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Original Article

The biogeography of ignorance: gaps in the knowledge of Amazonian amphibian biodiversity

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ABSTRACT

A large volume of biodiversity information is currently available in scientific repositories. However, its quality needs to be quantified, especially in megadiverse regions, such as the Amazon. In this study, we analyse the quality of Amazonian amphibian-sampling data, based on a robust database with >242000 occurrence records for 951 species. The data quality was based on three metrics: sampling completeness, taxonomic completeness, and temporal completeness. Subsequently, we built a knowledge ignorance map overlapping all the metrics. We also investigated potential drivers of ignorance represented by river density, protected-area density, species richness, human footprint index, and travel time to the nearest human settlement. Our findings indicated that only 14% of the Amazon is well sampled, with large sampling gaps and low taxonomic accuracy, especially in southern and southeastern Amazonia. Sampling efforts were sporadic and recent, limiting the understanding of the temporal dynamics of Amazonian amphibian biodiversity. Our results also highlighted areas of high ignorance in many spatially disjunct Amazonian regions. Amazonian sites with low river density and localities with low human footprint have few records. Sites with shorter travel times are better known, and therefore have a lower ignorance index. The density of protected areas and species richness are related to anuran ignorance only in small areas in the Amazon. Our findings highlight that the data quality of Amazonian amphibians has gaps, mainly influenced by accessibility and anthropization. These shortcomings require coordinated efforts in research, curation, and data sharing. Thus, this study sheds light on a widespread issue of biodiversity ignorance in the Amazon, serving as a warning about the quality of collected data and potential limitations to its use.

Keywords: sampling completeness; knowledge ignorance; knowledge gap; environmental policy

INTRODUCTION

The intensification of human-induced activities has negatively impacted natural ecosystems and their ecological processes (Hooper *et al.* 2005, Boivin *et al.* 2016, Sullivan *et al.* 2017, Tilman *et al.* 2017, Díaz *et al.* 2019, Rillig *et al.* 2021, McFadden *et al.* 2023). In some cases, these impacts exceed the recovery limits of ecosystems (Tilman *et al.* 2017, Tucker *et al.* 2018) and represent a global threat to biodiversity (Wolkovich *et al.* 2014). Tropical forests, once minimally altered by traditional populations, are increasingly affected by human activity, leading to significant losses in biodiversity and associated ecosystem services (Lewis *et al.* 2015, Nobre *et al.* 2016, Gatti *et al.* 2021).

The Amazon, the largest tropical biome in the world, spans ~6.7×10^6 km^2 and extends across nine South American countries (Brazil, Bolivia, Peru, Colombia, Ecuador, Venezuela, Guyana, Suriname, and French Guiana), forming the so-called Pan-Amazon region (RAISG 2020, IBGE 2021). This interconnected system encompasses not only tropical forests but also savannas, rivers,

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and unique ecosystems, playing a crucial role in global climate regulation (Nobre *et al.* 2016, Latrubesse *et al.* 2017). Among these ecosystems, the Amazon stands out as one of the largest remaining reservoirs of natural resources on the planet. It hosts the largest river drainage network in the world, responsible for ~20% of global surface freshwater (Salati and Vose 1984, Latrubesse *et al.* 2017, Hierro *et al.* 2019, Tigre 2019, Jézéquel *et al.* 2020). Moreover, the Amazon harbours the greatest biodiversity on Earth (dos Santos *et al.* 2015, Antonelli *et al.* 2018), an immense complexity of ecological interactions, and provides crucial ecosystem services for human well-being (Couto Pereira 2010, dos Santos *et al.* 2015). The region is also recognized for its significant genetic exchange across the Neotropics (Antonelli *et al.* 2018) and retains high potential for the discovery of new species (Moura and Jetz 2021, Zapata-Ríos *et al.* 2021).

Mapping Amazonian biodiversity to understand species distributions, ecological functions, and the ecosystem services is a crucial yet challenging task (Oliveira *et al.* 2016, Moura *et al.* 2018, Carvalho *et al.* 2023). It relies on the availability and quality of primary biodiversity data, such as species-occurrence records, genetic samples, and behavioural descriptions. Normally, these data are insufficient, poorly documented, or biased towards remote and densely forested regions (Titley *et al.* 2017, Stropp *et al.* 2020, Zapata-Ríos *et al.* 2021, Carvalho *et al.* 2023). As human-induced land-use changes and infrastructure construction intensify environmental changes, addressing these challenges and expanding biodiversity knowledge have become increasingly urgent (Moura *et al.* 2018, Andrade-Silva *et al.* 2022, Carvalho *et al.* 2023, Danu and Rodriguez 2023). These efforts are particularly critical in understudied areas, such as much of the Amazon rainforest, where they can help to mitigate the growing risks of species extinction (Danu and Rodriguez 2023).

Globally, infrastructure-related factors, such as urban centres, industrial projects, hydroelectric plants, and mining operations, play a significant role in driving knowledge about biodiversity (Moura *et al.* 2018, Andrade-Silva *et al.* 2022, Carvalho *et al.* 2023, Danu and Rodriguez 2023). These human-induced developments often channel more resources into ecological studies, resulting in biodiversity data that are disproportionately associated with areas of higher human activity (Mayor *et al.* 2012, Hand *et al.* 2014, Seiferling *et al.* 2014, Di Marco and Santini 2015, Rocha-Ortega *et al.* 2021, Andrade-Silva *et al.* 2022, Carvalho *et al.* 2023, Danu and Rodriguez 2023). In contrast, intact natural systems remain poorly studied. To address this disparity, biodiversity research must critically evaluate the biodiversity-data quality to identify the associated drivers from spatial and temporal perspectives (Meyer *et al.* 2016).

The accessibility influences biodiversity knowledge (Azevedo-Ramos and Galatti 2002, Oliveira *et al.* 2016, Andrade-Silva *et al.* 2022, Carvalho *et al.* 2023). Accessible sites (e.g. near to rivers, roads, or railways) reduce the costs and time for biodiversity sampling, whereas the opposite occurs in remote areas, such as the interior of dense forests. In the Amazon, however, railways are scarce and often used only for the transportation of minerals between mining operations and river ports. In many lowland areas, road construction is also hindered by the frequent lateral flooding of rivers, which creates obstacles during the rainy season. Historically, rivers have been the primary, and sometimes only, access routes into the Amazon forest, limiting biodiversity knowledge in areas far from navigable rivers (dos Santos *et al.* 2015).

The known or potentially expected species richness of a given location is another determining factor in selection of sampling areas by researchers. Species richness is a fundamental measure of local diversity and underpins many ecological models and conservation strategies (Schall and Pianka 1978, Pearson and Cassola 1992, Myers *et al.* 2000, Gotelli and Colwell 2001, Nneji *et al.* 2023). With limited financial resources for field studies (Costa and Magnusson 2010) and conservation, it is considered advantageous to prioritize research and preserve areas with a greater number of species. Therefore, biodiversity surveys often prioritize areas with higher potential species richness, resulting in uneven knowledge of biodiversity across heterogeneous environments, such as the Amazon.

