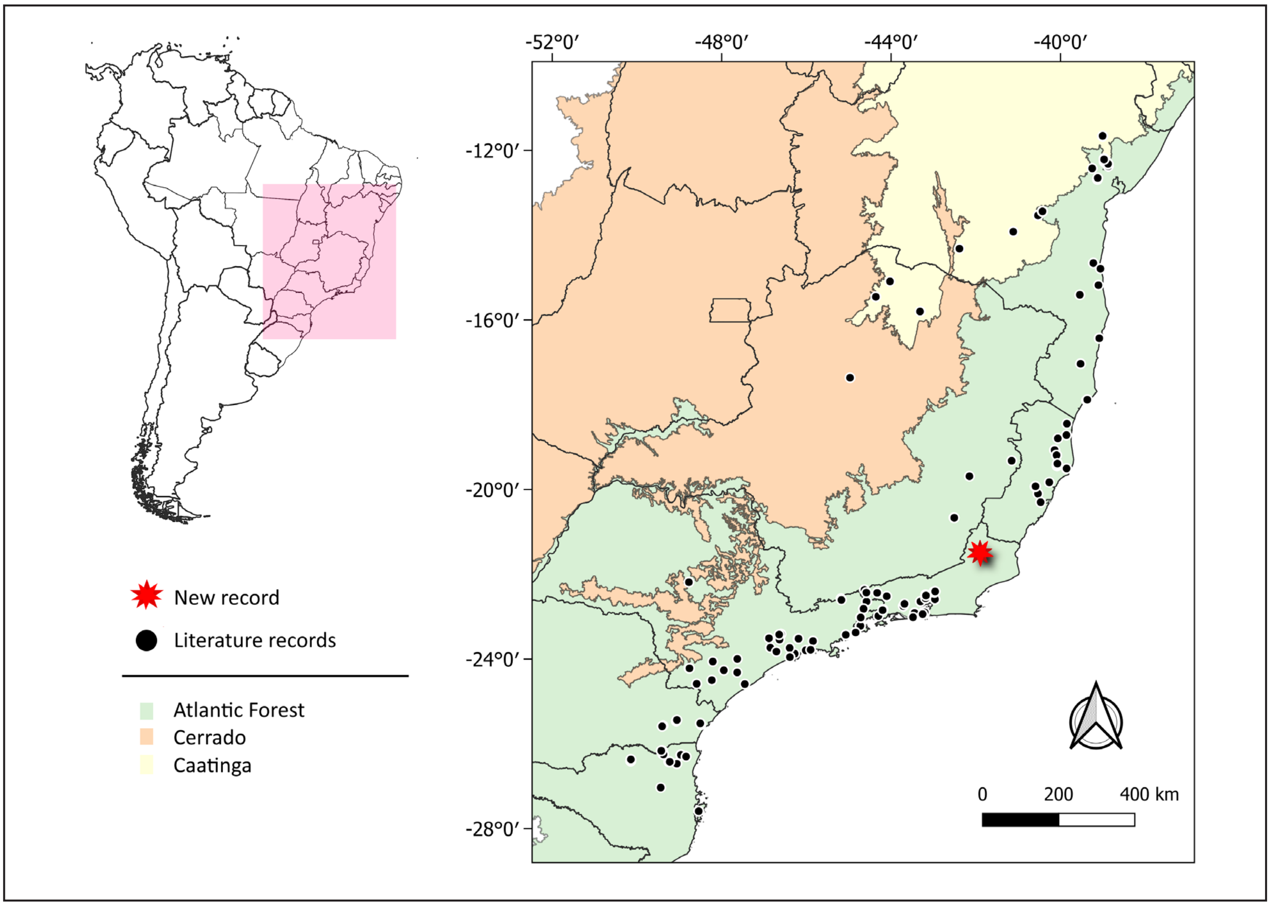

Figure 2. Distribution map of *Ceratophrys aurita*, including the new record from Cambuci, Rio de Janeiro, Brazil. Historical records based on supplementary material of Augusto-Alves *et al.* (2023).

support during the processing and curation of the specimen. Finally, we express our appreciation to the reviewers for their constructive comments, which significantly improved the quality of this note.

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