Animal Conservation

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The Importance of Environmental Heterogeneity in Evaluating the Conservation Status of Two Frog Species in a Changing Amazonian Interfluve

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ABSTRACT

Identifying the most effective criterion to assess the conservation status of vulnerable species in threatened tropical regions is crucial to evaluate recovery plans. We investigated the influence of environmental heterogeneity on the extent of occurrence (EOO), area of occupied habitat (AOH), and density variation of two Amazonian riparian frog species, *Allobates sumtuosus* and *Amazophrynella manaos*. We searched for the species in 86 sites in the Negro–Nhamundá Rivers interfluve between 2016 and 2019, using visual and acoustic searches in 250 × 10 m plots established on banks of small streams in *terra-firme* dense rainforests. EOO greatly overestimated the AOH for the studied species. This is likely due to the contrasting responses of the species to broad-scale environmental heterogeneity. The density index of the species varied in response to both abiotic and biotic factors, and few locations harbored high densities. Therefore, reserves to enhance the conservation of both species should be based on environmental determinants of intermediate density indices. The large EOO indicates resistance to threats at the species level. However, the species' restricted AOH suggests low resilience at the population level. This is critical given the current habitat degradation across the studied region. Extent of occurrence is likely to be a poor indicator of conservation status for many Amazonian frogs.

1 | Introduction

Conservation assessment is critical for species associated with threatened ecosystems. The extent of occurrence (EOO—the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known occurrence of the taxon) and area of occupancy (AOO—area within its EOO that is occupied by the taxon) are key criteria to assess the conservation status of species (i.e., criteria B (1 and 2)—IUCN Standards and Petitions Committee 2024; Brooks et al. 2019). Complementarily, density-index (DI) variation data (i.e., changes in the number of individuals per defined area between different areas where the species occurs) is useful to guide reserve allocation (Santini et al. 2018). However, occurrence and detailed ecological data for many tropical vertebrates is scarce (Carvalho et al. 2023), and only EOO is available for conservation assessments [i.e., The IUCN Red List of Threatened Species 2023; Internacional Union for Nature Conservation (IUCN) SSC Amphibian Specialist Group and Instituto Boitatá de Etnobiologia e Conservação da Fauna 2023]. This is especially worrisome for small and cryptic species associated with specific ecological conditions, for which EOO greatly overestimates AOO (Gaston and Fuller 2009; Jetz et al. 2008). Therefore, integrating environmental heterogeneity into spatial– and numeric–based metrics (EOO, AOO and DI) is needed to assess the conservation status of vulnerable species distributed in threatened tropical regions.

Amazonia harbors at least 10% of the known species on Earth, which are increasingly exposed to deforestation and forest degradation, such as edge effects, logging, fires, and extreme droughts (Flores et al. 2024). Therefore, characterizing EOO and AOO for vulnerable Amazonian vertebrates and their broad-scale environmental associations is required, but largely underexplored. EOO is a measure of resistance, based on the degree to which risks from threatening factors are spread across a species' geographical distribution, which is related to species' physiological tolerance (e.g., climatic conditions); whereas AOO is a measure of resilience, based on the degree to which species can recover against risks from spatially explicit threats (IUCN Standards and Petitions Committee 2024), and may be associated with the availability of specific environments (e.g., breeding sites). DI could be interpreted as a measure of population health and robustness (i.e., a proxy for vulnerability to extinction; Noss et al. 2002) and may vary in response to biotic and abiotic interactions (Santini et al. 2018). Variation in productivity, soil physical–chemical properties, topography, and climate (i.e., environmental heterogeneity: spatial nonuniformity of components or constituents of abiotic and biotic elements; Stein and Kreft 2015; Stein et al. 2014) is associated with the occurrence of many species of Amazonian vertebrates at broad scales (e.g., Mammals—Gonçalves et al. 2022; Frogs—Ferreira et al. 2018; Snakes—de Fraga et al. 2018; Birds—Borges 2013). However, it is unclear how environmental heterogeneity influences the proportion of an area occupied by species (AOO).

Area of occupancy is based only on occurrence data, which in most cases is biased by sampling effort (IUCN Standards and Petitions Committee 2024). In this context, the Area of Occupied Habitat (AOH) based on presence-absence Species Distribution Modeling represents a potential alternative for AOO (Marsh et al. 2023; Brooks et al. 2019). Moreover, understanding patterns of density-index variation and its environmental correlates within AOH gives an overall measure of resilience variation among occupied areas and is useful to support further conservation decisions. For example, a study indicated the best portion of a Central Amazonian reserve to protect two riparian frog species based on the relationship between site-scale environmental heterogeneity and their density-index variation (Jorge et al. 2016). Frogs are the most threatened vertebrates worldwide and a functionally diverse group in the riparian ecosystems of Amazonia, which have been severely degraded by human occupation (Barrow 2006). Hence, understanding the role of biotic and abiotic factors on density variation of riparian Amazonian frogs provides essential information to mitigate threats.

Density variation of Amazonian frogs is frequently associated with subtle changes in abiotic conditions (e.g., Moreno et al. 2023; Ferrão et al. 2018; Ferreira et al. 2018). However, the role of biotic interactions on density variation of ecologically similar but evolutionarily distinct species is unknown for Amazonian frogs. Investigating the role of both biotic and abiotic factors on species density variation at the site scale (i.e., realized niche), along with information on species' occurrence and occupancy patterns across broad-scale environmental gradients (i.e., fundamental niche), can help to advance our understanding of the role of stabilizing (i.e., increasing niche differences) and equalizing (i.e., decreasing fitness differences) mechanisms in mediating the coexistence of ecologically similar species in species-rich tropical regions.