In the Amazon, the Protected Areas have represented a significant knowledge gap regarding biodiversity (Carvalho *et al.* 2023). The low government investment in the management of protected areas and Indigenous Territories (Peres *et al.* 2023), coupled with bureaucratic limitations (Little 2005, dos Santos *et al.* 2015), discourages research in Amazonian protected areas, leaving their biodiversity largely unknown (Carvalho *et al.* 2023). However, protected areas have faced increasing threats in recent years owing to illegal activities, such as logging, land invasion, and mining, especially gold mining (Begotti and Peres 2019, Carvalho *et al.* 2023, Peres *et al.* 2023). Thus, places once considered important biodiversity refuges now face an uncertain future.

Here, we assess the current knowledge of the biodiversity of the Amazon and prioritizing areas for new inventories. To this end, we chose amphibians as taxa because they represent the third most species-rich taxon among terrestrial vertebrates (AmphibiaWeb Team 2023). Additionally, they are highly vulnerable to climate change and contamination of water, air, and soil (Amaral *et al.* 2019), and they make up 41% of species at risk of extinction listed by the International Union for Conservation of Nature (IUCN 2023). Thus, the amphibians are recognized as an important indicator of environmental changes (Toledo 2009, Becker *et al.* 2010, Amaral *et al.* 2019), being consistently included in environmental monitoring programmes. Therefore, sampling deficits and gaps can be extended easily to other terrestrial taxonomic groups in the Amazon.

To achieve our aims, we built amphibian-biodiversity-knowledge ignorance maps (Tessarolo *et al.* 2021, Castro-Souza *et al.* 2024a) with the following aims: (i) to assess the data quality of amphibian occurrence in the Amazon based on taxonomic, sampling, and temporal completeness; (ii) to spatialize the pattern of ignorance in Amazonian amphibian knowledge; and (iii) to identify the drivers associated with the spatial pattern of ignorance regarding Amazonian amphibians. Our hypotheses are as follows: (i) amphibian sampling is biased in the Amazon, with areas far from biome edges and large navigable rivers exhibiting high biodiversity ignorance; and (ii) river density, human footprint, and assumptions about species richness reduce ignorance, whereas travel time and density of protected areas increase ignorance about amphibian knowledge in the region.

MATERIALS AND METHODS

We built a database of Amazonian amphibian occurrences from four main sources as follows:

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i. Digitally accessible repositories (GBIF, SiBBr, SISBIO, Specieslink, and VertNet).
ii. Peer-reviewed articles, for which searches were conducted on AmphibiaWeb (https://amphibiaweb.org/amphibian/newspecies.html), Google Scholar (https://scholar.google.com.br/?Hl=pt), and Web of Science (https://www.webofknowledge.com) using the keywords 'Amphibia' AND 'Amazon' AND 'Checklist' OR 'Herpetofauna' OR 'New Record' OR 'New Species'. This step compiled data from 150 scientifc articles published in scientific journals containing information on amphibian species occurrences in the Amazon.
iii. 'Grey literature', i.e. technical reports from Environmental Impact Studies/Environmental Impact Reports, amphibian rescue, and monitoring in hydroelectric power plants in the Amazon.
iv. Our own data, i.e. personal records from the authors over 15 years, from 2007 to 2022, in the southern portion of the Brazilian Amazon (for more details, see Penhacek *et al.* 2024, 2025a, b).

Our dataset consists of 242724 occurrences within the limits of the Amazon domain, with 213072 species-level records for 951 amphibian species, available at: [Mendeley Dataset]. Version 1 DOI: 10.17632/ykk5xp94vr.1, and an additional 29652 records above the species level for 587 taxa.

Data quality metrics

The quality of biodiversity data is essential to ensure the reliability of ecological studies and the effectiveness of conservation strategies (Hortal *et al.* 2015, Cardoso *et al.* 2011, Tessarolo *et al.* 2021, Castro-Souza *et al.* 2024b). Incomplete, inaccurate, or biased data can lead to erroneous conclusions, affecting the prioritization of areas for conservation and the understanding of ecological patterns (Meyer *et al.* 2016, Isaac *et al.* 2020, Castro-Souza *et al.* 2024b, Penhacek *et al.* 2025b).

To evaluate the quality of amphibian data in the Amazon, we calculated three metrics, encompassing quality, spatial coverage, and sampling longevity, respectively: (i) taxonomic completeness (TaxC), which reflects the effort in taxonomic resolution made for a given grid cell; (ii) sampling completeness, representing the sampling effort in capturing the biodiversity of a grid cell; and (iii) temporal completeness (TC), representing the temporal effort in sampling a grid cell (for details, see Castro-Souza *et al.* 2024b). These metrics were calculated for grid cells of 0.5° resolution (~50 km × 50 km) at the Equator. We also calculated the three data-quality metrics with a different occurrence number of thresholds (Fig. 1B). Next, assuming a cut-off threshold of 25 occurrences per cell (description below), we constructed a map for each of the three quality indices (Fig. 1C). Finally, we summed the values of the three maps to generate a knowledge-ignorance map, with values rescaled between zero (high ignorance) and one (low ignorance) (Fig. 1D).

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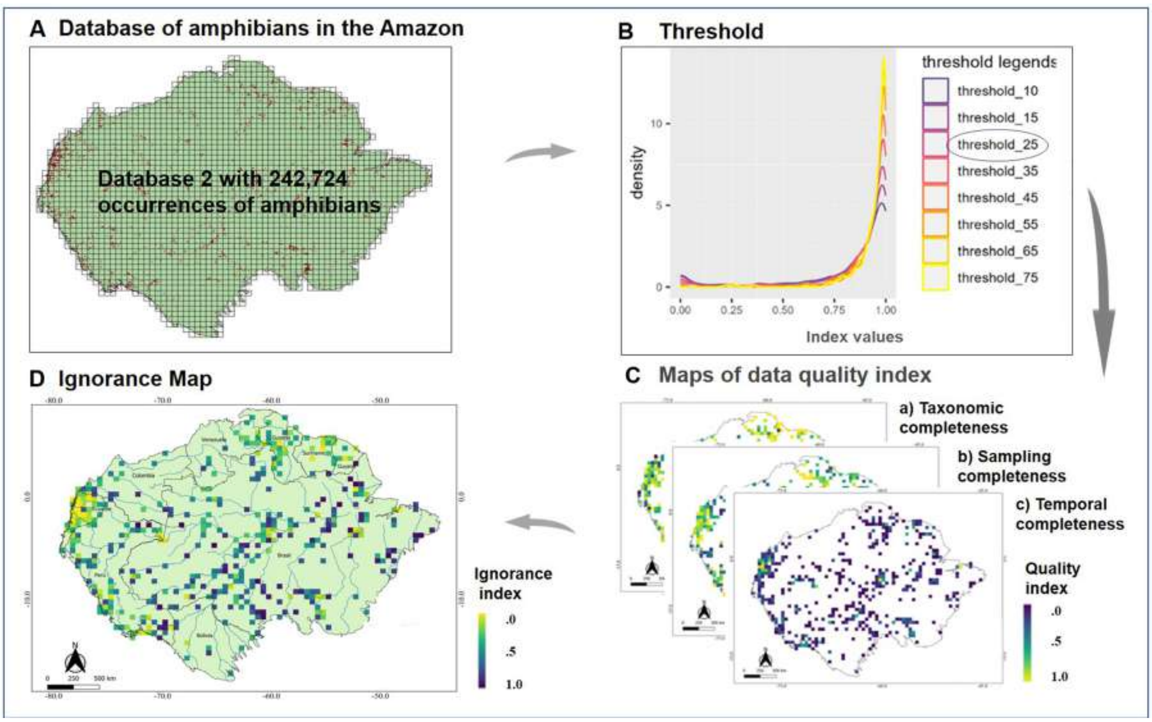

Figure 1. Methodological and analytical steps for constructing the biogeographical ignorance map. A, construction of amphibian databases through different search sources and plotting over the Amazon in a grid with 0.5° resolution cells. B, evaluation of the three sampling-quality indices with different cut-off thresholds for the number of amphibian occurrences within the cells. C, calculation and plotting of maps with the three sampling quality metrics with a threshold of 25 occurrences per cell. D, construction of the final knowledge ignorance map by summing the three metrics, rescaled from zero to one.

