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ECOSYSTEMS

Distribution and diversification of *Adelphobates*, emblematic poison frogs from Brazilian Amazonia

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Abstract: *Adelphobates* contains three species, and the inaccurate identification of *A. quinquevittatus* and the scarcity of records of *A. castaneoticus* complicate inference of their distributions; the latter species occurs in sympatry with *A. galactonotus*. Our objective was to revise the distributions of *Adelphobates* by compiling data and modeling habitat suitability, as range limits may be shaped by landscape features and biotic interactions. We initially analyzed the existence of operational taxonomic units within the nominal species and subsequently inferred the observed and potential distributions, taking into account the possible independent lineages for the three species, and we also generated a molecular timetree to understand the chronology of interspecific diversification events. *Adelphobates quinquevittatus* was found to have a more easterly distribution than previously described, and specimens with phenotypic variation were found to occur in areas inconsistent with the modeling, and *A. castaneoticus* was concentrated in the Tapajós-Xingu interfluve, surrounded by *A. galactonotus*. Models indicated that the right bank of the Xingu River is suitable for both species, indeed, both were found there. Despite *Adelphobates* species having their distributions delimited by major Amazonian rivers, estimated divergence times predate the formation of the modern river network, suggesting that other mechanisms were involved in their diversification.

Key words: Brazil nut, competition, Dendrobatidae, modeling, riverine barrier, species range.

INTRODUCTION

Despite increased sampling efforts and new technical procedures, which have led to a recent increase in the number of taxonomic descriptions of new anuran species in the Amazon, the region's true frog diversity is still probably underestimated (Guerra et al. 2020). In addition, inaccurate taxonomy can generate incorrect distribution patterns that consequently affect the interpretation of bioregionalization (Vasconcelos et al. 2019). For example, delimitation of bioregions based on IUCN distribution data differs considerably from that based on operational taxonomic units (OTUs) from genetic data (Godinho & Da Silva 2018, Vacher et al. 2020). Genetic delimitation of OTUs, even considering conservative divergence limits, resulted in more limited ranges and greater endemism of candidate species than with the IUCN taxonomy (Vacher et al. 2020). This is particularly important for so-called cryptic species complexes and for widespread species, especially those that occur in geologically complex areas likely to have favored diversification (Fouquet et al. 2012, 2021, Mota et al. 2020). Thus, taking into account genetic information and biogeographic ruptures in taxonomic evaluations should lead to extensive revision of the distribution of many taxa (Shaney et al. 2017, Vacher et al. 2020).

There is evidence that for the Amazonian anurans, distribution patterns can be influenced by the presence of large rivers (Godinho & Silva 2018, Réjaud et al. 2020), but climate and topographic variables also contribute significantly (Godinho & Silva 2018, Vacher et al. 2020, Moraes et al. 2022). Among the climatic variables, the distribution and diversification patterns of Neotropical anurans are influenced especially by those related to precipitation (Vacher et al. 2020, Lemes et al. 2022). This relationship is not unexpected given the ecophysiology of this group, associated with its low dispersal capacity and dependence on aquatic habitats for tadpole development, which makes it susceptible to specific local conditions (Moura et al. 2016, Lemes et al. 2022). In addition to the structural characteristics of the landscape, such as elevation and vegetation cover, and climatic variables, biotic interactions can also shape species distributions (Lemes et al. 2022). In the poison dart frogs (Dendrobatidae), for example, the competition between closely related species has already been associated with niche apportionment and delimitation of the distribution of species (Brown et al. 2008a, b, Twomey et al. 2008, Schulte et al. 2010, Ryan & Barry 2011).

Diversification processes in Andean dendrobatids occurred mainly in the early Oligocene (Santos et al. 2009), and resulted in a great diversity of species that have a high degree of endemism (Brown et al. 2011, Grant et al. 2017, Guillory et al. 2019). This may have occurred especially due to allopatric barriers generated by Andean orogeny and to the high variety of environments associated with altitudinal gradients, favoring specialization and the occupation of restricted niches (Roberts et al. 2007, Twomey et al. 2008, Vasconcelos et al. 2019). Meanwhile, in dendrobatids of the Amazonian lowlands, as well as the Aromobatidae (sister group to Dendrobatidae), most diversification occurred more recently, from the Miocene, and has been associated mostly with marine incursions and the organization of the modern Amazon drainage network (Santos et al. 2009, Réjaud et al. 2020). Unlike Andean species, dendrobatid distributions are broader and species do not appear to occupy very specialized niches (Caldwell & Myers 1990, Santos et al. 2009, Brown et al. 2011, Hoogmoed & Ávila-Pires 2012, Rojas et al. 2020).

Phylogeographic studies focusing on aromobatids from the Brazilian Amazon have frequently demonstrated that intraspecific diversification is common, especially within widely distributed species, and can often lead to the identification of candidate species (Amézquita et al. 2009, Simões et al. 2010, 2014, Kaefer et al. 2013, Maia et al. 2017, Réjaud et al. 2020, Fernandes et al. 2021). Nonetheless, there are relatively fewer studies focused on dendrobatids in the same region, for which the broad distributions currently proposed may reflect underestimation of local biodiversity due mainly to: (1) scarcity of faunal surveys in not very accessible areas where probable occurrence of a particular species has been attributed, and (2) scarcity of phylogeographic and taxonomic studies focused on the diversity of potential species complexes (Noonan & Gaucher 2006, Wollenberg et al. 2006, Rojas et al. 2020, de Medeiros et al. 2021). An example of this underestimation was the “ventrimaculatus” complex (Caldwell & Myers 1990), widely distributed in the Amazon basin, which after taxonomic and systematic revisions was subdivided into several species of *Ranitomeya* (Grant et al. 2006, 2017, Brown et al. 2011).

Recently, phylogeographic studies of widely distributed Amazonian species such as *Dendrobates tinctorius*, *Adelphobates galactonotus* and *A. quinquevittatus* resulted in the identification of genetically structured populations, although no candidate species have been identified so far (Noonan & Gaucher 2006, Rojas et al. 2020, de Medeiros et al. 2021). Important evolutionary processes were proposed as catalysts of this intraspecific divergence, such as isolation in forest refuges (Noonan & Gaucher 2006), the action of rivers as barriers (Rojas et al. 2020, de Medeiros et al. 2021), and river dynamics (de Medeiros et al. 2021), although no predominant process to explain diversification within the species already studied has emerged.

The dendrobatid genus *Adelphobates* Grant, Frost, Caldwell, Gagliardo, Haddad, Kok, Means, Noonan, Schargel, and Wheeler (2006), subject of this study, currently contains three species and is widely distributed in the *terra firme* (upland, non-flooding) forest of Brazilian Amazon. These are: *Adelphobates quinquevittatus* (Steindachner, 1864), *A. castaneoticus* (Caldwell & Myers 1990) and *A. galactonotus* (Steindachner, 1864) (Grant et al. 2006, 2017). All species have their distributions limited to the north by the Amazon River, with their longitudinal limits much less clearly defined (Frost 2021).

The true identity of *A. quinquevittatus* has been discussed for almost five decades as well as its distribution and natural history (Silverstone 1975, Myers 1982, Lötters 1988, Caldwell & Myers 1990, Martins & Haddad 1990, Lötters & Vences 2000, Grant et al. 2006, Brown et al. 2011). Initially, *A. quinquevittatus* was included in the "minutus" group and considered a species with highly variable color patterns and widely distributed throughout the Amazon basin (Silverstone 1975). Subsequently, there was an attempt to solve the taxonomic problem involving the "quinquevittatus" complex, when a partial revision of the group was presented, in which species with variations in size and color that had been, erroneously, placed in synonymy with *A. quinquevittatus* were separated into five species (Myers 1982). However, even after this revision, *A. quinquevittatus* was still considered quite variable in color and widely distributed in the Amazon (Grant et al. 2006, Brown et al. 2011). Caldwell & Myers (1990) and Martins & Haddad (1990) warned of the incorrect use of the nomenclature "*Adelphobates quinquevittatus*" and restricted the name "*Adelphobates quinquevittatus* Steindachner" *sensu stricto* to one species of color not so variable in relation to the holotype and restricted to the southwest of the Amazon, especially in the drainage of the Madeira River, and considered that variations regarding the color pattern would be discreet.

Adelphobates quinquevittatus was then redescribed as being a small size dendrobatid, measuring up to approximately 20 mm in body length, blackish body, with five longitudinal stripes that can be either light blue, yellow, greenish or white. The ventral region, from head to cloaca, has a light color (varying between light blue or white, with irregular black marks). The limbs are vibrant orange with the presence of well separated black points and they have small golden spots dorsally located at limb insertions, in addition to the absence of an internal metacarpal tubercle (Caldwell & Myers 1990). This species has diurnal habits and is sheltered in leaf litter (*serapilheira*) or on trunks fallen on the forest floor where females lay their eggs. Hatchling tadpoles are transported individually and deposited in phytotelmata (rainwater-filled plant structures) close to the ground, where they remain to metamorphose, frequently using for this purpose fruit capsules (*ouriços*) of the Brazil nut tree, which accumulate rainwater (Caldwell & Myers 1990, Martins & Haddad 1990, Caldwell

& de Araújo 2004, Rodrigues & Azevedo-Ramos 2004a).

Adelphobates castaneoticus is also a small size species, measuring between 18 and 23 mm. It has a black body with small stripes or white spots on the back and yellow or orange bright spots on the dorsal and ventral surfaces of the limbs (Caldwell & Myers 1990, Rodrigues & Azevedo-Ramos 2004b, Lima & Galatti 2011, Camera & Krinski 2014). However, Caldwell & Myers (1990) warned of geographical variation in the color pattern. This species shares with *A. quinquevittatus*, in addition to the small size, the absence of the internal metacarpal tubercle, as well as the presence of a gold or orange point, dorsally, in the insertions of the limb (Caldwell & Myers 1990). According to IUCN, the distribution of this species is extremely fragmented, being found mainly in the state of Pará, limited in the west by the Tapajós River and extending east to both margins of the Xingu River. However, the spatial distribution data currently presented in the literature is punctual and sparse, leading to uncertainty about its geographical range (Pinto et al. 2016). *Adelphobates castaneoticus* uses as a primary micro-habitat phytotelmata, such as the outer casing of Brazil nut fruits (*ouriços*), for the deposition and development of tadpoles. Tadpoles are extremely aggressive and prone to cannibalism; thus they are usually found alone, especially in *ouriços* and small pools (Caldwell & de Araújo 1998, 2004).

Adelphobates galactonotus is the largest species of the genus, reaching up to 42 mm (snout-to-vent length). It also occurs in eastern Amazonia, between the Amazon, Tapajós and Tocantins rivers, in the states of Pará, Mato Grosso, and Tocantins, extending east nearly to the Maranhão coast (Noonan & Wray 2006, Hoogmoed & Ávila-Pires 2012). Like the others, it is found in leaf litter on the forest floor and occurs frequently in areas with abundant presence of *ouriços*, although it can also be found in areas with some level of environmental impact or transition zones between Cerrado and Amazonian Forest (Estupiñan & Galatti 1999, Hoogmoed & Ávila-Pires 2012). Like *A. castaneoticus*, *A. galactonotus* also uses the *ouriço*, as well as adventitious pools and palm petioles, for tadpole deposition; tadpoles are transported individually mostly by males (Rodrigues et al. 2010). Throughout its distribution this species has several color patterns and may have the back with blocks or points in yellow, orange, red, white, blue, black or brown (Hoogmoed & Ávila-Pires 2012, Rojas et al. 2020).