The central goal of the present study was to investigate the influence of environmental heterogeneity on occurrence and occupancy patterns and density-index variation of two Amazonian frog species to identify the main threats to their conservation. The frogs *Allobates sumtuosus* Morales 2002 (Aromobatidae) and *Amazophrynella manaos* Rojas, Carvalho, Ávila, Farias, and Hrbek 2014 (Bufonidae) were used as models in the present study. The known distribution of *A. sumtuosus* is mostly within the Negro-Nhamundá Rivers interfluve (NNI—Amazonas state, Brazil), but diverging lineages may range further into the Guyana Shield and beyond the Nhamundá River (Motta et al. 2018; Simões et al. 2013), whereas *A. manaos* is known to occur 50 km further east until the Trombetas River (Rojas-Zamora et al. 2014).

We chose these species because they are broadly distributed across the interfluve in Central Amazonia, Brazil (Rojas-Zamora et al. 2014; Simões et al. 2013), and their known close association with specific breeding sites. They occur sympatrically and are syntopic only in some heterogeneous riparian environments in dense rainforests, and are locally abundant and highly detectable by visual and auditory surveys during the rainy season (Jorge et al. 2016; Menin et al. 2011; Lima et al. 2006). Despite the limited distribution records for these species, their current conservation status is "Least Concern" (IUCN 2023). Therefore, these species are good models to evaluate how contrasting conclusions of conservation assessments based on EOO or habitat-related AOO (hereafter AOH) can be related to the species' responses to environmental heterogeneity.

Specifically, we aimed to answer the following questions: (1) Is EOO or AOH the most appropriate metric to assign a threat category for the focal species; (2) How does the relationship between the occurrence (presence or absence) of the focal species and broad-scale environmental heterogeneity relate to their EOO and AOH? and (3) How do abiotic (i.e., site-scale environmental heterogeneity) and biotic factors (i.e., density of the other species) affect the density-index variation of the focal species across AOH?

For these questions we (1) hypothesized that EOO and AOH would produce contrasting conservation status for the focal species due to their specific association with riparian ecosystems; (2) predicted a large EOO for the species due to their expected wide distribution across climatic gradients, and a restricted AOH due to the species' patchy occupancy across edaphic, topographic, and productivity gradients; and (3) expected different effects of abiotic and biotic factors on each species' density-index variation across their AOH.

2 | Materials and Methods

2.1 | Focal Species

Allobates sumtuosus is a small [Snout-vent length range (SVLr): Males = 14–16 mm; females = 16–17 mm], diurnal, terrestrial, and cryptic species, whose tadpoles develop in isolated ponds, mainly on the margins of black-water streams, where males call intensively during the rainy season (Lima et al. 2006). The species has a generalist diet, although its most frequent prey items are ants (Formicidae) and springtails (Collembola) (see Juncá and Eterovick 2007 for the feeding ecology of a closely related species).

Amazophrynella manaos is a small (SVLr for 29 Males = 14–15.8 mm; and for 28 Females = 15.9–24.7 mm; Rojas-Zamora et al. 2014), terrestrial, diurnal, and cryptic species, whose tadpole development is in interconnected ponds mainly on the margins of black-water streams. The males actively call during the rainy season (Lima et al. 2006). Its diet overlaps greatly with that of *A. sumtuosus*, but its most frequent prey items are ants (Formicidae) and soil mites (Acarina) (Taveira et al. 2020).

2.2 | Study Area

The NNI has heterogeneous soils (Quesada et al. 2010) that sustain *terra-firme* (i.e., forests not flooded by large Amazonian rivers) submontane and lowland dense rainforests [Instituto Brasileiro de Geografia e Estatística (IBGE) 2004]. These forests are drained by acidic black– or less-acid clear–water streams. Topographical relief within the interfluve varies between 30 and 339 m a.s.l., and is limited to the south by the Amazon River and to the north by savanna vegetation (Figure 1). Annual precipitation (1970–2000) varied between 1971 and 3017 mm (Fick and Hijmans 2017).

2.3 | Sampling Design

We used visual and auditory searches for individuals of the species in 86 RAPELD [Rapid Assessment Program (RAP) surveys in Long–Term Ecological Research (LTER—PELD in Portuguese); Magnusson et al. 2005] riparian plots. Plots were separated by at least 1.1 km from each other. Plots were divided into 25 10-m wide subplots located along margins of 1st, 2nd, and 3rd order streams of four tributaries of the Negro River and five tributaries of the Amazon River (Figure 1). The number of subplots with at least one individual was recorded, generating a density index varying from 0 to 25.

Searches (one per plot—see exceptions below) were undertaken during the rainy season (November–March) from 2016 to 2019, between 0700–1000 and 1500–1730, periods when males were more actively calling. We resampled entirely those plots where no individual was recorded in first searches (mean 2 days between searches) to confirm absences. A previous study indicated that diurnal frogs were unlikely to go undetected in searches undertaken during the breeding season (Jorge et al. 2016). In that study, most of the absences were confirmed in second-round surveys (*A. sumtuosus* and *A. manauensis*; Jorge et al. 2016). Visual searchers were conducted using a 130-lm head torch (Kathmandu Panthon 130) to increase detectability for these cryptic frogs. Combining survey methods (visual and auditory) to search for abundant and aggregated frog species greatly improves detectability (McCarthy et al. 2013).