Taxonomic completeness

Taxonomic completeness serves as an indicator of data quality based on the taxonomic refinement carried out within a given grid cell. Cells where more time and resources have been invested in identifying organisms down to the species level tend to exhibit higher taxonomic completeness. Cells with low taxonomic completeness contain a high number of records identified above the species level (e.g. order, family, or genus) and require further effort and investment in taxonomic research.

We calculated TaxC for each cell (p_i) as the ratio of the number of primary occurrences identified at the species taxonomic level (s) divided by the total number of records (t), Equation 1 (following Castro-Souza *et al.* 2024b).

$$\text{TaxC} = s(p_i)/t(p_i) \tag{1}$$

Taxonomic completeness values range from zero to one, where zero indicates low taxonomic completeness, meaning that taxonomic knowledge requires further refinement, and one indicates that maximum taxonomic completeness has been achieved in the cell, meaning that all records in the cell have been refined fully to the species level.

Sampling completeness

To understand the spatial deficiency in amphibian data, we calculated the sampling completeness (SC) based on species accumulation curves (SCs) (Tessarolo *et al.* 2021). Only cells with >25 records were evaluated. For each cell, we performed local permutations with randomization of the sampled data to estimate the number of species expected to be missing if the sampling effort had been applied sufficiently. We also randomized each permutation 100 times, creating SCs. We then subtracted one from the angle of the resulting curve from each local permutation. This formula provided sampling completeness values ranging from zero to one. Values closer to one indicate that sampling in the cell was more complete and that local diversity is likely to be well represented by the collected data. On the contrary, values close to zero indicate insufficient sampling and that there is a higher probability that unsampled species are present in the region. For locations where completeness was calculated (<25 records), the SC values were categorized as follows: $\text{SC} < .5$, low completeness; $.5 \leq \text{SC} < .75$, medium completeness; and $\text{SC} \geq .75$, high completeness. Locations where completeness could not be calculated were considered unsampled (NA).

Temporal completeness

High sampling effort at a location might be efficient in capturing local biodiversity. However, if the effort is made only once, or during a single season of the year, it might introduce bias by failing to capture the true diversity of that locality owing to variations in the temporal, spatial, and population dynamics of the species present there (Castro-Souza *et al.* 2024a, b). For an adequate understanding of local biodiversity, it is desirable for sampling to be repeated over time. Thus, as a proxy for sampling quality, we measured TC as the number of years sampled (S) in a cell (pi) divided by the largest number of years sampled in a cell found in our database S(pi)max, Equation 2 (*sensu* Castro-Souza *et al.* 2024b), i.e.:

$$\text{TC} = \left[S(p_i)\right]/\left[S(p_i)_{\max}\right] \tag{2}$$

This index has values ranging from zero to one. Values close to zero indicate low temporal completeness, where all occurrences belong to a few sampling years, whereas values close to one indicate maximum temporal completeness (several years of sampling in the same location).

Sensitivity of quality indices to occurrence numbers in cells

We performed analyses with different occurrence thresholds per cell (Supporting Information, Fig. S1) to assess how the threshold settings for the minimum number of occurrences affect the results of the indices. We calculated SC using thresholds of 10, 15, 25, 35, 45, 55, 65, and 75 occurrences as the cut-off values per cell (Supporting Information, Fig. S1A). For TaxC and TC, in addition to the occurrence thresholds mentioned above, we calculated indices without a threshold value for occurrence records and for five occurrences (Supporting Information, Fig. S1B, C).

All cut-off thresholds showed a similar density pattern (Supporting Information, Fig. S1). However, by choosing higher cut-off thresholds, fewer cells are evaluated, which might represent an underestimation of the sampled area. On the contrary, very small thresholds for the number of occurrences introduce noise in the calculation of the index, potentially generating undesirable artificial values (Soberón *et al.* 2007, Tessarolo *et al.* 2021, Castro-Souza *et al.* 2024a). Therefore, we established a minimum cut-off threshold of 25 species records to perform all calculations, thus avoiding noise in the indices and loss of sampled area.

Mapping biogeographical ignorance

Advances in information technology have driven the production, storage, and dissemination of large-scale biodiversity databases worldwide (Sousa-Baena *et al.* 2014). However, it is crucial to acknowledge that these datasets have intrinsic limitations regarding quality, longevity, and spatial coverage (Ladle and Hortal 2013). Understanding, mapping, and integrating these gaps into biodiversity knowledge databases can be highly valuable for ecological research, enabling a more critical use of available data (Castro-Souza *et al.* 2024a).

The concern with incorporating such uncertainties into biogeographical knowledge dates back to Boggs (1949), who proposed an 'atlas of ignorance' to represent geographical variations in the level and precision of knowledge about spatially explicit phenomena (Tessarolo *et al.* 2021). Expanding on this idea, Ladle and Hortal (2013) established the conceptual foundations of 'biogeographical ignorance maps', incorporating metrics of data quality, longevity, and distribution coverage (Meyer *et al.* 2015, 2016, Stropp *et al.* 2016, Tessarolo *et al.* 2021).

Based on these concepts, we propose the construction of a biogeographical ignorance map for Amazonian amphibians, summarizing three metrics: TaxC, SC, and TC. The values of these three indices were summed (TaxC + SC + TC), rescaled to range from zero to one, then subtracted from one. The resulting map was designed such that values close to zero (dark cells) indicate low biogeographical ignorance, whereas values close to one (light cells) represent high ignorance. This innovative approach not only highlights knowledge gaps but also guides future research by directing efforts towards underexplored areas and enhancing the reliability of biodiversity studies.

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Drivers of knowledge ignorance

We constructed a piecewise structural equation model (piecewise-SEM) using five variables: two environmental (river density and known species richness), one anthropogenic (human footprint), one accessibility related (travel time to the nearest human settlement), and one conservation related (protected area density), to assess their effects on the amphibian biogeographical ignorance in the Amazon.

Using this model, we tested the hypothesis that species richness, river density, and human footprint negatively affect the mapped biogeographical ignorance. Furthermore, we hypothesize that the last two variables also indirectly affect biogeographical ignorance, positively influencing a better survey of the species richness of a site. For protected areas, our hypothesis is that, owing to the low investment in management and infrastructure in these areas, in addition to restrictive legislation regarding researcher access and data dissemination, especially in Indigenous Lands, a higher density of protected areas will positively affect biogeographical ignorance. In turn, travel time is expected to have a positive effect on biogeographical ignorance, decreasing the sampling effort of a site, hence the knowledge about the species richness of this site. We also believe that there is a correlation between travel time, river density, and human footprint, and between protected area density and human footprint, although not strong enough to undermine our analysis with these variables kept separate (Fig. 2; Table 1).