Based on morphological similarities it was suggested that *A. quinquevittatus* would be a sister species of *A. castaneoticus* (Caldwell & Myers 1990). However, later studies that included genetic data, besides morphology, allocated *A. quinquevittatus* to the basal position of the genus, sister to the clade formed by *A. castaneoticus* and *A. galactonotus* (Grant et al. 2006, 2017). Interestingly, these latter two occur in sympatry in the eastern Amazon, in addition to using similar resources for the deposition and development of tadpoles (Caldwell & Myers 1990, Rodrigues et al. 2010, Hoogmoed & Ávila-Pires 2012). However, especially with respect to *A. castaneoticus*, distributional data are extremely limited, and it is unknown whether they occur in syntopy in the same microhabitats.

Adelphobates species are specialists in forest habitats, however their distributions coincide with the “Arc of Deforestation”, the region with the highest rates of forest loss in the Amazon, promoted by illegal extraction of wood, monoculture, livestock and burning of anthropic origin (Laurance et al. 2001a, b, Fearnside 2005, Alencar et al. 2015, De Faria et al. 2017, Silva Júnior et al. 2021). In recent years, several colossal enterprises, such as the construction of hydroelectric power plants and large scale mineral exploration are taking place in this region and many others are in the planning phase (Fearnside 2016, Latrubesse et al. 2017). These impacts reduce forest environments and consequently the suitable habitat for these species. In this context, the inaccurate determination of the taxonomic identities of the populations and geographical distributions of the *taxa* may induce poor decision making regarding the conservation of these species.

Due to the aforementioned factors not yet clarified regarding the species of *Adelphobates*, we compile occurrence data in the scientific literature, publicly available faunal inventories in legally protected areas, online repositories, as well as field data, with the aim of delimiting with greater accuracy, and in light of updated taxonomic information, the distributions of the three species in this genus. Considering taxonomic changes in *A. quinquevittatus* and the consequent occurrences attributed to this species, as well as the demonstrated inaccuracy of *A. castaneoticus* distribution and its overlap with *A. galactonotus*, such information is urgently necessary.

Through a Maximum Entropy algorithm we model the probable distributions of these three species with the objective of estimating the suitability of the habitats, through climatic, topographical and vegetation cover variables. Then, we use this information to ascertain whether the occurrence records with greater taxonomic uncertainty would be outside the most appropriate areas. Modeling also allowed us to analyze the overlap of the suitable areas for the two sympatric species and to infer if there are different variables affecting the distribution of each of them. Using genetic determination via OTUs, we assessed whether there are independent genetic lineages within nominal species. Additionally, we generated the first dated phylogeny based on a comprehensive sampling of species within the genus.

MATERIALS AND METHODS

Study area

The study area is located south of the Amazon River and covers the main tributaries of its right bank, including the whitewater Juruá, Purus and Madeira rivers, and the clearwater Tapajós, Xingu and Tocantins rivers (Sioli 1984, Ríos-Villamizar et al. 2013). Whitewater rivers have turbid waters, due to the large amount of sediment they transport. They may have their headwaters in the Andes, as is the case of the Madeira River, or in the sedimentary lowlands, such as the Purus and Juruá rivers (Sioli 1984, Latrubesse 2003, Ríos-Villamizar et al. 2013). As for clearwater rivers, their headwaters occur in cratonic areas of the Central Brazilian archaic shield. These rivers are poor in suspended sediments and have crystal clear waters with greenish tones (Sioli 1984, Latrubesse 2003, Ríos-Villamizar et al. 2013).

The Madeira, Tapajós and Xingu rivers are three main tributaries where the sampling was concentrated. The Madeira River is located in the southwestern Amazon, a tropical climate region, with a short dry season (*Am* in the Köppen classification) (Alvares et al. 2013b), an average temperature of 28°C, and relative humidity of 85%. The average precipitation is 2500 to 3000 mm/year, with the rainy season peaking between January and February and the dry season between June and August (Radambrasil 1978). Topography is mostly flat, with altitudes generally below 100 m. The vegetation is mainly composed of different types of *Terra Firme* and floodplain forests, campinaranas and open vegetation such as pastures and savannas (Perigolo et al. 2017, Rosseti et al. 2017, 2018). The region of middle-lower Tapajós River has an *Am* climate (Alvares et al. 2013b), with an average annual temperature varying between 23°C and 29°C (Alvares et al. 2013a). In this basin, the annual rainfall varies between 1800 and 2300 mm (Mohor et al. 2015), with the rainy season between November and April, peaking in March, and the dry season between May and October, being July the least rainy month (Santos et al. 2014, 2015). Altitude varies from approximately 800 m at the sources of the Juruena and Teles-Pires tributaries to approximately 7 m near the mouth (ANA 2011). The vegetation is mainly composed of Ombrophilous Forests in the northern part of the basin and typical Cerrado savannas in the south (Mohor et al. 2015, Farinosi et al. 2019). The Xingu River basin, located further east than the two previously mentioned, also has a *Am* type climate (Alvares et al. 2013b), with average temperatures between 23°C and 29°C (Alvares et al. 2013a) and rates relative humidity, which can vary between 78% and 89% (Brasil 2009). Average annual precipitation varies between 1600 and 2500 mm in the lower reaches of the basin (Brasil 2009). The rainy season occurs between October and April and the dry season between May and September, with March being the wettest month and August the driest (Lucas et al. 2022). The regions at the headwaters of the Xingu River have altitudes of approximately 600 m, while near the mouth it is approximately 4 m (ANA 2011), with slopes of low to medium inclination (Brasil 2009). Most of the region is made up of transitional forests. To the north, rainforests are predominant, while to the south typical Cerrado vegetation is found (ANA 2011, Rizzo et al. 2020).

Sampling

For records of occurrence, as well as for genetic analysis, we sampled a total of 113 individuals (for location details, see Table I), 60 of which were *Adelphobates quinquevittatus* from 13

Table I. Sampling locations and number of individuals of *Adelphobates* (N) collected for this study. Geographic coordinates were not included for the purpose of protecting the species, which are the target of illegal trade.

A. quinquevittatus		***A. galactonotus***		***A. castaneoticus***	
Locality	N	Locality	N	Locality	N
Jirau Left	7	Brasil Novo	5	Santarém	1
Módulo Búfalo	8	Trairão	6	BR163	1
Teotônio Left	7	Morais Almeida	1	Flona Tapajós	5
Jaci Left A	1	Araguaína	1	Mojuí dos Campos	3
Jaci Left B	3			Uruará	4
Jaci Left C	5			Vitória do Xingu	4
Jaci Left D	4			Três Bueiros	6
Jaci Right A	6			Trairão	8
Jaci Right B	3			Morais Almeida	4
Morrinhos	2			Jacareacanga	3
Porto Velho A	5			Paranaíta	1
Porto Velho B	4				
Teotônio Right	5				
	60		13		40

locations in the Madeira River basin, 40 samples of *A. castaneoticus* from 11 locations in the Tapajós - Xingu interfluve, and 13 samples of *A. galactonotus* from the Tapajós - Xingu interfluve and Tocantins basin (Figure 1). Specimens of *A. quinquevittatus* were collected between 2008 and 2018, while *A. castaneoticus* and *A. galactonotus* were collected during field activity in 2018. Tissue samples were collected from both adults (muscle and liver) and tadpoles (tail fin) (Table II), preserved in 99% ethanol and stored in the tissue collection of the Amphibian Ecology Laboratory of the Instituto Nacional de Pesquisas da Amazônia (INPA).

For genetic analyses, we also used 42 fragments of the COI gene, being five of *A. quinquevittatus* generated and made available on Genbank by Grant et al. (2006): DQ502906, DQ502788, DQ502787, DQ502786, DQ502785; 36 of *A. galactonotus* generated and made available on Genbank by Rojas et al. (2020): KU597863, KU597864, KU597865, KU597866, KU597867, KU597868, KU597869, KU597870, KU597871, KU597872, KU597873, KU597855, KU597856, KU597857, KU597858, KU597859, KU597860, KU597861, KU597862, KU597854, KU597853, KU597852, KU597851, KU597850, KU597849, KU597848, KU597847, KU597846, KU597845, KU597844, KU597843, KU597842, KU597841, KU597840, and Lyra et al. (2017): KU494315, KU494314; and one for *A. castaneoticus* generated and made available on Genbank by Grant et al. (2006): DQ502780.

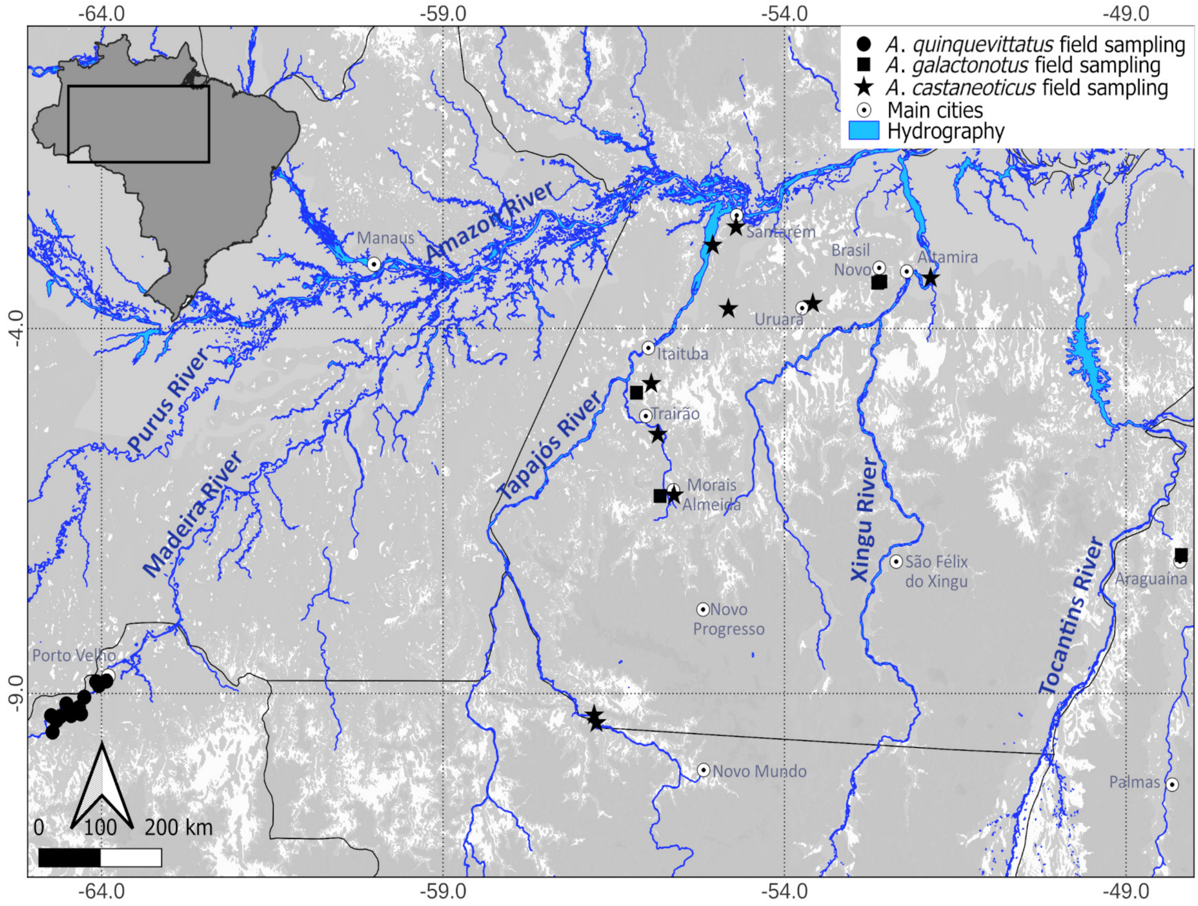

Figure 1. Field sampling for *Adelphobates quinquevittatus* (black dots), *A. castaneoticus* (black stars) and *A. galactonotus* (black squares). White circles correspond to the main municipalities located in the sampling area.

Table II. Type of tissues used for *Adelphobates* DNA extraction.