2.4 | Environmental Variables

2.4.1 | Broad-Scale Environmental Variation

To represent broad-scale environmental heterogeneity, we used five variables: (1) Precipitation Seasonality [PS—%; grain size (gs) = 1 km^2; Fick and Hijmans 2017]; (2) Walsh Index, which describes the severity of the dry season (WI; gs = 1 km^2; Amaral et al. 2013); (3) JERS (Japanese Earth Resources Satellite), which describes flooded-area extent during the high water of large Amazonian rivers (gs = 100 m^2; Hess et al. 2015); (4) Soil sand content (SA—%; gs = 1 km^2; Hengl et al. 2014); and (5) Soil Organic Carbon (SOC—ton/ha; gs = 1 km^2; Hengl et al. 2014).

These variables are related to physiological tolerance (i.e., PS, climatic conditions); temporal availability of breeding ponds (i.e., WI, more severe dry seasons, shorter hydroperiod of ponds); spatial availability of breeding sites (JERS—closer to flooding areas of large rivers, fewer unflooded stream-banks are available as breeding sites); quality of breeding ponds (e.g., SA—sandy stream-banks are more likely to form isolated and interconnected ponds, apart from stream margins); and growth requirements (e.g., SOC, productivity as a proxy for availability of food) of frog species.

We clipped the raster layers (i.e., broad-scale environmental variables) for the studied area extent and resampled them to 500-m^2 gs to extract the values using the *extract* function of the "Dismo" version (v.) 1.3.4 (Hijmans et al. 2017) R v. 4.3 (R Core Team 2023) package. Extracted values (i.e., values of the broad-scale environmental variables used in the presence-absence analyses—see subsection 2.5.2) refer to geographic coordinates recorded at the beginning of each plot (i.e., 1.5 m from stream margin) using a Garmin 64s GPS (error ± 3 m/Datum WGS 1984). The distribution of sampling sites across broad-scale environmental gradients within the study area is found in Figure S1.

2.4.2 | Site-Scale Environmental Variation

To represent the environmental heterogeneity that varies at finer scales, we used the stream pH, which directly influences the pH of ponds on stream banks (Jorge et al. 2016), as water