Model variables

Accessibility

To calculate the travel time to the nearest human settlement, we used the raster produced by Nelson *et al.* (2019). This raster considered human settlements with a population density of 300 inhabitants/km^2 and an estimated population ranging from 5000 to 110000000 inhabitants (level 12 of Nelson *et al.* 2019). For each pixel, the travel time was calculated considering eight directions: four orthogonals and four diagonals. The pixel values represent the time (in minutes) from the central point of the pixel to the nearest human settlement. For our analysis, we cropped the global raster to the Amazon domain, then increased the resolution of the pixels to 0.5° (~50 km × 50 km). We summed the time spent in each 30″ pixel (~1 km × 1 km) originally available (Nelson *et al.* 2019).

Environmental (i)

To calculate river density, we used the global database HydroRivers, provided by HidroSHEDS (Lehner and Grill 2013) (https://www.hydrosheds.org/products/hydrorivers). We quantified the number of 0.01° cells (~1 km × 1 km) with the presence of rivers up to the sixth order in the Amazon. Then, we calculated the number of cells with river presence within each 0.5° (~50 km × 50 km) cell in the study area. Finally, we divided the number of river cells by the total number of 0.01° cells in each 0.5° cell (2500), obtaining values between zero and one. This gave us density results ranging from zero (when there are no rivers in the cell) to one (when all 2500 0.01° cells contain rivers).

Environmental (ii)

Known species richness was calculated by quantifying the number of species present in each 0.5° grid cell (~50 km × 50 km), based on our primary database (Database 1). This dataset comprises 213072 occurrence records for 951 species.

Conservation

To quantify protected area density, we divided the protected areas in the Amazon, obtained from the Amazonian Socioenvironmental

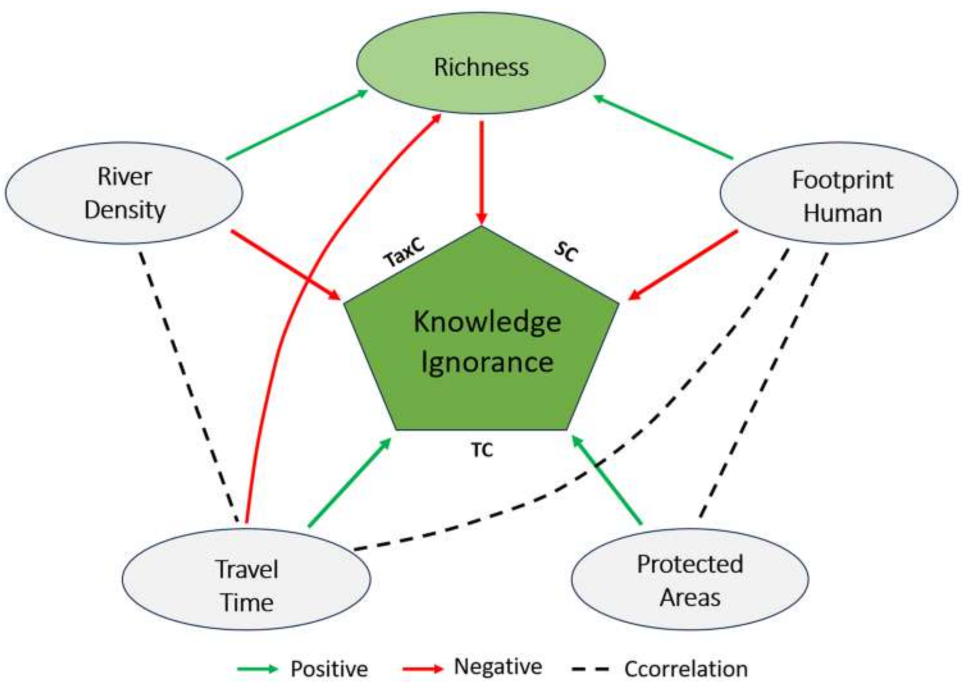

Figure 2. Hypothetical model to test the effect of five variables on the biogeographical ignorance of amphibian knowledge in the Amazon. Continuous lines and arrows indicate unidirectional effects, whereas dashed lines indicate correlational effects between two variables. Abbreviations: SC, sampling completeness; TaxC, taxonomic completeness; TC, temporal completeness.

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Table 1. Environmental, economic, and social variables responsible for the increase in biogeographical ignorance regarding amphibian knowledge in the Amazon.

Hypothesis	Correlation with other variables	Relationship to ignorance	Assumptions
Accessibility			
Travel time (Tt)	Tt with Dr and Hfp	Direct and indirect positive	Longer travel time increases the cost of research expeditions, discouraging researchers and raising knowledge ignorance at the site
Environmental			
River density (Dr)	Dr with Hfp and Tt	Direct and indirect negative	The presence of navigable rivers facilitates river access for researchers to a location of interest for research, encouraging higher sampling rates and reducing the lack of knowledge about biodiversity in this region
Richness of known species (SR)		Direct negative	Locations with either reported higher species richness or favourable environmental characteristics (such as habitat heterogeneity) tend to attract greater sampling efforts. This occurs because, owing to limited resources, researchers prioritize areas where there are indications (such as historical data or promising ecological conditions) that the diversity might be more representative
Conservation			
Protected area density (Dap)	Dap with Tt and Hfp	Direct and indirect positive	Protected areas in the Amazon generally have low infrastructure and research support resources. Furthermore, there are regulations that restrict researcher access, particularly in Indigenous Lands, owing to the risk of disease transmission to Indigenous peoples and/or the exploitation of natural resources through biopiracy
Anthropization			
Human footprint (Hfp)	Hfp with Dap and Tt	Direct and indirect negative	A larger human footprint enables greater infrastructure and a higher number of researchers, increasing the sampling rate and reducing knowledge ignorance

Information Network, RAISG (RAISG 2024; https://www.amazoniasocioambiental.org/es/mapas/#api-anchor-home), into 0.01° (~1 km × 1 km) raster cells. Then, we calculated the number of protected cells within each 0.5° (~50 km × 50 km) cell in the study area. Finally, we divided the number of protected cells by the total number of 0.01° cells in each 0.5° cell (2500), obtaining values between zero and one. A value of zero indicates no protected areas in the cell, whereas values between zero and one reflect variable densities, from low to high, of protected areas in the cell.

Anthropization

We extracted the average value of the human footprint (HFP) from 2000 to 2020, available in a raster with a resolution of 30 arc-seconds (~0.008°) from the figshare repository (https://doi.org/10.6084/m9.figshare.16571064), provided by Mu *et al.* (2022). The raster consists of eight distinct sub-indices, which capture different aspects of human pressures on the global land surface, here cropped for our study area. These sub-indices include: (i) built-up environment extent; (ii) population density; (iii) electrical infrastructure; (iv) agricultural areas; (v) pastures; (vi) roads; (vii) railways; and (viii) navigable rivers (Keys *et al.* 2021). For our analysis, we increased the resolution of the cells to 0.5° (~50 km × 50 km) by summing the values of the indices present in the 30″ cells originally provided.