	A. quin*	***A. gal***	***A. cas***
Adult muscle	9	1	6
Tadpole tail fin	51	12	24
Total	60	13	40

*** de Medeiros et al. 2021.**

DNA extraction, amplification and sequencing

Total DNA was extracted from muscle tissues from adult individuals or tadpole tail fins using Promega® Wizard Extraction Kit (Table II). We used the primers CHMF4 and CHMR4 (Che et al. 2012) for amplification of the COI mitochondrial gene. The ribosomal 16S gene is widely used in interspecific studies as a good phylogenetic marker in Dendrobatidae species (Grant et al. 2006) or even at the intraspecific level in Aromobatidae species (Kaefer et al. 2013, Simões et al. 2014, Maia et al. 2017). However, this gene also seemed to be poorly resolute in phylogeographic studies, at least in the genus *Adelphobates*. This was evidenced by the low haplotypic diversity in the species studied so far (Rojas et al. 2020, de Medeiros et al. 2021), and probably reflects differences in nucleotide substitutions rates, being for COI 1.04 ± 0.27 substitutions per site per 100 millions of years (Myr), and for 16S, 0.07 ± 0.03 substitutions per site per 100 Myr (Mueller 2006). For this reason, we chose the marker COI as it was more informative. We purified and precipitated the amplified fragments and subsequently sequenced them using an ABI 3031x (Applied Biosystems®) sequencer, following the manufacturer's instructions. We edited the sequences obtained with BioEdit v 7.2.5, and the aligned homologous regions using Muscle (Edgar 2004), implemented in Mega X (Kumar et al. 2018).

Identification of Operational Taxonomic Units (OTUs)

For species delimitation, we used the genetic distances of COI fragments from the alignment of 37 unique haplotypes sequenced during this study (eight from *A. castaneoticus*, five from *A. galactonotus*, and 24 from *A. quinquevittatus*) and 30 unique haplotypes available on Genbank (29 from *A. galactonotus*, and one from *A. quinquevittatus*). We used the Assemble Species by Automatic Partitioning (ASAP) online tool and compared the three substitution models available in the tool: JC69, K80 and p-Distance (Puillandre et al. 2021). ASAP is a method to delimit species based on genetic distances and is recommended for analysis from a single locus (Puillandre et al. 2021). We acknowledge that a phylogenetic tree built from a single locus can differ considerably from the species tree (Tang et al. 2014), but our objective was to estimate the number of possible OTUs, considering that at least two of the species of *Adelphobates* have already shown genetically structured populations (Rojas et al. 2020, de Medeiros et al. 2021).

Estimation of Divergence Times

We estimated divergence times between species via *Beast implemented in Beast 2.6.3 (Bouckaert et al. 2019), using the COI gene. For this analysis, the best nucleotide substitution model was defined by PartitionFinder 2.1.1 (Lanfear et al. 2017). The Molecular Clock Model "Relaxed Clock Lognormal" and the prior "Coalescent Constant Population" were also applied in the analysis. The nucleotide substitution rate applied for COI was 1.04 ± 0.27 substitutions per site per 100 Myr following the proposal by Mueller (2006). As calibration points, we used the average and confidence intervals proposed by Santos et al. (2009), which dated the node of the Dendrobatinae subfamily at 28.74 ± 4.45 million years ago (Ma) and the node of the genus *Adelphobates* at 10 ± 2.5 Ma. We performed two independent runs of two 4 x 10^8 generations, sampling trees every 5,000 generations and discarding 10% of the total trees as burn-in. We combined both runnings using the LogCombiner tool (Rambaut & Drummond 2014), executed at Beast 2.6.3 (Bouckaert et al. 2019), with parameter convergence verified using tracer 1.7. Finally, we used Figtree (Rambaut & Drummond 2012) to view and edit the tree.

For divergence times estimates we used COI sequences available on Genbank for a representative of each genus of the Dendrobatinae subfamily: *Oophaga histrionica* DQ502816; *O. granulifera* HQ841107; *O. pumilio* DQ502907; *Excidobates mysteriosus* MF614318; *Dendrobates tinctorius* MF069439; *Andinobates victimatus* MF614296; *Phyllobates terribilis* DQ502861. The species *Minyobates steyermarki*, belonging to a monotypic sister genus of *Adelphobates* (Guillory et al. 2019), was not included in the analysis because the only sequence available on Genbank corresponds to a non-homologous fragment.

Survey of occurrence and distribution data

For elaboration of distribution maps, we compiled occurrence data recorded in the scientific literature, such as peer-reviewed articles, notes and checklists, as well as publicly available faunal reports on legally protected conservation areas, and other types of faunal surveys. We only used data on occurrence that included a photographic record, morphological description, or identification by expert taxonomists. We choose not to include in the map reports or articles that only mention a possible occurrence in a given location. This was particularly important for *A. quinquevittatus*, considering the problematic taxonomic history of the species. We represent, with a yellow star, some occurrences attributed to *A. quinquevittatus* but which present notable discrepancy with the most recent taxonomic description (Caldwell & Myers 1990), especially in relation to spot patterns and coloration. We also obtained occurrence data for the three species during field activities, as well as from samples donated by other researchers, whose identification was confirmed through COI gene sequencing.

We produced the distribution map using QGIS 3.20 Odense, and the vector and raster layers available on electronic sites from Instituto Brasileiro de Geografia e Estatística (IBGE – https://www.ibge.gov.br) and Ministério do Meio Ambiente e Mudança do Clima (MMA - https://www.gov.br/mma). The representations of *Adelphobates* species distributions were defined by Minimum Convex Polygon. We also used the distribution vector layers provided by IUCN to compare the distributions prior to the present study.

Distribution Modeling

For distribution modeling, we used the same data set of the distribution map. When two occurrences were less than 5 km apart, we eliminated one of them to avoid the model overlapping, giving preference to points with some genetic information confirming taxonomic determination (Radosavljevic & Anderson 2014). We also removed from modeling occurrences of specimens different from the current description in color pattern.

To test the effect of environmental variables on the suitability of habitat and distribution of species, we modeled their distributions using bioclimatic and elevation data available in the WorldClim database (http://www.worldclim.org), along with the data on vegetation cover available on EarthEnv (https://www.earthenv.org/landcover). For all variables, we used

30” layers of resolution (approximately 1 km). Initially, we had 19 bioclimatic variables (Bio 1 - Bio 19), elevation, seven historical climate predictors (maximum, minimum and medium temperature, precipitation, wind velocity, water vapor pressure and solar radiation) and six vegetation variables (perennial trees of wide leaves, deciduous trees of wide leaves, perennial/deciduous trees of thin leaves, mixed forests, shrubs and herbaceous vegetation).

After trimming the mask of all variables to the area of interest in QGIS, Brazilian Legal Amazon, we excluded from the model variables with more than 70% correlation, based on the Pearson’s correlation coefficient (r). With the selected independent layers we performed a Principal Component Analysis (PCA), to identify those variables that contribute most to the environmental variability of the area. For both analyzes, the packages “raster” (Hijmans et al. 2015), “rgdal” (Bivand et al. 2015) and “vegan” (Oksanen et al. 2007) were installed in R environment (R Core Team 2022). Finally, we got the 11 independent layers that contributed most to the area of interest, namely: annual temperature range (Bio 7), average moist quarter temperature (Bio 8), warmer quarter precipitation (Bio 18), colder quarter precipitation (Bio 19), elevation, water vapor pressure for December - beginning of the rainy season to the region (Vapr 12), solar radiation for April - final from the rainy season to the region (Srad 4), perennial trees of wide leaves (PTWL), mixed forests (MF), shrubs (S) and herbaceous vegetation (HV).

We performed the distribution modeling using the Maximum Entropy algorithm, Maxent 3.4.4 (Phillips et al. 2017), with environmental variables and previously selected points of occurrence as inputs. The maximum number parameter of interactions was changed to 5,000, the percentage of random tests for 30% and 15 bootstrap replicates were applied. We considered satisfactory for a more careful adjustment of the model Area Under Curve (AUC) values above 0.7, indicating that the estimated distribution is not random, but determined by the selected variables (Phillips et al. 2006).

We cut the final map obtained from the average replications by the minimum threshold value (Minimum training presence logistics threshold). We considered the presence omission test value lower than 0.15 and $p < 0.05$ to be satisfactory. A binary map of presence or absence was thus generated, which was finally multiplied by the output layer of Maxent 3.4.4 (Phillips et al. 2017) to generate the habitat suitability map and thus predict the potential distribution of the species. Furthermore, we considered the minimum threshold value as the most appropriate choice for *Adelphobates* species, since it allowed to include low suitability values in the model when a species is present (Rodríguez-Rodríguez et al. 2020). In the case of *A. castaneoticus*, occurrence information is extremely scarce, and *A. quinquevittatus* is still subject to potential taxonomic problems. Thus, the choice of this threshold allows the elaboration of a less restrictive model that can broadly cover the potential areas of occurrence.

RESULTS

Identification of Operational Taxonomic Units (OTUs) and divergence times

We recovered the three species of *Adelphobates* described by the current taxonomy using ASAP, considering the three replacement models provided by the tool (JC69, K80 and p-distance) and *p* values less than 0.001. Additionally, we did not detect cryptic intraspecific lineages under each of the three nominal species. The dated tree based on 67 unique haplotypes of COI confirmed *A. quinquevittatus* in the basal position of the genus and *A. castaneoticus* and

A. galactonotus as sister species. The divergence between *Adelphobates* and *Oophaga*, the phylogenetically closest genus in our analysis, occurred on average 18.51 Ma (24.9-12.5 Ma 95% HPD). *Adelphobates quinquevittatus* diverged from the clade formed by *A. castaneoticus* and *A. galactonotus* an average of 12.63 Ma (18.2-7.0 Ma 95% HPD), and average divergence time for these last two is 6.99 Ma (11.3-2.7 Ma 95% HPD) (Figure 2).

Distribution

Our distribution map confirmed the occurrence of all three species limited to the area south of the Amazon River. Using records based on confirmed identification of photographs, *Adelphobates quinquevittatus* is not demonstrably present in Bolivia, Peru, Ecuador, or Colombia, although its distribution is likely to enter Bolivian territory (Figures 3 and 4). Furthermore, this species has not been confirmed in far western Brazil and is found predominantly in the south-central Amazon, mostly in the Madeira river basin. Westernmost specimens purportedly of this species in the mid and upper Purus and Juruá basins show noteworthy differences relative to the description of *A. quinquevittatus* stricto sensu (Figures 3 and 4), such as less vibrant limbs color, as well as points in the limbs not being black, borders of the points in the limbs not being smooth and uniform and the presence of spots on the distal tip of the snout, apparent absence of golden spots on the insertions of the posterior and previous limbs (Figure 6a,