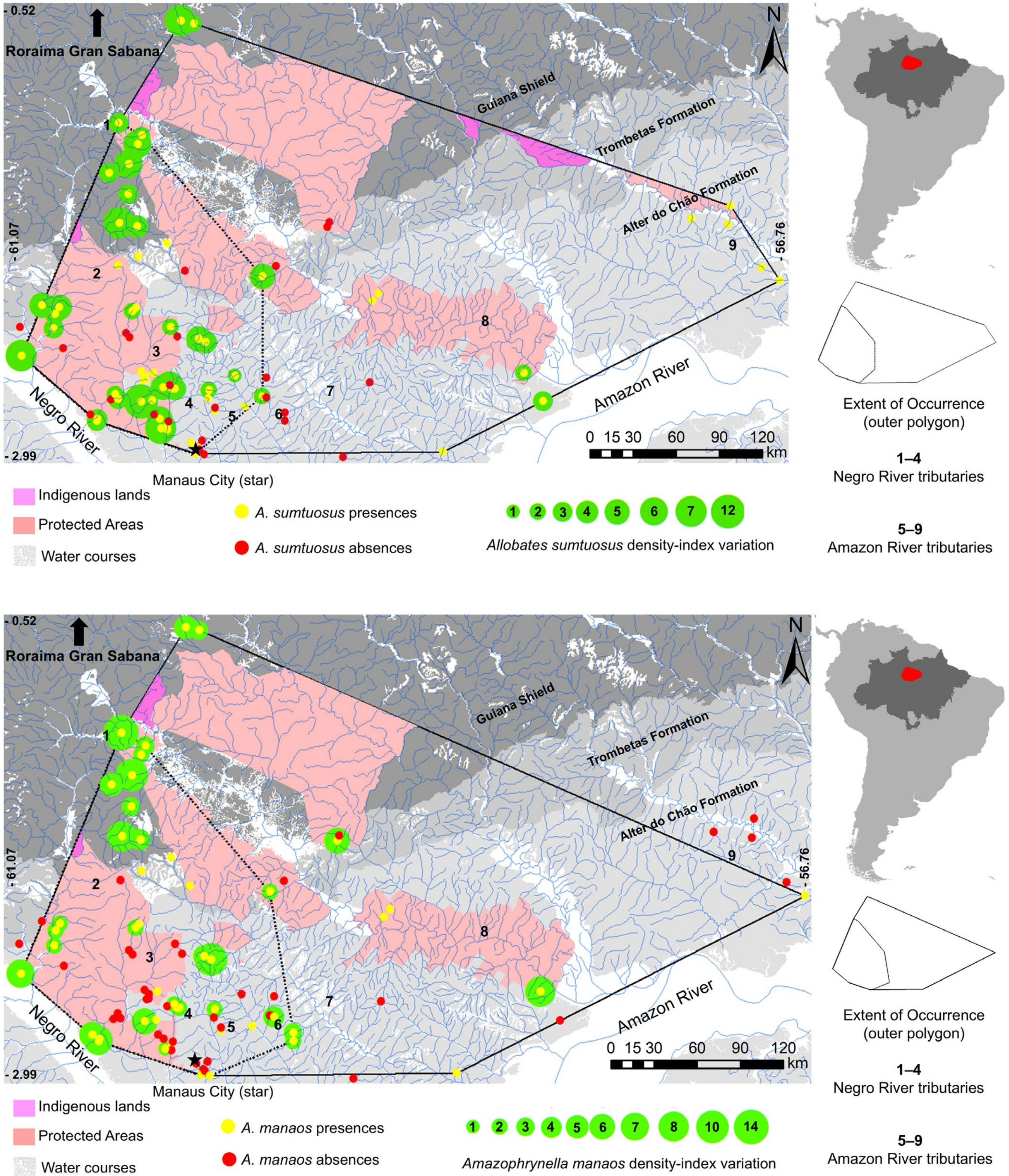

FIGURE 1 | Presences (yellow dots), absences (red dots), and density-index variation (green circle size) for *Allobates sumtuosus* (top map) and *Amazophrynella manaos* (bottom map) within their Extent of Occurrence (EOO; MCP—Minimum Convex Polygon), within the Negro-Nhamundá Rivers interfluve (NNI), between the Amazon River and the Gran Sabana, State of Roraima. Gray colors represent different geological formations; pink indicates indigenous lands; salmon Protected Areas, and lines are stream and river networks within the following drainage systems: Negro River (1) Camanaú, (2) Apuaú, (3) Cuieiras, and (4) Tarumã-Açú; and Amazon River (5) Puraquequara, (6) Rio Preto, (7) Urubu, (8) Uatumã, and (9) Nhamundá. The dashed polygon within the species' EOO is the MCP calculated without dispersed and extreme eastward points. This specific portion of the species' EOO is under severe degradation. Inset map (top right of each map) shows the limits of South America (light gray shadow), Brazilian Amazonia basin (dark gray shadow) and the study area (red polygon).

pH restricts the development of tadpoles of some frog species; stream discharge (SD), which is related to the intensity of flooding events after heavy rains that can wash away adults, eggs, and tadpoles; and canopy openness (CO—as the mean of six equidistant measurements obtained along plots), as radiant heat penetration may influence the survival of adults of the focal species. Detailed procedures used to obtain site-scale variables are given in Jorge et al. (2020). Geographic coordinates of the sampling sites and the data used in this manuscript can be assessed at https://ppbiodata.inpa.gov.br/metacatui/data/RafaelFilgueiraJorge. Descriptive statistics and correlation matrices are given in Tables S1–S3.

Multicollinearity was low [VIF—Variance Inflation Factor < 5 in all cases; see James et al. 2017 for VIF thresholds] for all predictor variables in all analyses (Tables S4 and S5). We detected spatial autocorrelation (i.e., Moran Index) associated with pH (within 2.7 and between 13 and 19 km; $p < 0.05$) and CO (within 3 km; $p < 0.05$), but not for the response variables (density-index variation of each species) or for SD in any distance class ($p > 0.05$; Table S6), so autocorrelation is unlikely to cause type I error in statistical tests (Legendre et al. 2002). VIF and autocorrelation analysis were conducted in the "MASS" v. 7.3.60 (Venables and Ripley 2002) and "pgirmess" v. 2.0.3 (Giraudoux 2023) R packages.

2.5 | Spatial and Statistical Analyses

2.5.1 | Extent of Occurrence and Area of Occupancy

We used presences (*A. sumtuosus*, $N = 62$; *A. manaos*, $N = 47$) to estimate species EOO, which is defined as the area within a minimum convex polygon (MCP) enclosing presence records, using the *eoo* function of the "red" v. 1.6.1 (Cardoso 2017) R package. We estimated the species' AOH as a proxy for AOO using a presence-absence model-based Species Distribution Modeling approach.

The steps to calculate AOH were as follows: we (1) estimated presence-absence Generalized Linear Models (GLMs), as described below; (2) created raster stacks with the raster layers (broad-scale environmental variables—resampled for 2×2 km grain size) used in GLMs; (3) projected the occurrence probability for each species across their entire EOO by multiplying the coefficients from GLMs by the cell values of raster stacks using the *predict* function of the "car" v. 3.1.3 (Fox and Weisberg 2019) R package; (4) converted the occurrence probability maps into presence-absence maps based on True Skill Statistic (TSS = sensitivity + specificity − 1). For this, we used probability thresholds ranging from 0 to 1 to create presence-absence maps at every 0.01 units and estimate sensitivity (proportions of presences projected to be in unoccupied areas) and specificity (proportion of absences projected to be in occupied areas) for each one; (5) chose the threshold that maximized the TSS to produce the final presence-absence maps; (6) multiplied the number of "presence" cells by 4 ($km^2 = 2 \times 2$ km cell size as recommended by IUCN) to estimate initial AOHs (i.e., broad occupied habit type—terra- firme dense rainforest); and (7) divided the initial AOHs by the average drainage density (km/km^2) calculated over the entire initial AOH of each species to estimate the final AOHs (i.e., specific occupied habitat type—riparian zones).

The seventh step was taken to account only for riparian environments within the AOHs (i.e., drainage density within AOH; Figure S2). Our results on EOO and AOH only refer to NNI. We define "contrasting conservation status" at the first research question as EOO:AOH ratio $< 10\%$ correspondence in area size, for example: a species with an EOO = X km^2 should have an AOO = X/10 km^2 and either EOO or AOO (AOH here) should indicate the same conservation status for that species (IUCN Standards and Petitions Committee 2024). Map processing was conducted in ArcGis Desktop v. 10.8.2 (ESRI 2011).

2.5.2 | Presence–Absence and Density Variation Analyses

We used Generalized Linear Models (GLMs—binomial distribution) to estimate how much of the variation in presences (*A. sumtuosus*, $N = 62$; *A. manaos*, $N = 47$) and absences (*A. sumtuosus*, $N = 24$; *A. manaos*, $N = 39$) of the focal species could be explained by broad-scale variables (i.e., extracted values from raster layers of each broad-scale environmental variable from each sampling location—fundamental niche).

We used GLMs (negative binomial distributions for aggregated counting data) to estimate how much of the density-index variation of the species ($N = 55$ plots with data for all site-scale variables) could be explained by biotic (i.e., each focal-species density-index variation as predictor of the density-index variation of the other species) and abiotic (i.e., stream and stream bank characteristics) variables (i.e., realized niche).