Statistical analysis

To assess taxonomic completeness as a measure of sampling quality, we used the 'TaxC' function described above (proposed by Castro-Souza *et al.* 2024b). For sampling completeness, we used the KnowBR package (Lobo *et al.* 2018). To calculate temporal completeness, we used the 'TC' function described above (proposed by Castro-Souza *et al.* 2024b).

Path analyses

To investigate the determinants of biogeographical ignorance in amphibian knowledge across the Amazon, we used two distinct analytical approaches. First, for a global analysis, we used piecewise structural equation models (piecewiseSEM) in the R environment (piecewiseSEM package; Lefcheck 2016). This method allows the evaluation of direct and indirect causal relationships between ecological variables (e.g. river density, protected area density) and the rate of biogeographical ignorance of amphibians, mediated by intermediate drivers, such as species richness.

We constructed a hypothetical model based on known ecological relationships, including direct and indirect pathways (Fig. 2). Predictor drivers were selected based on a literature review (e.g. Carvalho *et al.* 2023) and ecological hypotheses (Table 1). We used the variance inflation factor (car package) to assess multicollinearity among drivers in each pathway. Drivers with a variance inflation factor higher than three were excluded or replaced until collinearity was reduced. We present the standardized coefficient for each direct and indirect pathway. We calculated the indirect effect of each pathway by multiplying the coefficient of the driver on species richness by the coefficient of species richness on biogeographical ignorance. The significance of all pathways was determined using maximum likelihood. Model fit was assessed using Shipley's test of d-separation (Fisher's C statistic; $P > .05$ indicates good fit).

Path analysis using piecewiseSEM assumes that the relationship between variables is uniform across geographical space, which is unrealistic for highly complex historical phenomena at large

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spatial scales (Hortal *et al.* 2011, Gouveia *et al.* 2013), as observed in the vast and structurally complex Amazon. To relax this assumption, we additionally implemented, as a second step, a geographically weighted path analysis (GWPath), developed by Barreto *et al.* (2019) in the spgwr package (Bivand *et al.* 2017) for R.

Unlike traditional path analysis, which uses ordinary least squares regression, GWPath uses geographically weighted regressions (GWR) to fit the regressions composing the path model (Barreto *et al.* 2021). In the GWPath framework, path coefficients can vary regionally based on a Gaussian weighting function that assigns greater weights to geographically closer grid cells (Fotheringham *et al.* 2009, Barreto *et al.* 2021). Here, we used regionalizations based on a 1000 km bandwidth, which has been reported in previous studies to be the optimal width for capturing large-scale patterns in coefficient variation (Davies *et al.* 2011, Ficetola *et al.* 2017, Barreto *et al.* 2019, 2021). All analyses were conducted in the R environment (R Development Core Team 2022). All cartographic projections, including the biogeographical ignorance map and the regionalization of predictor driver effects, were created using QGIS v.3.4 (https://qgis.org/downloads) with the Blues colour palette.

RESULTS

The assessment of amphibian sampling data from the Amazon revealed crucial insights into the quality of currently available data. Despite our dataset housing >11% of the globally described amphibian species (Frost 2024) and >242000 occurrence records, we identified extensive sampling gaps and high knowledge ignorance throughout the Amazon. This result highlights the difficulty in understanding and interpreting the distribution patterns of Amazonian amphibians.

Taxonomic completeness

Taxonomic completeness (i.e. taxonomic refinement) was assessed for 38.8% of the Amazon (i.e. 990 cells) with ≥25 amphibian occurrence records, both at the species level and above the species level (Supporting Information, Fig. S2). Of these cells, 81.6% (808) are taxonomically refined (TaxC > .75), another 7.4% of the cells (73) are moderately well resolved taxonomically (.5 < TaxC < .75), and 11% of the cells (109) have poorly resolved taxonomic information (TaxC < .5) (Supporting Information, Fig. S2). Therefore, 61.2% of the cells (1562 of 2552) do not have sufficient data to be assessed according to the criteria set here (minimum of 25 records per cell), representing sampling gaps that lack diversity sampling for amphibians. The northeastern, northwestern, and southwestern regions of the Amazon have taxonomically well-resolved samples, whereas the southeastern, northwestern, and northern regions of the Brazilian Amazon predominantly show cells with low taxonomic resolution (TaxC < .5).

Sampling completeness

Only 17.1% of the cells with ~50 km resolution (437 cells in the study area) have >25 records at the species level (Supporting Information, Fig. S3). Of these analysed cells, 86.7% (365) were considered well sampled, with SC values ≥ .75. Another 5.5% of the cells (24) are considered moderately well sampled, with .5 < SC < .75, and 7.8% of the cells (34) are poorly sampled, with SC < .5. The well-sampled regions are mainly in the north, between Venezuela and French Guiana, in the west, primarily in Ecuador, and in the north, centre, and south of Peru. In the Brazilian Amazon, well-sampled cells are distributed primarily in the northwest region, in the basins of the Negro and Solimões rivers, in the centre, in the Amazon River basin, and in the southwest, in the basins of the Purus and Juruá rivers in the state of Amazonas, in addition to the southeast, along the Tapajós River basin in the state of Mato Grosso and the lower Xingu River basin in the state of Pará (Supporting Information, Fig. S3). The completeness analysis also reveals large sampling gaps in the Amazon (82.9%) according to the threshold established here, especially in the southern, southeastern, central-northern, central-western, and northwestern regions (Supporting Information, Fig. S3).

Temporal completeness

Our database showed a time span between the first and last sampling of 204 years (1818–2022). We calculated the temporal coverage for 34% of the study area through occurrences that included the year of the record in the database (869 of 2552 cells). The values for the TC index were low, with ~99% (860 cells) having TC < .5, indicating that most amphibian sampling in the Amazon is temporally sporadic (Supporting Information, Fig. S4). Few cells showed good temporal completeness (TC > .5), and these were concentrated mainly in the Ecuadorian Amazon, with smaller clusters in the eastern, central, and western regions of the Brazilian Amazon (Supporting Information, Fig. S4).

Biogeographical ignorance map

Only 16.5% of the Amazon (422 of 2552 cells) showed values for the three previously evaluated metrics. Significant taxonomic, spatial, and temporal biases were observed across the entire Amazon, especially in the southern, southeastern, central, northwestern, and northeastern regions (Fig. 3). Among the sampled cells, the majority exhibited high ignorance, particularly in the southeastern portion of the Brazilian Amazon (Fig. 3). Areas with low ignorance, although scattered throughout the Amazon, were concentrated mainly in the western region, in the Peruvian and Ecuadorian Amazon, and to the north, between eastern Venezuela and French Guiana. In Brazil, cells with low ignorance were spread across the entire Amazon, but with the highest concentration in the Amazon River basin, extending from east to west, in addition to other smaller areas in the northwestern and southwestern regions of Brazil (Fig. 3).