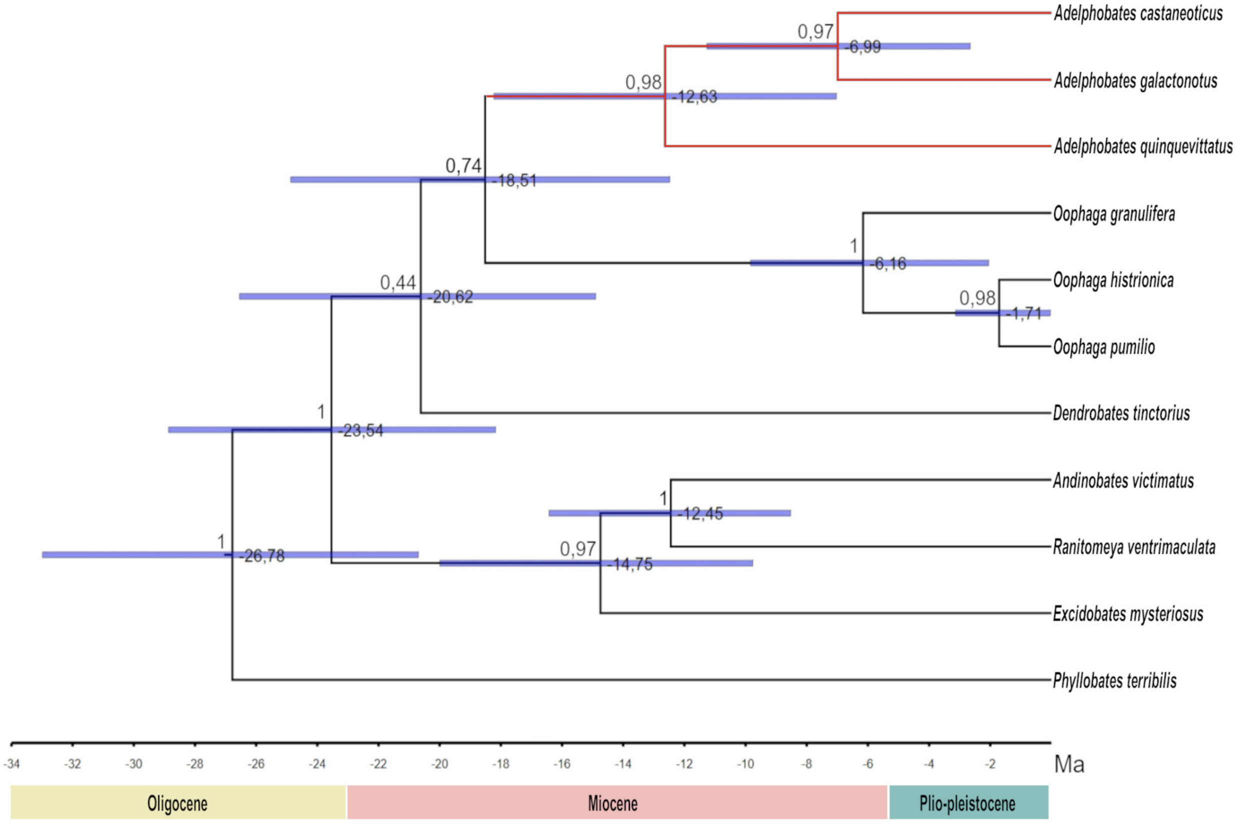

Figure 2. Divergence times among *Adelphobates* species, obtained from *BEAST, using 67 unique haplotypes of COI mtDNA. The values above the nodes correspond to the posterior probability, and values below the nodes to the average node height (age). Horizontal bars indicate the confidence intervals for the divergence times (95% HPD). Representatives of other Dendrobatinae subfamily genera were used as outgroups.

b, c). We refer to these as *Adelphobates* aff. *quinquevittatus*. Another atypical specimen also identified as *Adelphobates* aff. *quinquevittatus* in the extreme northeast of the distribution shows further color differences (Figure 6d) and probably represents another taxon. Thus, based on current information, the distribution *A. quinquevittatus* is delimited by the Amazon River to the north, without reaching its margin, the Purus to the west, Juruena to the east, and the Cerrado biome to the south.

The distribution of *A. castaneoticus* is limited to the north by the Amazon River, west by the lower Tapajós, and south by the Teles Pires (a right bank tributary of the upper Tapajós); however, it appears to be absent on the middle Tapajós in the Jamanxim-Teles Pires interfluve. Its distribution extends to the east to both margins of the Xingu River, but apparently not reaching far beyond that. During our field work, we documented some of the first records of the species midway between the Tapajós and Xingu rivers, suggesting that it occurs continuously in this region, apparently surrounded geographically by *A. galactonotus* (Figures 3 and 4).

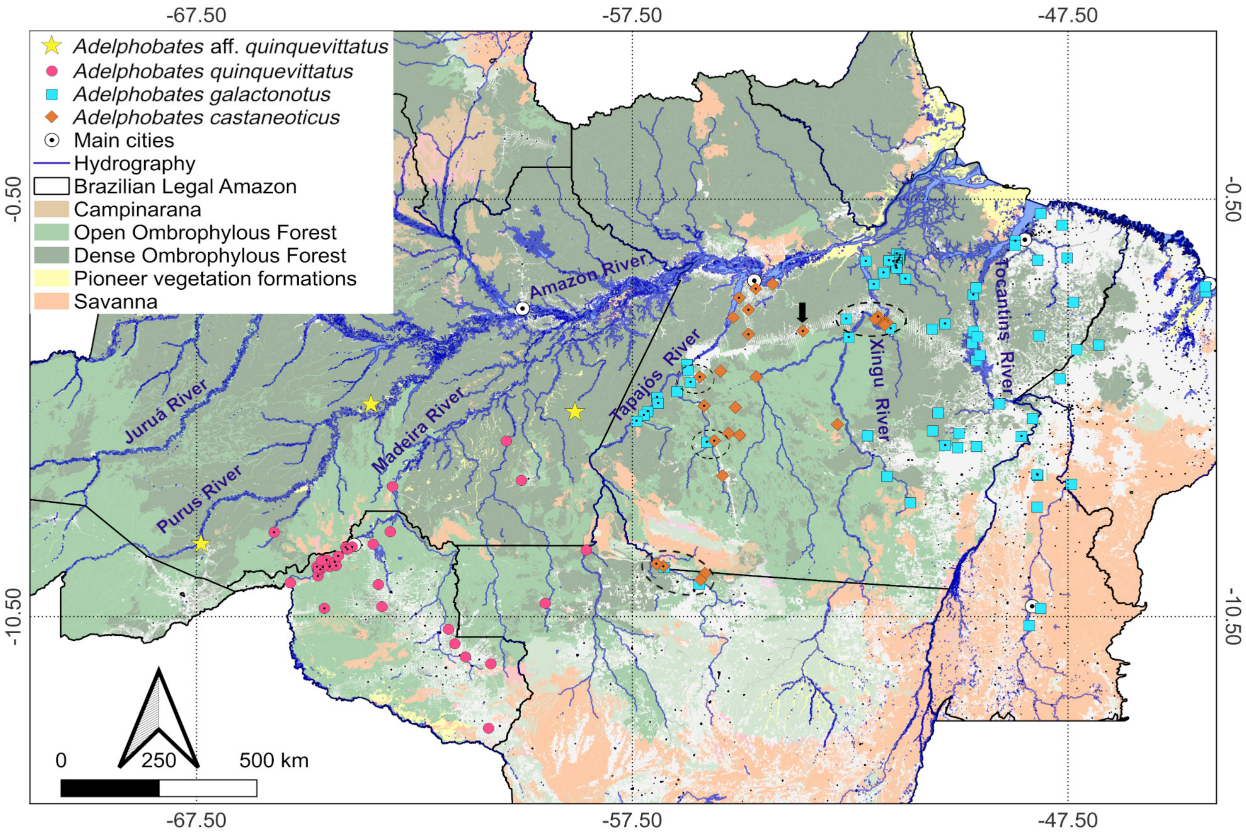

Figure 3. Distribution of *Adelphobates* species proposed by the present study. The pink dots, orange rhombus and blue squares correspond to the confirmed occurrences of *Adelphobates quinquevittatus*, *A. castaneoticus* and *A. galactonotus* respectively, identified by the survey carried out in this study. Stars represent putative *A. quinquevittatus* with some marked phenotypic variation. The black arrow indicates the unprecedented occurrence recorded for *A. castaneoticus* in the municipality of Uruará, Pará state. The circles with dashed lines indicate the four contact zones between *A. castaneoticus* and *A. galactonotus* distributions. Shapes with black dots inside are also identified by DNA sequencing. Stars represent putative *A. quinquevittatus* with some marked phenotypic variation. Background colors reflect different types of vegetation.

For *Adelphobates galactonotus*, the mapped points describe an area that surrounds and at least partially overlaps that of *A. castaneoticus*, where very few records have been documented. The distribution occupies much of southeastern Amazonia east of the Tapajós River, extending east and south beyond the limits of the Amazon into regions dominated by drier and more open vegetation types (Figures 3 and 4).

Modeling of habitat suitability

The distribution modeling also confirmed the highest habitat suitability south of the Amazon River for the three species (Figure 5). AUC values were equal to 0.97 ± 0.02 for *A. quinquevittatus*, 0.95 ± 0.02 for *A. castaneoticus* and 0.92 ± 0.02 for *A. galactonotus*, which resulted in excellent adjustments of the model considering the acceptable cut-off of 0.7 (Phillips et al. 2006). In addition to the AUC values, the omission test values were 0.09, 0.06 and 0.04 for *A. quinquevittatus*, *A. castaneoticus* and *A. galactonotus*, respectively, and the *p* values of the models were less than 0.001 even for other thresholds.

Six variables contributed approximately 90% of the total model for each species (Table III). Three variables were common to the three species, namely: Srad 4, Vapr 12 and Bio 19. HV was one of the six most important variables shared exclusively between *A. quinquevittatus* and *A. castaneoticus*. Bio 18 was exclusively shared between *A. castaneoticus* and *A. galactonotus*, and PTWL shared between *A. quinquevittatus* and *A. galactonotus*. Among the six most important for each species, each presented only one exclusive variable, being Bio

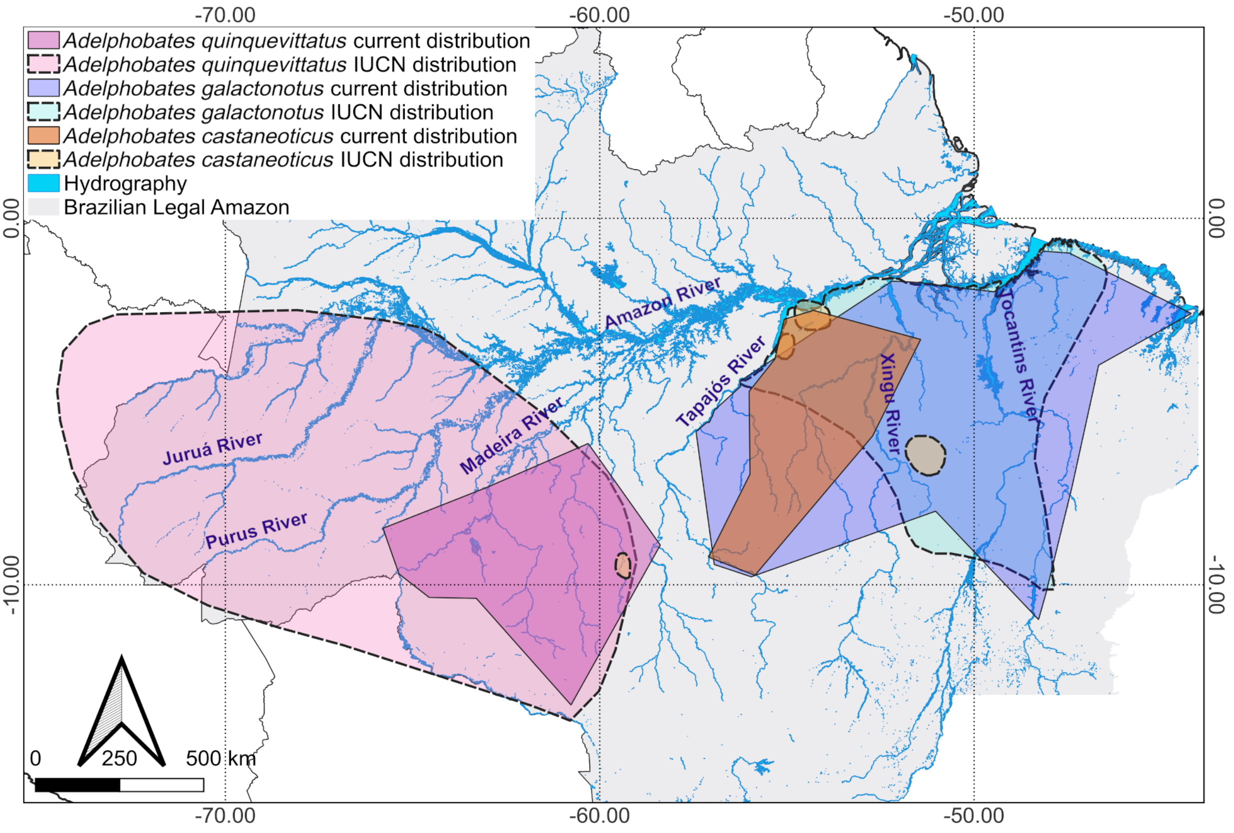

Figure 4. Distribution of *Adelphobates* species proposed by IUCN compared to the present study. Polygons correspond to *Adelphobates quinquevittatus* (pink), *A. castaneoticus* (orange) and *A. galactonotus* (blue).