For both GLMs, we first constructed a model considering only linear terms, and additionally constructed models including second-order polynomial-transformed terms individually for each predictor variable (i.e., five additional models for presence-absence GLMs and four for density-variation GLMs). We then used the Akaike Information Criteria (AIC) from the *stats* v. 4.3.2 R package (R Core Team 2023) to evaluate the contribution of transformed terms to polynomial models relative to linear ones. The final models included linear and polynomial terms only when those polynomial-transformed variables reduced the AIC by at least two units compared to the linear model (Tables S7 and S8). We did not include biotic variables in the presence–absence analysis (i.e., the fundamental niche). We undertook the GLM analyses using the "lme4" v. 1.1.35.1 (Bates et al. 2015) and "MASS" v. 7.3.60 (Venables and Ripley 2002) R packages.

3 | Results

3.1 | Discrepancies Between the *Extent of Occurrence and Area of Occupied Habitat*

Allobates sumtuosus and *A. manaos* occur broadly (results for EOO and AOH are in thousand km^2) in the NNI (EOO = 55.9 and 51.7, respectively), but occupy a restricted portion within their range [area AOH initial = 43.4 (cutoff threshold = 0.77; TSS = 0.52), area AOH final = 2.38 (area initial AOH/18.24 km/km^2 average drainage density); area AOH initial = 46.6 (Cutoff threshold = 0.59; TSS = 0.39); area AOH final = 2.49 (area initial AOH/18.77 km/km^2 average drainage density), respectively]. EOO and AOH final gave contrasting (EOO:AOH final < 5% ratio) conservation status for the studied species ("Least Concern" versus "Near threatened", respectively). Therefore, using AOH as a proxy for AOO seems better to assign a threat category for them due to EOO:AOH ratio inconsistencies.

3.2 | Relationship Between Species Presence–Absence and Broad-Scale Variables

The final presence–absence GLMs included linear (*A. sumtuosus*: PS, WI, and JERS; *A. manaos*: WI, JERS, SA, and SOC) and polynomial–transformed (*A. sumtuosus*: SA and SOC; *A. manaos*: PS) terms (Table S4). Both species were detected across a wide range of PS and WI gradients, although estimates of occupancy probability were patchy across the study area (Figure 2). This likely explains the species' large EOO, but restricted AOH final. *A. sumtuosus* was positively associated