Drivers of biogeographical ignorance of amphibians in the Amazon

Our results indicate that river density, travel time, and human footprint were the main variables directly influencing the ignorance of amphibian knowledge in the Amazon (Standardized Coefficient (Std) = −0.27, P = .001; Std = 0.20, P = .001; and Std = −0.17, P = .001, respectively). The results revealed that ignorance is lower in areas close to rivers and with a higher human footprint (Fig. 4). River density was also the only variable with a positive effect on species richness; the higher the river density, the greater the species richness sampled. Travel time to the nearest human settlement also had a direct influence on sampling ignorance; the longer the travel time, the higher the ignorance. However, its effect was not significant for species richness. In contrast,

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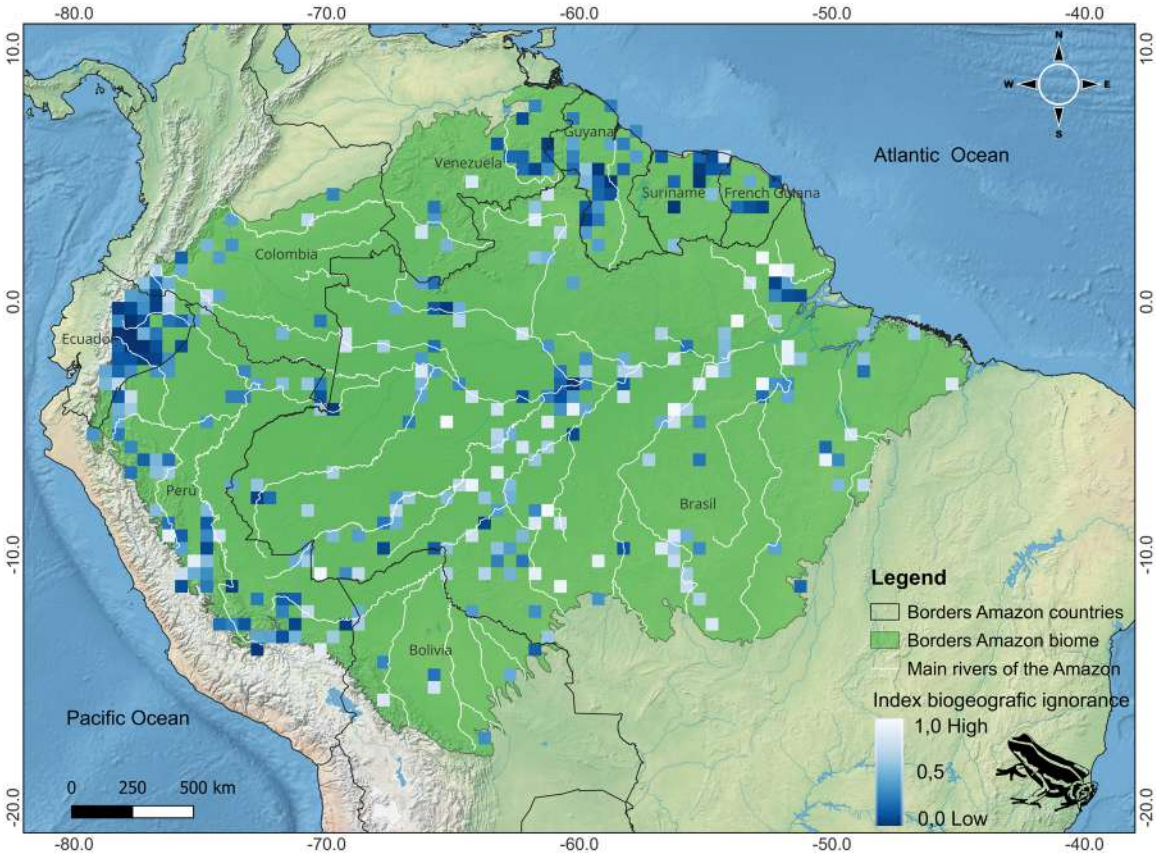

Figure 3. Map of biogeographical ignorance regarding amphibians in the Amazon, projected onto a 0.5° raster cell (~50 km × 50 km). Values close to one indicate greater ignorance, whereas values close to zero indicate less biogeographical ignorance. Locations where ignorance could not be calculated were considered non-sampled (NA).

there were no effects of protected areasdensity or species richness on the ignorance of amphibian knowledge in the Amazon. Our results also indicate indirect effects of the three variables (river density, travel time, and human footprint) mediated by species richness, but with a low effect value (Fig. 4; Supporting Information, Table S1).

Our results also indicate that the relative strength of the effects of the tested variables on ignorance is not spatially constant across all Amazon regions (Fig. 5). Although it is the strongest explanatory variable of amphibian ignorance in the Amazon (see Fig. 4), river density has a stronger effect on modulating ignorance, particularly in the central, eastern, and northwestern regions of the Amazon (Fig. 5; Supporting Information, Table S2). Travel time, although the second strongest variable in the global analysis, predominantly affects ignorance only in fragmented regions, mainly in the northern, northwestern, northeastern, central, and southeastern regions of the Amazon. Human footprint has a predominant effect on ignorance only in two opposite regions: one in the eastern and southeastern Amazon and another, smaller, in the northwestern region in southern Peru. Although protected areasdensity and species richness did not have significant effects on ignorance in the global analysis, they did have specific effects in explaining ignorance in the region, with the former being predominant in the western region, and the latter in parts of the northern and northwestern regions of the Amazon (Fig. 5; Supporting Information, Table S2).

DISCUSSION

Our results revealed important insights into the biases present in the available data on amphibian diversity in the Amazon. This conclusion is qualitatively similar to findings in several other taxa within this biome (Oliveira *et al.* 2016, Andrade-Silva *et al.* 2022, Carvalho *et al.* 2023), highlighting a common limitation in the understanding of Amazonian biodiversity. Our analyses involved the largest amphibian occurrence database for the biome, consolidating records that encompass >11% of the global amphibian diversity (Frost 2024), the highest diversity observed for any biome (Penhacek *et al.* 2024). Despite the extensive nature of the database, totalling >242000 occurrences, it is important to emphasize that this representation corresponds to <20% of the currently available amphibian records for the Amazon (Penhacek *et al.* 2024). This limitation arises from significant data gaps, notably the lack of geographical coordinates, a 'Wallacean deficit', and taxonomic incompleteness, a 'Linnean deficit' (Hortal *et al.* 2015), issues frequently observed in data from scientific collections (Hortal *et al.* 2015, Peterson *et al.* 2015, Anderson *et al.* 2020, Stropp *et al.* 2020, Araujo *et al.* 2022, Penhacek *et al.* 2024, 2025b).

When examining our data geographically, we observed a strong spatial bias, with areas of high taxonomic completeness concentrated mainly in the north and west of the Amazon, whereas vast regions in the south and southeast remain with low taxonomic resolution. The taxonomic deficit, or 'Linnean deficit', which