7 the most important for *A. quinquevittatus*, MF the most important for *A. castaneoticus*, and Bio 8 the third most important for *A. galactonotus*.

Adelphobates quinquevittatus distribution modeling recovered the same pattern of confirmed occurrences, in which the mid- and upper-Madeira River basin showed the highest suitability. Adjacent areas, with fewer occurrences, were also less suitable. Modeling also did not indicate suitable areas in the far west

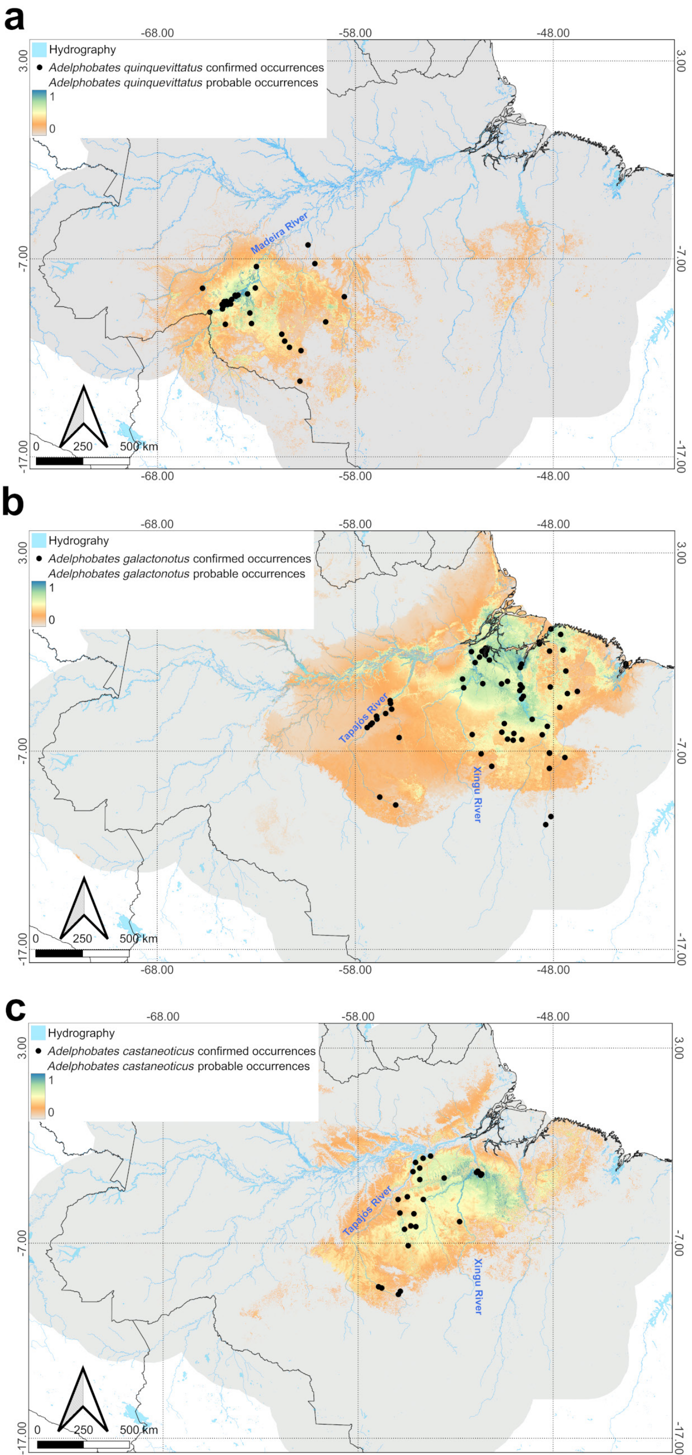

Figure 5. Environmental habitat suitability for the occurrence of (a) *Adelphobates quinquevittatus*, (b) *A. castaneoticus*, and (c) *A. galactonotus* based on bioclimatic, historical climatic, elevation, and vegetation data. Black dots represent occurrence data obtained from field-based samples and in confirmed occurrence data from the literature.

of the Amazon, as well as in much of Acre and Peru, but pointed to occurrences on the border with the Bolivian Amazon (Figure 5a). Regarding *A. castaneoticus* and *A. galactonotus*, sympatric species, the modeling considered unsuitable or poor many areas with confirmed occurrences. In the case of *A. galactonotus*, all the western and extreme southern occurrences lie in poorly suitable areas. For *A. castaneoticus*, most occurrence records are in areas of intermediate suitability, while the most suitable areas have few confirmed records. Still, considering only the most suitable areas for both species, there is a wide overlap especially along the right margin of the Xingu River (Figure 5b, c).

DISCUSSION

Delimitation of OTUs through ASAP recovered the three species of *Adelphobates* formally described, demonstrating that, despite genetically structured populations in *A. quinquevittatus* (de Medeiros et al. 2021) and *A. galactonotus* (Rojas et al. 2020), those populations would not represent candidate species, according to the marker used. Considering the absence of independent intraspecific lineages, our distribution map confirmed the occurrence of the three species of *Adelphobates* south of the Amazon River. However, significant differences in distributions were found when compared to the maps or descriptions most frequently used in the literature (Figure 4) (Rodrigues & Azevedo-Ramos 2004a, b, Rodrigues et al. 2010, Frost 2021).

Species distributions

Adelphobates quinquevittatus

According to the distribution provided by IUCN (Rodrigues & Azevedo-Ramos 2004a), *A. quinquevittatus* would extend through the Brazilian state of Acre and western Amazonas, to Iquitos, Peru, and would also enter considerably in Bolivian territory. According to Frost (2021), there would be confirmed occurrences only from the Madeira River Basin in Rondônia and Amazonas, and also in the Pando Department in Bolivia. However, due to changes in *A. quinquevittatus* classification, these distributions no longer apply. Occurrence records prior to the taxonomic review of Caldwell & Myers (1990) to Peru, Ecuador and even Guyana, which presented morphological description or photographic record (Silverstone 1975, Meede 1980, Myers 1982, Schulte 1986, 1999,

Table III. Percent-based contribution of the six main variables (which correspond to approximately 90% of the total model) for species distribution models obtained by maximum entropy algorithm. The variables are arranged from highest to lowest contribution.

Order of importance	*A. quinquevittatus*		*A. galactonotus*		*A. castaneoticus*	
	Variable	Importance	Variable	Importance	Variable	Importance
1	Bio 7	35.9035	Bio 19	27.4513	MF	38.1678
2	Srad 4	17.2272	Bio 18	18.9283	Srad 4	12.239
3	Vapr 12	15.8257	Bio 8	15.78	Vapr 12	11.7376
4	HV	8.8461	Srad 4	11.1927	Bio 19	11.1311
5	Bio 19	7.2767	Vapr 12	9.781	HV	8.8461
6	PTWL	5.5913	PTWL	4.666	Bio 18	6.9263

Lötters 1988), were later attributed to other species, especially from *Ranitomeya* (Silverstone 1975, Meede 1980, Myers 1982, Schulte 1986, 1999, Lötters 1988, Lötters & Vences 2000, Grant et al. 2006, Brown et al. 2011). The occurrence of *A. quinquevittatus* in two localities of Peru, Iquitos and Loreto (Schulte 1999), for example, had already been questioned by Lötters & Vences (2000) given the absence of photographic and material record stored of these specimens. However, Frost (2021) mentions that Lötters et al. (2007) provided a report to these occurrences, making this information ambiguous. What Lötters et al. (2007) really claim is that although there has been a taxonomic review by clarifying *A. quinquevittatus*'s "identity", identification problems still persist and this species continues to be confused with cryptic species of *Ranitomeya*, especially in southeastern Peru and Guyana. The image purported to be *A. quinquevittatus* from Loreto, Peru (Schulte 1999), does not resemble in any aspect the description of Caldwell & Myers (1990). For this reason we excluded occurrences for Peru from our distribution map.

The possibility of *A. quinquevittatus* occurrence in the Department of Pando, Bolivia, bordering the state of Rondônia in Brazil, has already been suggested (De la Riva 1990, De la Riva et al. 2000, De la Riva & Reichle 2014). In addition, Lötters et al. (2007) mention a personal communication of Reichle S to Jungfer KH on an occurrence in this region. This occurrence is totally plausible given the similarity of the environment, the absence of physical barriers and, of course, to the fact that species do not recognize political boundaries. However, as the occurrence has not yet been formally registered, this has not been included in our map.

According to our results, *A. quinquevittatus* has a reduced distribution and is limited to the easternmost portion compared to the distribution provided by IUCN (Rodrigues & Azevedo-Ramos 2004a) (Figures 3 and 4). In addition to the occurrences in the Madeira River basin, in the states of Amazonas and Rondônia, we found records of occurrence in the state of Mato Grosso, covering the Aripuanã River basin (Vogt et al. 2007, São-Pedro et al. 2009), tributary of the right margin of the Madeira River, and Juruena River (Bernarde & Machado 2009), tributary of the left margin of the Tapajós River. Most records of occurrence that affected knowledge about the distribution of this species are in faunal surveys of Conservation Units (UCs), which consist of restricted diffusion informal publications. Some of these fauna survey reports are not even available on the websites of their respective UCs. In addition, in our map proposal, the distribution of this species did not reach the western Amazon, the two westernmost records (upper Juruá and Purus Rivers) showing remarkable morphological differences in relation to *A. quinquevittatus* sensu stricto (Caldwell & Myers 1990). Therefore, it is very likely that these specimens are not *A. quinquevittatus*.