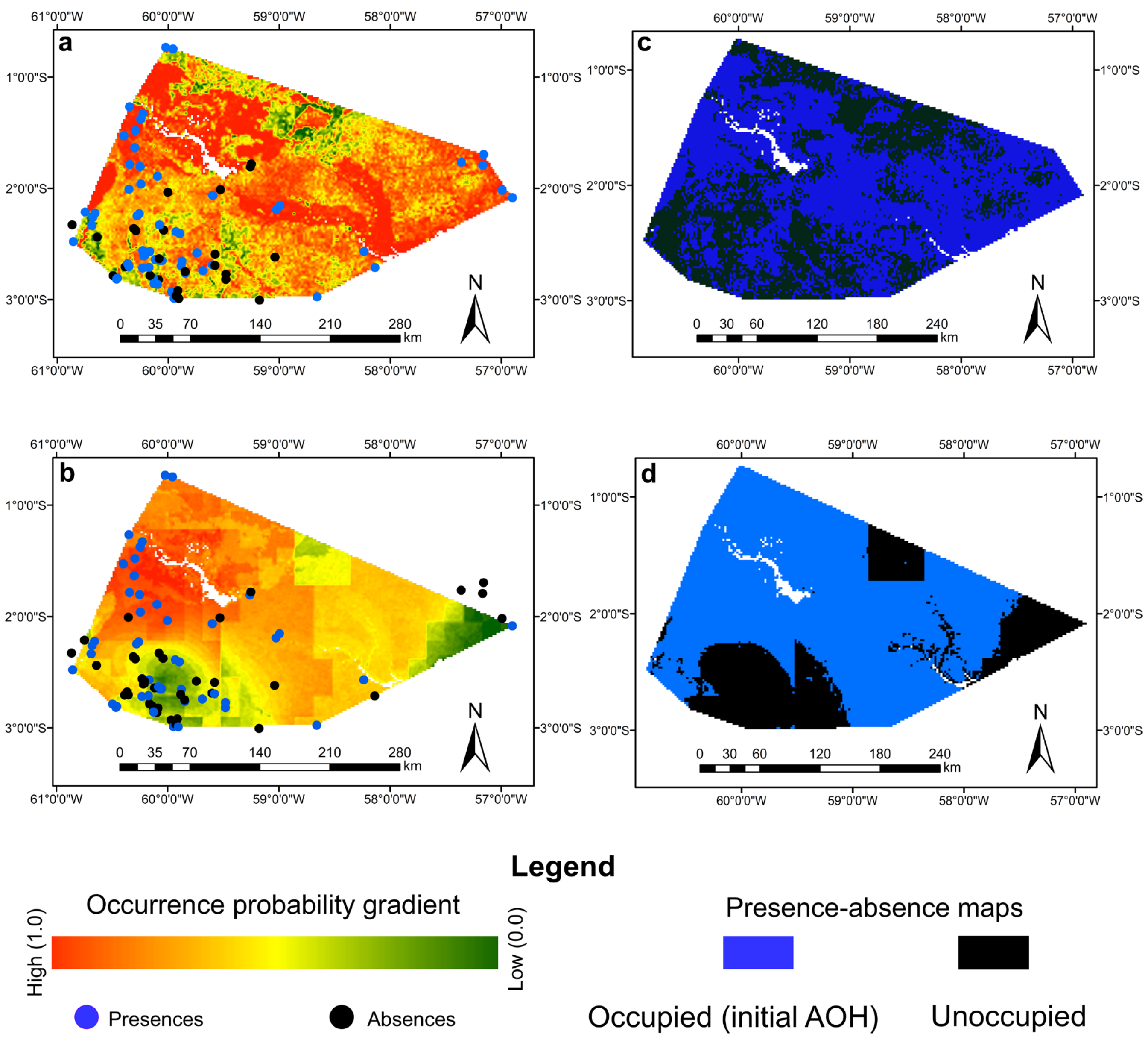

FIGURE 2 | Presence-absence model-based Species Distribution Modeling maps. Left: Occurrence probability maps based on the coefficients of the presence-absence Generalized Linear Models for (a) *Allobates sumtuosus* and (b) *Amazophrynella manaos*. Right: Presence-absence maps (initial Area of Occupied Habitat—AOH) generated from occurrence probability maps based on True Skill Statistics (TSS) thresholds for (c) *A. sumtuosus* (threshold = 0.77) and (d) *A. manaos* (threshold = 0.59). Initial AOH estimates (*A. sumtuosus* = 43.4 thousand km^2; *A. manaos* = 46.6 thousand km^2) likely represent the broad environmental type occupied by the studied species (i.e., *terra-firme* dense rainforests). Circles on "a" and "b" and colors on "c" and "d" maps represent presences (blue) and absences (black). Colored bars for "a" and "b" maps represent high (red) and low (green) occurrence probabilities.

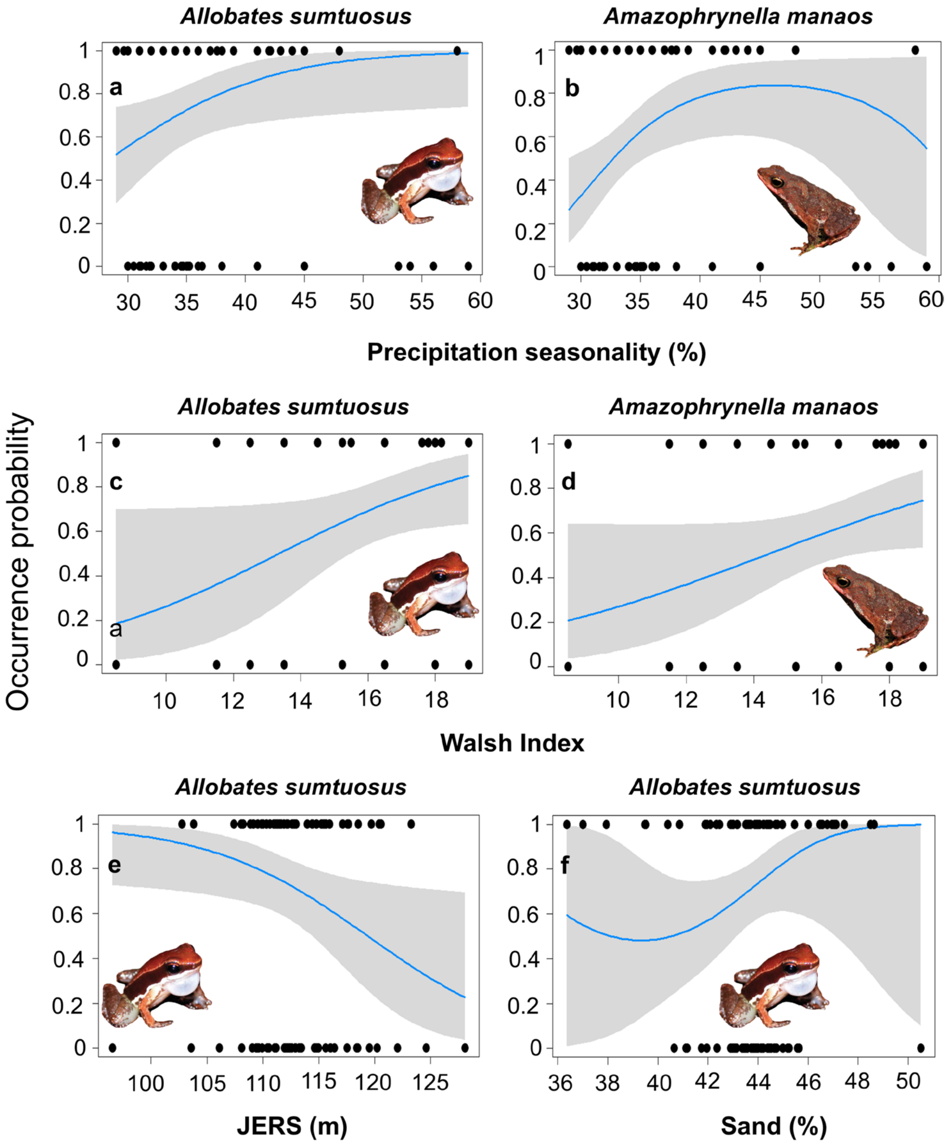

FIGURE 3 | Relationships between the probability of occurrence of *A. sumtuosus* (a, c, e, f) and *A. manaos* (b, d) and broad-scale environmental variables estimated in Generalized Linear Models (GLMs—binomial distribution) using presences (*A. sumtuosus*, *N* = 62; *A. manaos*, *N* = 47) and absences (*A. sumtuosus*, *N* = 24; *A. manaos*, *N* = 39) of the studied species from 86 sampling sites. a, b—Precipitation seasonality (%); c, d—Walsh Index; e—JERS (m); and f—Soil sand content (%). Plots only present statistically significant relationships. JERS, Japanese Earth Resources Satellite. Photos: AP Lima.

with PS, whereas *A. manaos* avoided areas at PS extremes (Figure 3a,b). Both species seem not to tolerate severe dry conditions (Figure 3c,d), although they showed distinct responses to other variables. *A. sumtuosus* was also associated with the flood zone of large rivers with sandy soils (Figure 3e,f), variables that did not significantly influence *A. manaos* distribution. SOC did not significantly affect either species' distribution (Table S4).