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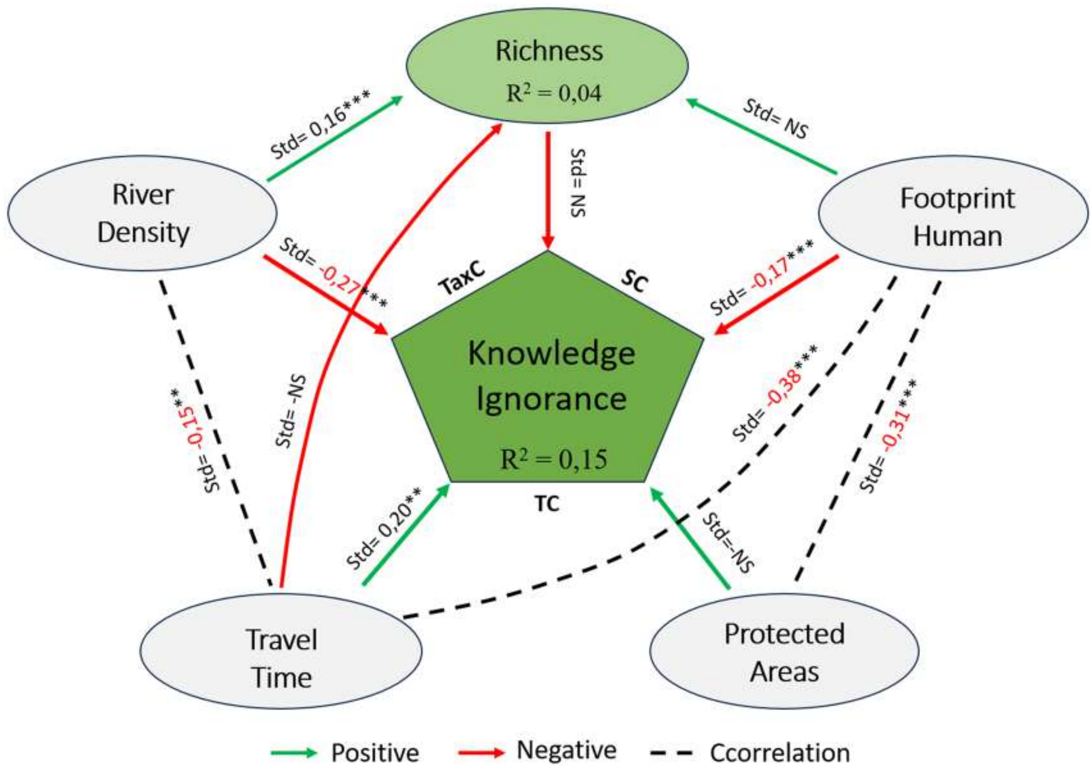

Figure 4. Piecewise structural equation models derived from hypotheses exploring the relationships between biogeographical ignorance of amphibian knowledge in the Amazon and environmental, economic, and social variables. The values next to the lines indicate the magnitude of the standardized regression coefficient. Indirect effects were calculated by multiplying the effect of the variable on species richness by the effect of species richness on biogeographical ignorance. Red values represent negative relationships and black values represent positive ones. Abbreviations: Std, Standardized Coefficient; NS, non-significant effects; SC, sampling completeness; TaxC, taxonomic completeness; TC, temporal completeness. Asterisks indicate the significance level for the relationship: *$P < .01$, **$P < .001$, and ***$P < .0001$.

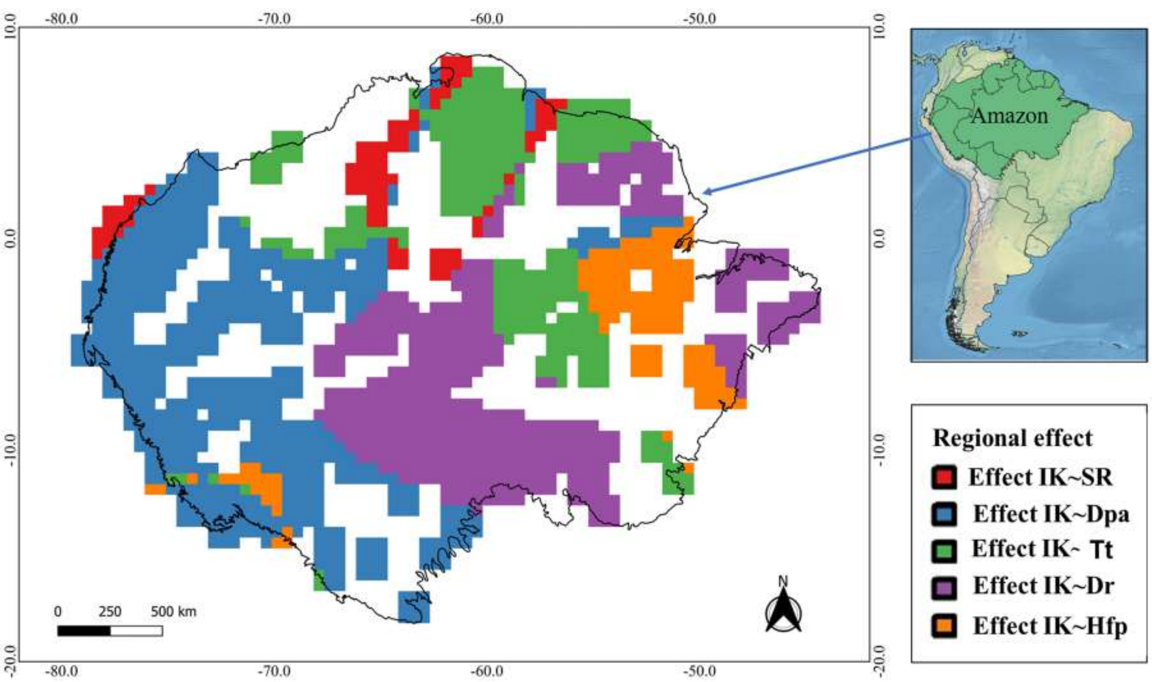

Figure 5. Geographically weighted path coefficients estimating the regional relationship between biogeographical ignorance in amphibian knowledge and natural, economic, and social predictor variables. Drivers with the strongest total effect on amphibian knowledge ignorance. Abbreviations: Effect IK, the effect of the predictor variable on knowledge ignorance; Dpa, protected area density; Dr, river density; Hfp, human footprint; SR, species richness.

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represents our lack of knowledge regarding the taxonomic identity of species (Cardoso *et al.* 2011, Hortal *et al.* 2015), is considered the most fundamental of all biodiversity knowledge gaps (Soberón *et al.* 2007). It is estimated that ~86% of terrestrial species and 91% of marine species are still unknown to science (Mora *et al.* 2011, Castro-Souza *et al.* 2024a). In short, spatial patterns of biodiversity cannot be discussed if we do not know which species we are dealing with (Castro-Souza *et al.* 2024a). This same uneven distribution was observed in sample completeness, with the northern, northwestern, and western regions exhibiting the best sample completeness, contrasting with undersampled or even unexplored areas in other regions, particularly the south and southeast. These sampling deficits are the main obstacles to the effective use of primary biodiversity data for species distribution modelling and for understanding regional ecological patterns and dynamics (Ladle and Hortal 2013). However, the exuberant biological diversity of the Amazon requires specialized taxonomic expertise, which is not always readily available. The lack of investment in biological assessments and the limited number of specialized taxonomists result in poorly resolved taxonomic records and, consequently, in low taxonomic completeness in datasets (Lawton *et al.* 1998, Magurran and Queiroz 2010).

Although previous studies have demonstrated a significant correlation between the number of species and higher taxonomic richness, such as genera, families, and orders, justifying their use in biodiversity monitoring programmes to reduce costs, especially in countries with limited financial resources (e.g. Balmford *et al.* 1996a, b, Bates *et al.* 2007, Heino and Soininen 2007, Carneiro *et al.* 2010, Kallimanis *et al.* 2012, Rosser and Eggleton 2012, Bennett *et al.* 2014, Bhusal *et al.* 2014, de Oliveira *et al.* 2020), a high variability in effect sizes across these studies was observed, indicating the need for prior evaluation before adopting simplified monitoring approaches (de Oliveira *et al.* 2020). Moreover, there are particularities in the ecological functions and ecosystem services specific to each species. Therefore, the adequate refinement of species data remains essential for a solid understanding of population dynamics within ecological communities.