One of the few herpetofaunal surveys carried out on the upper Juruá River mentions the occurrence of *A. quinquevittatus*, but there is no photographic record for a comparison of coloring (Bernarde et al. 2011). In this same survey there is a specimen identified as *Adelphobates* sp. n. (Figure 6a) which resembles another identified as *A. quinquevittatus* in the upper Purus River (Figure 6c) in Brown et al. (2011). Both specimens have less brilliant limbs, as well as less dark points, edges of the dark spots on the limbs are not smooth and unifom, and as well as presence of spots on the distal tip of the snout, which are absent in *A. quinquevittatus*. In addition to these differences, apparently the golden spots on the insertions of the hind and front limbs are absent. In the Lower Purus River, a specimen identified as *A. quinquevittatus* also differs

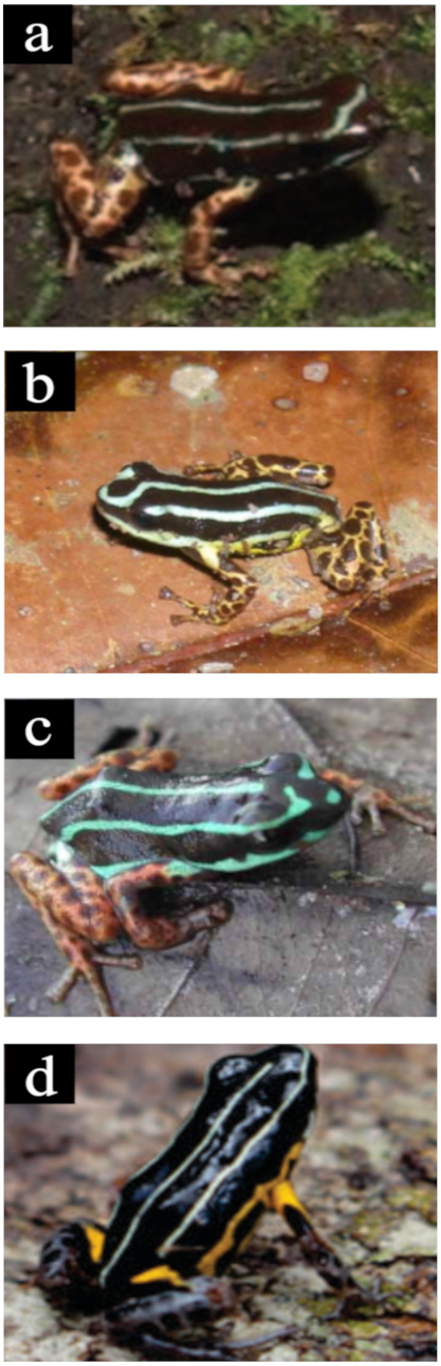

Figure 6. a. *Adelphobates* sp. n. in Igarapé Esperança at Resex Riozinho da Liberdade, Acre, (the article mentions the occurrence of *A. quinquevittatus* as well, but lacks corresponding photograph), Bernarde et al. (2011); b. *A. quinquevittatus* in Herpetofauna RDSU, Carauari-AM, Waldez & Souza (2008); c. *A. quinquevittatus* near the municipality of Boca do Acre, Amazonas, by Paulo Roberto Melo-Sampaio in Brown et al. (2011); d. *A.* aff. *quinquevittatus* at Estação Ecológica do Alto Maués in Ferreira (2021).

considerably in color pattern (Figure 6b) (Waldez & Souza 2008). In ESEC Alto Maués, extreme northeast of probable distribution, a specimen identified as *A.* aff. *quinquevittatus* also has remarkable variations regarding color, especially of the limbs, as well as the points in the limbs, in addition to the coloration of the side bands to the body (Ferreira 2021). Thus, the distribution of *A. quinquevittatus* is currently located in the south-central Amazon, not reaching the right margin of the Amazonas River to the north and being limited by the Purus River to the west, by the Juruena River to the east and by the Cerrado (non-Amazonian savannas), to the south (Figure 4).

In some of the localities of the Brazilian Amazon, where specimens that were identified as *A. quinquevittatus* have variation in color, there are species of *Ranitomeya* with confirmed occurrence, some of them with similar color pattern. This is the case of *R. toraro* (Boca do Acre; Upper Juruá River), *R. sirensis* (Rio Branco, Upper Purus River) and *R. ventrimaculata* (Taraucá, Acre), as well as *R. yavaricola*, with possible occurrence at the border between the district of Loreto in Peru, and the extreme west of Amazonas, in Brazil (Brown et al. 2011) (Figure 7). Although this species is originally described with limbs completely bronze (Perez-Peña et al. 2010), some morphotypes found in online image repositories have a pattern of stripes and dots similar to the alleged *A. quinquevittatus* found in the Upper Juruá River and Upper Purus River (Figure 7). GBIF (Global Biodiversity Information Facility - GBIF.org) database mentions the occurrence of *R. yavaricola* in the state of Amazonas, near the course of the Middle Juruá River, although there are no photos of the specimens. According to Caldwell & Myers (1990), during the field activities in the state of Rondônia, no other adult dendrobatids were found in the locations where *A. quinquevittatus*

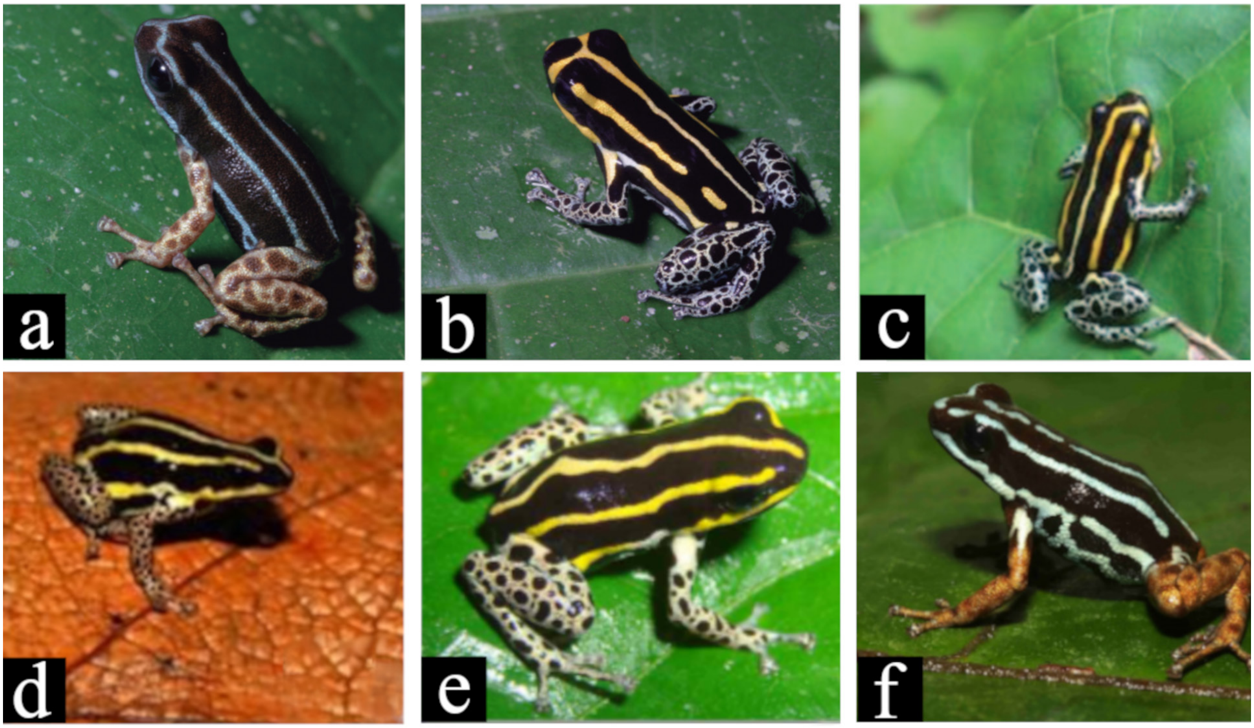

Figure 7. a and b: Sympatric *Ranitomeya toraro* and *R.* cf. *cyanovittata* at RESEX Riozinho da Liberdade, Acre, photos by Taran Grant in Grant et al. (2017); c. *R. ventrimaculata* at Resex Riozinho da Liberdade, Acre, Bernarde et al. (2011); d. *R. toraro* at Parque Estadual Chandless, Acre, Silva (2015); e. *R. sirensis* at Rio Branco, Acre, in Brown et al. (2011); f. *R. yavaricola* by Giuseppe Gagliardi at http://www.dendrowiki.org.

were recorded. Similarly, tadpoles from other dendrobatids were not found in *ouriços* where *A. quinquevittatus* tadpoles were collected during the samples of de Medeiros et al. (2021). On the other hand, the co-occurrence of *Ranitomeya* species is common in the same area. Therefore, identifying specimens with similar color patterns such as *A. quinquevittatus* requires caution. Identification in regions where there are already other similar species of confirmed *Ranitomeya* can benefit from the incorporation of ecological data, considering that there are differences in the use of resources especially for the deposition of eggs and development of tadpoles; vocalization, since apparently if the species of *Adelphobates* vocalize, it is inaudible (Caldwell & Myers 1990), unlike some *Ranitomeya* species (Brown et al. 2011); habitat, since *Adelphobates* is predominantly terrestrial, while some species of *Ranitomeya* are arboreal (Brown et al. 2011); in addition to the use of molecular data. Added to this, the fact that the distribution modeling of *A. quinquevittatus* did not identify as suitable areas where there are records of specimens with notable phenotypic variation, indicates that there is a need for a more cautious taxonomic analysis and that these specimens probably do not belong to *A. quinquevittatus*. Although habitat suitability modeling has its limitations, the map we generated presented reliable results, given that besides the high value of AUC, the omission error test showed a low value which indicates a small probability of type II errors, that is, of false absence in occupied areas.

Adelphobates castaneoticus

Adelphobates castaneoticus is the least-known species of the genus in many aspects, including its distribution. This may be a consequence of the apparent low detectability of the species in the field. According to Caldwell & Myers (1990), four observers sampled a forest environment almost every day during two months, but only 15 adults, two juveniles and 36 tadpoles were collected. According to IUCN (Rodrigues & Azevedo-Ramos 2004b), the distribution of *A. castaneoticus* is disjunct, forming four areas: two of them on the right margin of the Tapajós River, near the confluence with the Amazon River; one on the left margin of the Juruena River; and one on the right margin of the Middle Xingu River (Figure 4). Frost (2021) mentions a few known occurrences, such as the holotype collected in Volta Grande of the Xingu River, and other specimens from Taperinha (near the confluence of the right margin of the Tapajós River with the Amazonas River) and Novo Progresso, on the right margin of the Jamanxim River. The map we propose to *A. castaneoticus* shows a less fragmented distribution compared to the IUCN and broader when compared to Frost (2021) (Figure 4).

Based on our survey over a large area of the Xingu-Tapajós interfluve, *A. castaneoticus* does occur in the region. This interfluve historically consisted of a “blank” area in the internationally published herpetofauna surveys, because in addition to the difficult access, this area is primarily composed of indigenous lands mosaics (Barros, unpublished data). Thus, the records of occurrence mainly derive from faunal surveys conducted in UCs (Barros et al. 2014), in addition to the unprecedented occurrence we recorded in the municipality of Uruará, almost exactly in the intermediate position of the Tapajós and Xingu Rivers, during the field surveys of the present study. The two northernmost polygons in the map provided by IUCN were also confirmed on our map. However, in relation to the southernmost polygons, we found no occurrence that confirms the species in these locations. The most western of these is in the Aripuanã River basin in the state of Mato Grosso (Rodrigues & Azevedo-Ramos 2004b) and coincides with the distribution of *A. quinquevittatus* (CNEC 2002, São-Pedro et al. 2009). The polygon located more to the east lies on the right margin of the Middle Xingu River, near São Félix do Xingu, and although we found some mentions in reports, we did not find the original document where it appears and for this reason we do not include it in our distribution proposal. More recent records also indicated the presence of *A. castaneoticus* in the Teles Pires Basin, *Cristalino* region, between the states of Mato Grosso and Pará (Caldwell 2010, Rodrigues et al. 2015). During our samples on the field, we recorded occurrences along the right margin from the Tapajós River to the south, but when we reached the confluence with the Jamanxim River, the distribution of *A. castaneoticus* followed only the right margin of this river, not occurring in the Tapajós-Jamanxim interfluve.

While confirmed occurrences of *A. castaneoticus* exist along the right margin of the Xingu River, specifically in the Volta Grande region, these forest fragments have exhibited considerable degradation, marked by evidence of fires and felled trees. In a broader context, our observations of *A. castaneoticus* specimens collected from various localities reveal a noteworthy pattern. These specimens were predominantly found in well-preserved fragments with few discernible signs of ecological disruption (Barros et al. 2014, Rodrigues et al. 2015, Torralvo et al. 2022). This trend suggests vulnerability of this species to environmental degradation, a threat that has become more pronounced in recent years in this region.

Adelphobates galactonotus

The distribution of *Adelphobates galactonotus*, as proposed by the IUCN (Rodrigues et al. 2010), had previously undergone a comprehensive revision by Hoogmoed & Ávila-Pires (2012). This revision resulted in a new distribution map that extended to the Maranhão coast, the northern states of Mato Grosso within the Cristalino region, and Tocantins, particularly in the Tocantins River basin. The primary modification in our revised distribution proposal involves the inclusion of locations along the right bank of the Tapajós River, in the interfluvial region with the Jamanxim River, and the addition of occurrences in the central region of Tocantins, specifically Palmas.