3.3 | Biotic and Abiotic Determinants of the Species' Density Variation

The final density-index GLMs included only linear terms (Table S5). Biotic and abiotic variables had different effects on species density-index variation. *A. sumtuosus* density was higher on margins of more acidic streams, and that of *A. manaos* was higher on margins of less acidic streams (Figure 4a,b). The species' densities had a marginally significant positive relationship with each other (Table S5). In spite of the estimated positive association between the densities of the two species, the highest density-index values were observed in areas with low to intermediate density of the other species (Figure 4c,d). SD and CO did not influence the density variation of either species (Table S5).

4 | Discussion

We showed that the EOO and AOH estimated in the present study gave very different conservation statuses for the study species, based on criteria and recommendations of the IUCN guidelines (e.g., geographic range; IUCN Standards and Petitions Committee 2024). These results can be explained by the varying extents and forms that different broad-scale variables influenced the occurrence probability of each species. Niche differences probably determine their sympatric coexistence at broad spatial

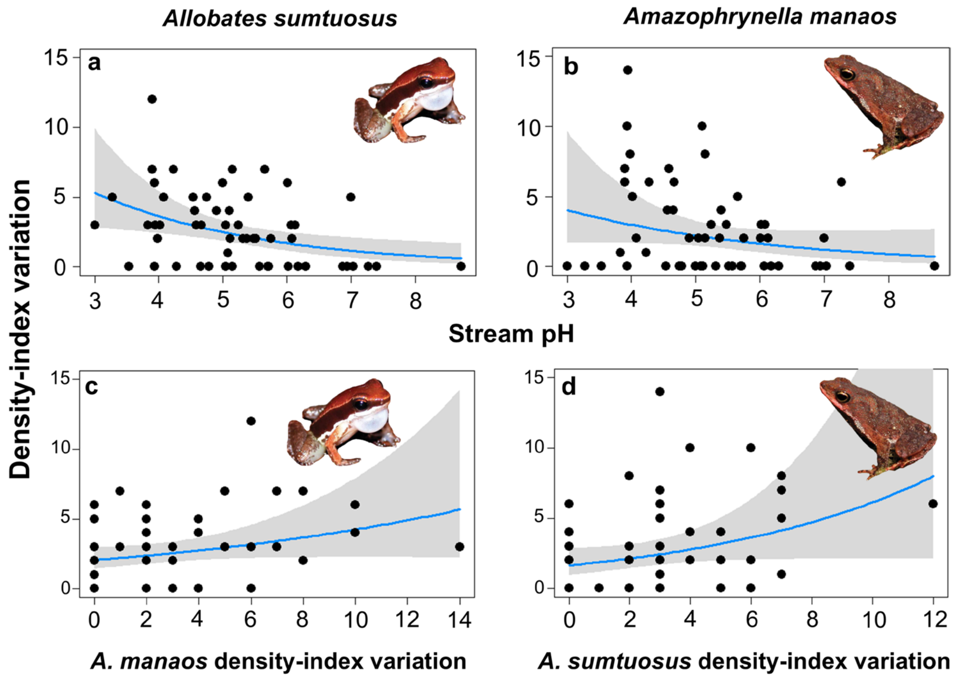

FIGURE 4 | Relationships between density-index variation (i.e., the number of subplots with at least one individual recorded during surveys—generating a density index varying from 0 to 25 per plot) of *A. sumtuosus* (a, c) and *A. manaos* (b, d), and stream pH (a, b) and the other species density-index variation (c, d) estimated in density variation Generalized Linear Models (GLMs—negative binomial distribution) from 55 sampling sites. Plots only present statistically significant relationships. Photos: AP Lima.

scales. At the site scale, biotic and abiotic factors determined differentially the species density variation between sampling sites. This may be a case of syntopic coexistence governed by the interplay of niche and fitness difference mechanisms (i.e., based on the relationships between the species' density variation and biotic and abiotic local predictor variables; Carroll and Nisbet 2015). Some biological characteristics (i.e., physiological tolerance to precipitation seasonality) of the study species are likely to enhance their resistance to threats (i.e., large EOO). Of relevant concern is that the categorization based only on EOO for the studied species masks their likely low resilience against threats (i.e., reduced AOH), due to the species response to other environmental characteristics related to reproduction (i.e., availability of breeding sites). Based on the distribution of densities across the species' AOHs, few areas are suitable to maintain large populations of the species. The ongoing habitat degradation and climate change pose a severe threat for the studied and many other riparian species in the study area.

Generalist breeding species have large niche breadths, reflecting their broad geographic range, whereas specialist breeding species have a restricted geographic area related to their narrow niche breadths (e.g., Odonata—Olsen et al. 2022). However, the niche breadth of species that tolerate wide ecological conditions is positively related to occupancy area, whereas the niche breadth of species associated with specific ecological conditions is negatively related to occupancy area (e.g., Birds—Hurlbert and White 2007). The studied species have a high occurrence probability throughout much of the precipitation seasonality gradient (i.e., large niche breath/tolerance for climatic conditions), a broad biogeographic pattern found for Amazonian anurans (Vacher et al. 2020). This may explain the species' large EOO. However, their patchy occupancy is concentrated in narrow portions of gradients related to temporal availability of breeding sites (i.e., both species—WI) and spatial availability and quality of breeding sites (i.e., *A. sumtuosus*—JERS and SA, respectively), probably causing their restricted AOHs. These results may also explain the larger EOO and smaller AOH for *A. sumtuosus* in relation to the smaller EOO and larger AOH for *A. manaos*.