In turn, the temporal analysis revealed that sampling is predominantly recent, especially in the Brazilian Amazon, with a concentration in the last two decades. Furthermore, temporal completeness showed that most samples are sporadic, with 99% of the evaluated cells presenting low temporal completeness. This sampling pattern in the Amazon creates a significant bias, hindering the proper understanding of the temporal dynamics of species and the impacts that anthropogenic environmental changes and climate change might have on biodiversity and its ecosystem services. The situation is exacerbated further by the slow accumulation of temporal records in the Amazon in comparison to the rapid loss of habitat owing to human threats (Sousa-Baena *et al.* 2014, Stropp *et al.* 2020). The Amazon is now at the threshold of making a rapid transition from a largely forested landscape to a non-forested one, and the changes are happening too quickly for species, people, and ecosystems to respond adaptively (Boulton *et al.* 2022, Albert *et al.* 2023). Consequently, many of the populations studied in the past might no longer be present today owing to environmental changes in their original habitats.

It is widely recognized that the Amazon still lacks comprehensive knowledge of its biodiversity (Oliveira *et al.* 2016, Stropp *et al.* 2020, Andrade-Silva *et al.* 2022, Araujo *et al.* 2022, Carvalho *et al.* 2023, Penhacek *et al.* 2024, 2025b), including amphibians, as evidenced by the present study. Thus, in conjunction with the metrics, the analysis of sampling ignorance revealed significant gaps, especially in the southern, southeastern, central, northwestern, and northeastern regions, highlighting the need for focused efforts in these areas to improve data quality. This represents a significant risk, particularly for the southern and southeastern regions of the Amazon, where all three metrics tested indicated low completeness (high ignorance of knowledge). These areas are part of the so-called 'Deforestation Arc', where industrial and agribusiness expansion has generated high deforestation rates, leading to the possible extinction of species before they are even described by science, resulting in the loss of biological heritage and ecosystem services (Albert *et al.* 2023).

As previously highlighted in several studies, logistical factors of accessibility and human influence emerge as the primary determinants of biodiversity knowledge in the Amazon (Hopkins 2007, Santos *et al.* 2015a, Oliveira *et al.* 2016, Stropp *et al.* 2020, Albuquerque *et al.* 2021, Araujo *et al.* 2022, Carvalho *et al.* 2023, Daru and Rodriguez 2023, Penhacek *et al.* 2024, 2025a, b). The low sampling rate of biodiversity in the region can be attributed to a series of complex and interconnected factors. The vast geographical extent of the Amazon, often covered by dense forests, coupled with its varied topography, presents significant logistical challenges for the systematic collection of biological data. These difficulties make scientific excursions expensive and prevent continued sampling, which is important for understanding the temporal dynamics of biodiversity in the face of anthropogenic and climatic changes. Furthermore, the limited infrastructure in some parts of the region, particularly in relationship to roads and research centres, contributes to sampling gaps. Historically, rivers have been the main transportation routes, influencing the distribution of research and sampling efforts, which are concentrated primarily in areas with greater fluvial access.

Recent studies have also highlighted that knowledge of biodiversity within protected areas is scarce, with >70% of these areas represented by <0.01 species records/km^2 (Oliveira *et al.* 2017, Andrade-Silva *et al.* 2022). Considering that National Protected Areas and Indigenous Territories (ITs) cover ~51% of the Amazon territory (RAISG 2024), the low sampling rate in these regions results in extensive gaps in the knowledge of Amazonian biodiversity. Although these areas were once symbolic of refuges for biodiversity owing to the minor anthropogenic changes they suffered, this reality has currently changed (Laurance *et al.* 2012). Increasing invasions by land grabbers, miners, and loggers, often illegal, fuelled by anti-environmental policies, especially in Brazil, have been altering these environments negatively and putting their biodiversity at risk (Laurance *et al.* 2012, Begotti and Peres 2019, 2020, Ferrante and Fearnside 2020, Siqueira-Gay *et al.* 2020). Thus, the lack of knowledge about biodiversity within these areas can lead to the extinction of many species even before they are described and studied by science. Overcoming these obstacles will require coordinated efforts, with serious government policies focused on the environment, investment in research and monitoring, in addition to the commitment of all to the conservation and sustainability of the region.

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Our findings show that factors such as river density, human footprint, travel time, and density of protected areas affect ignorance unevenly across different regions of the Amazon. For example, river density and human footprint have stronger negative effects on ignorance in the central, eastern, northwestern, and southeastern regions, facilitating the study of biodiversity in these locations, whereas travel time positively influences ignorance mainly in fragmented and difficult-to-access regions, such as the north and northeast. Furthermore, the density of protected areas, although not significantly affected in the overall analysis, negatively affects ignorance in large areas in the western Amazon, demonstrating that they constitute essential points of support for research in this region. These regional variations indicate that ignorance about amphibians is not a uniform phenomenon, but rather conditioned by a combination of geographical, social, and environmental factors.

Recognizing this spatial variation is essential to direct research and conservation efforts more effectively. By recognizing that ignorance is shaped differently in each region of the Amazon, it is possible to adapt approaches to studying and protecting biodiversity. Strategies that do not consider these specificities might fail to mitigate knowledge gaps, especially in areas with high species diversity or with more difficult access. In short, understanding how different factors influence ignorance in different regions of the Amazon is essential to optimize resources allocated to conservation and increase the effectiveness of scientific research on amphibians in the region.

CONCLUSION

This study provides a comprehensive analysis of the quality of amphibian sampling in the Amazon, revealing challenges faced not only by amphibians but also by several other taxa within the biome (Oliveira *et al.* 2016, Carvalho *et al.* 2023). The geographical analysis showed that well-resolved data are predominantly concentrated in the northern and western Amazon, whereas vast regions in the south, southeast, north-central, and northwest remain characterized by high taxonomic and sampling ignorance. Temporally, sampling is predominantly recent, which hinders the understanding of long-term species dynamics and their responses to environmental changes, such as deforestation and climate change.

The analysis also highlighted that accessibility, particularly through river density and human influence, are key determinants of the quality of biodiversity sampling in the Amazon. The lack of knowledge within protected areas (which cover >50% of the Amazon territory) further exacerbates the gaps in biodiversity data. This data deficiency poses an additional risk to the conservation of undescribed species and to the ecological balance of the biome.

The study further emphasized the urgency of overcoming the logistical and financial challenges that hinder the collection of biological data, especially in remote areas. Addressing the gaps and biases in sampling Amazonian biodiversity is crucial not only for understanding its richness but also for formulating effective conservation policies. Without solid data, it becomes challenging to predict and mitigate the impacts of environmental change, which compromises the ecosystem services of the Amazon, vital for global balance.

Finally, the results reveal the complexity of the relationship between the lack of knowledge about amphibians and socio-environmental factors in the Amazon. The uneven distribution of the impacts of these variables suggests that conservation policies and research strategies must be tailored to local realities. Rather than adopting a one-size-fits-all approach for the Amazon, regional specificities should be taken into account to optimize research and conservation efforts.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

DATA AVAILABILITY

The data underlying this article are available in the article and in its online Supporting Information.

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