Apparently the distribution of *A. castaneoticus* is spatially concentrated and surrounded by the distribution of *A. galactonotus*. In fact, field surveys did not detect both species in the same locality, indicating that the distributions despite being sympatric are probably not syntopic. Often distributions were interspersed on the right margin of the Tapajós River and along the Transamazônica road (between the Tapajós and Xingu Rivers) where our field sampling was concentrated. In the field, three distributional "contact zones" were identified, all in Pará State: in Itaituba, where the species are separated by the Jamanxim River; in the municipality of Trairão; and another between the municipalities of Brasil Novo and Vitória do Xingu. Considering the occurrence records, another contact zone exists between southern Pará and northern Mato Grosso, in the Cristalino region (Figure 3). This information reflects the importance of field sampling that, by enabling the recording of new occurrences, contributes to a more accurate determination of geographical distributions and also to the formulation and testing of ecological hypotheses.

Forest management by pre-Columbian societies (Levis et al. 2017) may have affected the distributions of these frogs. There is a high density of Brazil nuts (*Bertholletia excelsa*) near to the margins of the rivers, forming large stands called "*castanhais*" (Cohn-Haft et al. 2007, Levis et al. 2017, Rossetti et al. 2018), with evidence of anthropic origins (Scoles & Gribel 2011, 2015, Shepard & Ramirez 2011, Ribeiro et al. 2014). Given that *ouriços* of Brazil nuts are often used by *Adelphobates* species for the deposition and development of tadpoles, the formation and dispersal of nuts by humans may have been important to broaden the distribution of these species. The existence of these *castanhais* is recent considering the evolutionary history of the species. The divergence between *A. castaneoticus* and *A. galactonotus* dated here was an average of 6.8 Ma (3.11 – 10.68 Ma 95% HPD), a much older time than expected for human occupations in South America, then a multifactorial approach to understanding the relationships between these two species should not be discarded. In the presence of competition, it is plausible that its intensity was accentuated during colder and drier periods when forest habitats were reduced (Haffer 1969, Rocha & Kaefer 2019). Conversely, in warmer and more humid conditions, the opportunities for spatial occupation may have expanded with the broadening of forest environments (Haffer 1969, Rocha & Kaefer 2019). The expansion of *castanhais* by human populations, and the resulting increase in suitable sites for tadpole deposition and development, could have potentially influenced interspecific competition. Nevertheless, these hypotheses remain untested and warrant further in-depth investigation.

The distribution modeling of *A. galactonotus* resulted in large areas with a high density of confirmed occurrences, but low suitability, especially on the right margin of the Tapajós River. These occurrences are also isolated by an extensive area that is poorly suited in the Tapajós-Xingu interfluve, where in fact few records have been confirmed. The occurrences in the central area of the state of Tocantins were outside the predicted area for distribution, which would constitute an error of omission (type II error). However, the value of the omission test (0.06) was well below the recommended as adequate (0.15), almost being the conservative limit (0.05). This indicates that despite a possible omission error, it lies within a margin predicted by the modeling. The area of highest suitability for this species is concentrated in the Xingu-Tocantins interfluve, where occurrence records indicate high density of records. The presence of *A. galactonotus* in less suitable areas may be attributed to several non-excludable factors, including the possibility that the sample obtained may not comprehensively represent the species' true distribution. Biases can also be introduced by the modeling process, even when the model appears to fit well based on AUC values and when consistent results are achieved across various tests. Furthermore, habitat suitability is determined based on current data, and a given species' distribution can be influenced by historical and ecological processes, such as the presence of physical barriers, niche boundaries, environmental changes, and ecological interactions. In some instances, isolated populations in areas of low suitability might represent remnants of more suitable environments from the past, or they could be the outcome of ecological interactions, including interspecific competition, which may lead less competitive species to occupy less suitable areas. It is worth noting that these hypotheses have yet to be rigorously tested.

The distribution modeling of *A. castaneoticus* resulted in intermediate to high suitability in the Tapajós-Xingu interfluve, a pattern that contrasts with *A. galactonotus*. This divergence underscores that, despite being sister species and sharing sympatric ranges, while possessing relatively similar general biology, there exist discernible distinctions in their ecological requirements, resulting in some degree of niche differentiation. Nevertheless, on the right margin of the Xingu River, there is a substantial area of high suitability, which coincides with regions also deemed suitable for *A. galactonotus*. Despite the high suitability, confirmed occurrences in this specific area are scarce, with one of the exceptions being documented during a fauna survey conducted for the Environmental Impact Study for the construction of the Belo Monte hydroelectric plant. During field investigations, we conducted sampling up to a distance of approximately 60 km from the right margin of the Xingu River, visiting *castanhais* sites that were identified. However, probably due to the severe environmental degradation in this area, we failed to locate any specimens.

Interspecific interactions

In Dendrobatidae, documented instances of competitive interactions have been observed between sympatric and parapatric species, as well as cases of intraspecific competition (Twomey et al. 2008, Ryan & Barry 2011, Fouilloux et al. 2022). These interactions typically revolve around the competition for suitable sites for tadpole deposition and development, which are critical resources for individual fitness. In this context, it is plausible that *A. castaneoticus* may have enjoyed a competitive advantage over *A. galactonotus*, either in the past or in the present, potentially leading the latter to occupy peripheral areas with lower suitability. This could offer an explanation for the more centralized distribution pattern of *A. castaneoticus* in the Tapajós-Xingu interfluve and the surrounding distribution of *A. galactonotus*. This hypothesis gains further support from the observation that *A. galactonotus* appears to be a more generalist species, capable of inhabiting transitional environments between humid forests and the Cerrado, areas with sandy terrain, and even environments subject to some degree of environmental disturbance, in contrast to *A. castaneoticus*, which has been exclusively recorded in pristine forest habitats (Torralvo et al. 2022). This distinction may be indicative of *A. castaneoticus* greater sensitivity to environmental changes and the potential evolutionary selection of aggressive tadpole behavior, granting them a competitive edge in selecting their habitat. The aggressive behavior of *A. castaneoticus* tadpoles, including their ability to swiftly eliminate potential predators and competitors such as Odonata larvae and other tadpoles, including conspecifics that occupy the same ouriço, has been documented (Caldwell 1993, Caldwell & de Araújo 1998). This behavior was also observed in a pilot study (de Medeiros LA, unpublished data), wherein *A. castaneoticus* tadpoles were observed to attack and eliminate *A. galactonotus* tadpoles in an environment simulating developmental pools.

An interesting example of how this type of interaction can influence species distributions was observed in two dendrobatids, *Ameerega trivittata* and *A. bassleri* (Twomey et al. 2008). These have parapatric distributions in an elevation gradient in Peru: *A. trivittata* occurs predominantly in lowland areas, while *A. bassleri* occurs predominantly in high altitude areas, although occasionally the reverse occurs for both species. Both share important resources for tadpole development and in some locations they can occur in sympatry, so competition in these areas is expected (Twomey et al. 2008). Field experiments along an altitude gradient indicated that the survival of *A. trivittata* is strongly affected by *A. bassleri*, on the other hand, the latter was not affected by *A. trivittata*, regardless of elevation. It is possible, in this case, that the absence of *A. bassleri* in lowlands is due to physiological constraints, while that of *A. trivittata* in the highlands is a consequence of competitive exclusion by *A. bassleri* (Twomey et al. 2008).

Competition is considered an important ecological interaction that influences the distribution of species, especially when dealing with evolutionarily related or ecologically similar species (Twomey et al. 2008), and as it is possible that this is the case for these two species of *Adelphobates*. The potential competitive interactions between *A. castaneoticus* and *A. galactonotus* offer a promising avenue for further research, addressing critical questions regarding the impact of interspecies competition on their distribution, ecological dynamics, and evolutionary history.

Evolutionary history

The biogeographic history of *Adelphobates* in the Amazon has not yet been carefully investigated. In a previous study, Noonan & Wray (2006) proposed potential explanations for the biogeographic history of what was then the genus *Dendrobates*. This genus formerly included the current taxon *Adelphobates*, whose phylogenetic relationships were the subject of ongoing debate at the time. Noonan & Wray highlighted the paraphyly within the 'tinctorius' and 'ventrimaculatus' groups, to which *A. galactonotus* and *A. castaneoticus*, along with *A. quinquevittatus*, were assigned. They suggested that these three species formed a monophyletic clade with an estimated origin dating back to 6–23 million years ago (Noonan & Wray 2006). The origin of this clade has been dated based on four specimens, being one from *A. galactonotus* of unknown origin, one from *A. quinquevittatus* from the Ituxi River and two from *A. castaneoticus* from Santarém, and the relationships between the three species were not well resolved. This time interval would weaken a hypothesis based on the influence of the Amazon River on the diversification of *Adelphobates*, because it precedes the period suggested for the consolidation of the modern course of this river (Hoorn et al. 2010, Latrubesse et al. 2010).

The estimated timing of key events resulting from Andean tectonic activities, which played a direct role in isolating drainage systems, aligns with phylogenetic data for fish in the northwestern region of South America. Particularly significant are the events that occurred after 12 Ma (Albert et al. 2006). During the middle to late Miocene, the northwestern region of South America underwent significant geological transformations, primarily driven by the uplift of the Andes (Hoorn 1994, de Gamero 1996, Latrubesse et al. 2010). Geological evidence indicates that the area now encompassing the upper Amazon once consisted of extensive wetland environments, including swamps and shallow lakes. Well-defined drainage channels were notably scarce during this period (Hoorn 1994). This situation changed during the early Pliocene due to alterations in drainage patterns, leading to large-scale flow, including sediment transport from the Andes toward the Atlantic Ocean (Latrubesse et al. 2010). Consequently, the current morphology of the Amazon basin gradually took shape between the late Miocene and the early Pliocene (Hoorn et al. 2010, Latrubesse et al. 2010, Albert et al. 2018).

The hypothesis suggesting that the origin of the genus *Adelphobates* to the south of the Amazon River is linked to the establishment of the modern course of the river gains support from the fact that the sister clade of *Adelphobates*, *Minyobates steyermarki* (Rivero, 1971), is distributed north of the Amazon River, within the Guiana Shield. However, the estimated divergence between *Adelphobates* and *Minyobates*, which falls within the range of 22 to 10 million years ago (Mya), as proposed by Guillory et al. (2019), still exhibits relatively limited overlap with the different timeframes suggested for the establishment of the current Amazon River course. In our analysis, we estimate the node separating *Adelphobates* from the nearest clade, which was included in our study (*Oophaga*), to be approximately 18.51 Ma (with a range of 12.48 to 24.9 Ma). This estimate is based on 67 unique haplotypes sampled across a wide distribution of the genus and aligns with the estimate proposed by Guillory et al. (2019).

It is not uncommon to find older diversification events dating back to the Miocene in Amazonian anurans. The region's significant environmental changes during this period may have had a profound impact on populations that are particularly sensitive to environmental fluctuations and possess limited dispersal abilities (Godinho & Silva 2018, Réjaud et al. 2020). For species within the Dendrobatidae and Aromobatidae families, the events that occurred during the Miocene, including the Andes uplift and subsequent drainage network reorganization, marine incursions, and habitat alterations, played a pivotal role in driving extensive diversification. This process involved a complex network of migrations and colonization of new, more suitable environments, with a particular intensification over the last 10 Myr (Santos et al. 2009, Réjaud et al. 2020). For instance, the ancestor of *Adelphobates* is believed to have originated from dispersal events around an estimated average of 21 Mya, stemming from the still-developing eastern Andes before the formation of the Amazon floodplain (Santos et al. 2009).