Concern related to the restricted AOH found for the species is exacerbated by the fact that few areas harbor high densities, meaning their resilience is not homogeneous across their AOH. The sympatric coexistence of the species seems to be mediated by niche differences across broad-scale environmental gradients (i.e., spatial resource partitioning), and their positive density relationships where they are syntopic could be explained by the storage-effects hypothesis (i.e., stable coexistence), given their varying degrees of association with similar site-scale environmental gradients (i.e., pH, increasing niche differences at local scales—stabilizing mechanisms). The different responses of the studied species to stream pH and the contrasting distribution of their higher densities may be explained by the Intermediate Disturbance Hypothesis, as their distinct reproductive requirements may lead them to outperform the other at more suitable areas for each one (i.e., competitive interactions—equalizing mechanism; Chesson 2018, 2000). Antagonistic interactions are expected between ecologically similar species with highly overlapping diets (Lanuza et al. 2018; Letten et al. 2017). However, the studied species have generalist diets and the main apparent limiting resource (i.e., reproductive sites) for the species is distinct, which may cause intra-specific competition to be stronger than inter-specific competition. Nevertheless, more direct manipulations would be necessary to evaluate these hypotheses, and many factors other than competition may be involved.

4.1 | Conservation Implications

Considering only EOO, the threat category for the focal species would be, and currently is, Least Concern, but our AOH final estimates indicate a Near Threatened status for *A. sumtuosus* and *A. manaos*. Given the current and projected degradation of the studied area, governmental institutions in charge of conservation plans should give special attention to the threats faced by riparian and habitat-specific breeding species in Amazonia. The riparian ecosystem of nonflooded forests (where the studied species occur) in Amazonia represents a very tiny portion of *terra-firme* dense rainforests, which may also explain the restricted AOHs found here. Our results showed that the loss of small portions of the most suitable riparian areas occupied by the studied species may cause substantial loss of their AOHs.

Given their large EOO, the species probably have high resistance against ongoing threats at the species level (i.e., reduced extinction risk of the species as a whole), but their restricted AOH suggests very low resilience at the population level (i.e., decreasing viability of local populations being affected by threatening factors), which is of relevant concern as most of the areas harboring higher densities within their AOHs are not protected. Deforestation, with an annual rate of more than 55 km^2/year in Amazonia, is projected to decrease 80% of the geographic area of the Critically Endangered primate *Saguinus bicolor* (Gordo et al. 2021), which mostly overlaps with that of the occupancy area of the studied species. Human settlements in Amazonia expand over headwaters, causing severe downstream degradation (Barrow 2006). Therefore, the ongoing degradation of nonriparian environments in Amazonia may even exacerbate the negative effects of environmental change on riparian biodiversity. Climate change may also cause severe negative effects on the population dynamics of the studied species by increasing the length and severity of dry seasons (Ferrante et al. 2023).

The implications of our results go far beyond the species studied. In central Amazonia, many vertebrates are closely associated with or exclusively found in riparian ecosystems (e.g., Birds—Bueno et al. 2012; Snakes—de Fraga et al. 2011). We highlight that using only EOO (i.e., MCP) to assess the conservation status of riparian species in Amazonia, mainly for those depending on specific breeding sites (i.e., ponds) may blur the real risks and threats faced by them (Marsh et al. 2023; Herzog et al. 2012; Jetz et al. 2008). Despite the robustness and easy use of MCP to represent the EOO even for fish species (e.g., Tagliacollo et al. 2021), there are drawbacks to its use for organisms living along curvilinear features of the landscape (i.e., stream networks; Joppa et al. 2016). For management purposes, we recommend the use of initial AOH as the probable extent area (i.e., broad occupied habitat type—e.g., *terra-firme* dense rainforest) and use the final AOH (accounting only for riparian ecosystems) for AOO for riparian species that rely on streams or stream-side ponds to reproduce. Further studies using the presence-absence model-based SDM approach as used herein should produce more precise estimates of AOO based on AOH for riparian species.

It is important to highlight that (1) any metric will only approximate the real conservation status of a given species when all known biological and ecological characteristics of those species are considered in the evaluations and (2) all riparian organisms should be treated at least as vulnerable—as the ecosystem they rely on is already considered vulnerable (Castello et al. 2013). Therefore, the most effective way to conserve riparian organisms is by developing a biome-scale river-catchment-based conservation plan to protect terrestrial and aquatic ecosystems in Amazonia (Castello et al. 2013). Most Amazonian biodiversity, including human beings, relies directly or indirectly on riparian ecosystems of *terra-firme* dense rainforests for provisioning services (Junk et al. 2024; Castello et al. 2013). The limited budget destined for ecological research is the main cause of occurrence-data scarceness, preventing effective conservation actions for many Amazonian species (Carvalho et al. 2023). Creating a more audacious ecosystem-based conservation plan (i.e., river catchment-based plan; Bland et al. 2016) involving local communities could increase public awareness towards conservation and attract more finance to fill sampling gaps in Amazonia.

Author Contributions

Rafael F. Jorge and Albertina Pimentel Lima conceived the ideas and designed the methodology. Rafael F. Jorge collected and analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Statement

The data that support the findings of this study are openly available in https://ppbiodata.inpa.gov.br/metacatui/data/RafaelJorge.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.