In the case of *Amazophrynella* species (Bufonidae), which are distributed across the Amazon, the primary western and eastern clades exhibit subclades with distributions constrained by the North-South orientation of the Amazon River (Moraes et al. 2022). These toads share certain characteristics with *Adelphobates*, including small body size (similar characteristic especially to *A. quinquevittatus* and *A. castaneoticus*), an affinity for leaf litter in *terra firme* forests, and the use of small temporary pools for reproduction (Fouquet et al. 2012, Rojas et al. 2018). The divergence between the northern and southern subclades of these toads is traced back to the Middle Miocene. During this period, it is proposed that northern subclades originated through dispersal events from the south or other vicarious factors. This occurred before the consolidation of the present-day Amazon River, and the river is considered to have played a secondary role as a barrier (Moraes et al. 2022), rather than being a primary cause of vicariance (Rojas et al. 2018). As for the divergence between *Adelphobates* and *Minyobates*, this remains a subject of ongoing investigation, with vicariance not yet conclusively ruled out. Current data suggest that during the Miocene, marine incursions might have resulted in the isolation of various land fragments within the Amazon, as well as the eastern slope of the Andes, the Guiana Shield, and the Brazilian Shield. These geological events promoted diversification in species, as observed in upland birds of the genus *Xiphorhynchus* (Aleixo 2004).

Marine incursions, involving the migration of marine waters across the Atlantic Ocean, have been documented in Brazil's northern region, particularly in the extreme east of the Amazon. These events are substantiated by geological evidence observed in the Pirabas and Barreiras Formations, situated within the Marajó Basin at the mouth of the Amazon River (Lundberg et al. 1998, Rossetti & Júnior 2004). Isotopic analyses of fossils from the Pirabas Formation, dated to the Early-Middle Miocene (between 23–12.1 Mya), have revealed strong evidence of marine influence and the existence of a cyclical coastal environment (Alvim et al. 2021). However, the precise timing, duration, and scale of these marine incursions remain a subject of ongoing study. In some cases, it is estimated that sea levels may have risen between 30 to 100 meters above the present-day level during warmer periods (Nores 2020). More radical hypotheses suggest that marine transgressions could have been as high as 50 meters above the current sea level, extending across the Atlantic Ocean. Such events may have isolated the Amazon into two main regions, the Guiana Shield and the Brazilian Shield (Nores 2020). The hypothesis of the vicariant origin of the genus *Adelphobates*, resulting from its isolation on the Brazilian Shield due to marine incursions, deserves further examination, especially considering the alignment between estimates of divergence times and geological events. In this context, the role of the Amazon River as a secondary barrier, restricting *Adelphobates* to its southern margin after its establishment, represents a plausible hypothesis.

Adelphobates quinquevittatus has its distribution separated from those of *A. galactonotus* and *A. castaneoticus* by the Tapajós River. The effect of this river as a barrier has already been attributed to some species and populations of amphibians (Simões et al. 2014, Maia et al. 2017), reptiles, (Moraes et al. 2016, de Oliveira et al. 2016), birds (Ribas et al. 2012, Harvey & Brumfield 2015, Silva et al. 2019, Maximiano et al. 2020), and mammals (Alfaro et al. 2015, Saldanha et al. 2019, Guimarães et al. 2021). Although the Tapajós River currently limits the distributions of *Adelphobates* species, Santos et al. (2009) found a time interval ranging from 12.5 – 7.5 Ma for the divergence between *A. quinquevittatus*, the basal species of the genus, and the ancestor of *A. galactonotus* plus *A. castaneoticus*. We obtained an average divergence of 12.6 Ma (18.2-7.0 Ma) for the same node. However, these estimates precede those inferred for most of those other taxonomic groups, for which the Tapajós River started to act as an effective barrier to the genetic divergence between populations or sister species, which occurred in a relatively simultaneous interval of time, during the Pleistocene (Birds: Ribas et al. 2012; Primates: Alfaro et al. 2015; Anurans: Maia et al. 2017). Recently, estimates of divergence between anuran and lizard species between opposite margins of the middle Tapajós River resulted in a wide range of times, from the Middle Miocene to the Pleistocene, although they were mostly concentrated within the limits of the Pliocene (Moraes et al. 2020). This period was also inferred for lineage divergence of the marsupial species complex *Marmosops pinheiroi* between opposite margins of the same river (Guimarães et al. 2021).

In contrast to other rivers with substantial sediment loads that enable geochronological inferences through the analysis of sedimentary deposition, cratonic rivers, including those within the Brazilian shield such as the Tapajós, pose unique challenges for dating analyses. These rivers, due to their current paucity of sediments, present limitations in conducting dating studies (Sioli 1984, Fricke et al. 2017, Toczeck et al. 2019). As a result, there is a notable absence of precise ages for the onset of these rivers in the Brazilian shield (RADAM Brasil 1975). Many of the inferences concerning their history rely on dating the divergence of a limited number of taxa (Ribas et al. 2012, Alfaro et al. 2015, Maia et al. 2017, Silva et al. 2019, Guimarães et al. 2021, Moraes et al. 2022). In addition, the basins of these rivers have numerous geological faults, as well as paleochannels that indicate intense neotectonic activity, which reorganized river courses and modified landscapes (Rossetti 2014). It is conceivable that vicariance events associated with what is now the Tapajós River basin have taken place on multiple occasions and at varying points in time (Moraes et al. 2020). These events might have been triggered by proto-rivers that once flowed into the craton, and which are now the tributaries of the Tapajós River. Importantly, some of these vicariance events could have occurred before the establishment of the present-day Amazon River (Hoorn et al. 2010, Latrubesse et al. 2010). Alternatively, these vicariance events might have been shaped by the more recent course changes influenced by drainage reorganization and tectonic reactivations (RADAM 1975, Rossetti 2014, Toczeck et al. 2019). Additionally, climate changes, leading to fluctuations in water volume, could have either intensified or reduced its effectiveness as a barrier (Irion et al. 2006, Moraes et al. 2016).

The Tapajós River possesses an asymmetric basin, where left-margin tributaries drain recent areas of the Solimões sedimentary basin, whereas right-margin tributaries traverse eroded terrains of the Brazilian shield (RADAM 1975, Toczeck et al. 2019). This transitional zone, situated at the boundaries of geologically distinct domains, has the potential to create ecotonal areas and dynamic landscapes, thus offering opportunities for specialization (Moraes et al. 2016, 2020). Much like the Amazon River, the Tapajós River may have served as a limiting factor in shaping the distributions of *A. quinquevittatus*, *A. castaneoticus*, and *A. galactonotus* since the establishment of its modern course. However, the absence of precise dating for the emergence of the Tapajós River, coupled with the lack of fossil records for Amazonian anurans and substantial disparities in marker replacement rates, along with the inherent limitations of DNA-based divergence dating methods, necessitates cautious consideration when establishing potential links between river ages and diversification events.

The current dendrobatid biota endemic to the Amazon basin emerged between the Miocene-Pliocene transition and the present day, characterized by rapid in situ diversification driven by the establishment of suitable geoclimatic conditions for maintaining a tropical forest environment (Santos et al. 2009). The divergence between *A. castaneoticus* and *A. galactonotus*, with an estimated mean time of 6.99 Ma (ranging from 11.3 to 2.7 Ma), aligns well with this prediction. Santos et al. (2009) similarly estimated the same event to have occurred on average approximately 8 Mya (with a variation of ± 2 million years). Despite these species now occurring in sympatry, with no apparent physical barriers, the dynamics of the region, including the presence of paleochannels, raise the possibility that they might have originated from a vicarious event, potentially associated with an extinct barrier, before coming into secondary contact. In dendrobatids, intraspecific competition poses limitations to population expansion, particularly concerning resources used for tadpole deposition and development (Twomey et al. 2008, Gray et al. 2009). In cases of intraspecific competition, divergent selection may favor the existence of extreme phenotypes, thereby reducing niche overlap and alleviating the effects of competition (Pfennig et al. 2007, Martin & Pfennig 2009). Natural selection or sexual selection reinforcing the maintenance of these divergent phenotypes may ultimately lead to reproductive isolation and speciation (Wang & Summers 2010, Richards-Zawacki & Cummings 2010). This mechanism could have operated in the ancestor of *A. castaneoticus* and *A. galactonotus*, given the significant morphological variations between the two species, both in terms of size and aposematic coloration patterns. Periods of increased aridity throughout the Neogene, when forest environments were reduced, and resources for tadpole development became scarcer, might have intensified intraspecific competition within the ancestral species of this clade. In this scenario, phenotypic divergence and the capacity of these new phenotypes to exploit different niches, as observed in *A. galactonotus* today, could have provided a significant adaptive advantage.

Our objective is not to establish a specific cause for the events that gave rise to *Adelphobates* species, but rather to present a comprehensive exploration of the historical and ecological backdrop within which they evolved, and to consider how these factors may have played a role in their diversification. Instead of seeking a singular cause, we aim to put forth hypotheses that can be subject to future testing using alternative methods and datasets, as a means to elucidate the narrative of this genus. From our preliminary findings, it is evident that these organisms present a promising model for investigating a wide range of biological hypotheses, given their intriguing natural history, behavior, and evolutionary patterns.

Implications for conservation

While all *Adelphobates* species are currently classified as ‘Least Concern’ according to the IUCN, it is worth noting that the most recent update was in 2004. In the case of *A. castaneoticus*, there is limited information available regarding its distribution, and it is evident that its conservation status necessitates reevaluation (Rodrigues & Azevedo-Ramos 2004a, b). Despite their ‘Least Concern’ classification, it is crucial to recognize that all these species inhabit regions within the ‘Arc of Deforestation’, an area experiencing the highest rates of deforestation in the Amazon. This deforestation is primarily driven by illegal logging, monoculture, livestock farming, and anthropogenic fires (Laurance et al. 2001a, b, Fearnside 2005, Alencar et al. 2015, De Faria et al. 2017, Latrubesse et al. 2017, da Silva et al. 2018). The states of Pará, Mato Grosso, Amazonas, and Rondônia, where *Adelphobates* species are known to occur, have accounted for nearly 90% of the total deforestation in the Legal Amazon (Assis et al. 2019, INPE 2021). On top of that, several large enterprises such as the construction of hydroelectric dams and large-scale mineral exploration, both through legal and illegal means, are taking place in this region. This trend is expected to persist in the years to come, further exacerbating the environmental challenges in the area (Fearnside 2016, Latrubesse et al. 2017, Villén-Pérez et al. 2022). These environmental impacts have resulted in the reduction of forested habitats, significantly affecting these species. For instance, the Madeira River basin, where *A. quinquevittatus* is primarily found, faces the highest levels of environmental vulnerability and has experienced severe disruption due to recent dam construction (Latrubesse et al. 2017). The species inhabits areas of pristine forest, and as forest degradation intensifies, suitable habitats are diminishing. This directly impacts the species' ability to survive and reproduce, as its occurrence has never been documented in open vegetation or pasture areas (Bernarde 2007, Bernarde & Macedo 2008, Turci & Bernarde 2008, da Silva et al. 2018, de Medeiros et al. 2021). Besides the on-site environmental impacts, the illegal international trade in pets, driven by the attractive beauty and diverse color patterns of these species, poses a significant threat (Rodrigues & Azevedo-Ramos 2004a, b, Rodrigues et al. 2010). Frequently, both adult frogs and tadpoles are offered for sale on various websites outside of Brazil, particularly in Europe and Asia. The convergence of these multiple threats could have severe consequences for the populations of *Adelphobates* species in the very near future.

Finally, we believe it is important to highlight that, considering these updated distributions and our modeling of potential areas of occurrence of the species, we hope that the information presented here can serve as a useful source to guide future selection of priority areas and strategies for the conservation of these species.

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Author contributions

LAM, EG, IK and MCH conceived the study. LAM and EG carried out the sampling in the field and performed the analyses. LAM wrote the original draft of the manuscript. All the authors discussed the results, made corrections and critical suggestions to the manuscript, and approved the final version for submission.