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Tree cover and habitat type mediate taxonomic and phylogenetic anuran diversity in Southeastern Peru



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ABSTRACT

Understanding the drivers that shape anuran diversity is crucial for identifying conservation hotspots, particularly as global anuran declines threaten the reduction of their ecosystem functions across food chains. While studies have examined the influence of environmental and anthropogenic factors, few have explored their effects on multiple facets of diversity or considered how their effects vary across habitat types. Using an extensive dataset from Southeastern Peru, Western Amazonia, we quantified taxonomic and phylogenetic anuran diversity and used linear mixed-effects models to assess how environmental and anthropogenic drivers influenced them. We found a total of 4010 anuran individuals from 88 species, 29 genera, and 10 families across 20 sites and 72 plots. Observed and standardized data showed that floodplain forests supported ~35 % higher taxonomic and phylogenetic diversity than terra firme forests, and models further revealed the significance of forest type in driving anuran multifunctional diversity. Yet, terra firme forests display a stronger effect of tree cover on diversity, resulting in higher anuran diversity in terra firme forests with higher tree cover. Forest degradation negatively influenced anuran phylogenetic diversity, suggesting that anthropogenic disturbances may be filtering species based on their evolutionary identity. These findings highlight the importance of a multifaceted diversity approach to understanding anuran diversity patterns and its drivers. Further, maintaining habitat diversity and tree cover is fundamental to protect anuran diversity in tropical rainforests.

1. Introduction

Anurans are integral components of ecosystems and play an important role across food chains (Cloyd and Eason, 2017). They modulate ecosystem functions such as energy and nutrient flows across aquatic and terrestrial ecosystems, through their effects on algae and arthropod communities (Osborne and McLachlan, 1985; Whiles et al., 2006; Hocking and Babbitt, 2014; Cortes et al., 2014). Anurans also provide ecosystem services including pest control, water quality regulation, and act as bioindicators (Vitt et al., 1990;

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Hocking and Babbitt, 2014). Anuran populations worldwide are in decline (Stuart et al., 2004; Whiles et al., 2006; Green et al., 2020), facing unprecedented challenges from anthropogenic disturbances, habitat loss, emerging diseases, and climate change (Collins and Storfer, 2003; Blaustein and Bancroft, 2007; Hof et al., 2011; von May et al., 2019; Iglesias-Carrasco et al., 2022). A third of all anuran species are classified as vulnerable or endangered (2429 out of 7878 species) (AmphibiaWeb, 2025; IUCN, 2025). While many studies have examined how anthropogenic and environmental factors influence anuran diversity (Campbell Grant et al., 2020; Green et al., 2020), most focus on taxonomic diversity, often overlooking other facets such as phylogenetic diversity that can reveal ecological and evolutionary processes and ecosystem functioning (Kraft et al., 2007; Emerson and Gillespie, 2008; Srivastava et al., 2012; Cadotte et al., 2013; Pyron and Wiens, 2013). Moreover, the magnitude of these effects may differ across regions and habitat types since they have distinct species composition and natural histories (Griffin et al., 2025; Sun et al., 2025). Identifying how these drivers vary among key anuran habitats is thus essential for developing effective conservation strategies, particularly in highly threatened ecosystems such as the Amazon rainforest.

Environmental conditions are key for anuran diversity as they influence anuran survival, reproduction, and habitat availability (Buckley and Jetz, 2007). Water availability is especially important to anuran life cycles as they are generally sensitive to desiccation, with 66 % of anuran species relying on aquatic environments for their reproduction and early development (Liedtke et al., 2022). Precipitation, precipitation seasonality, and the interaction between precipitation and temperature influence anuran distribution worldwide (Buckley and Jetz, 2007; Hillman et al., 2008; Pyron and Wiens, 2013). Whereas higher humidity and smaller distances to water bodies tend to support greater anuran diversity at local and landscape scales (da Silva et al., 2012; Rojas-Ahumada et al., 2012), tree cover has been found to influence anuran diversity at landscape scale, as trees provide essential habitats, regulate temperature, retain moisture, and offer food resources for anurans (Skelly et al., 2005; Werner et al., 2007). Furthermore, higher tree cover is often associated with higher habitat diversity, which can promote a greater number of anuran species (Herrmann et al., 2005; Eigenbrod et al., 2008). Additionally, anuran communities differ in species compositions across forest types (von May et al., 2009; Bernarde et al., 2013; Menin et al., 2019; González-Abella et al., 2021), likely reflecting differences in environmental conditions such as vegetation structure and microhabitat types. This suggests that forest type may itself be an important driver of anuran diversity, while other drivers could interact with it and exert distinct effects across habitats.

Anthropogenic disturbances such as land use change, environmental pollution, and introduction of pathogens pose significant threats to both local and global anuran diversity (Collins and Storfer, 2003; Hof et al., 2011; Scheffers et al., 2019; Iglesias-Carrasco et al., 2022). Land-use change, including deforestation and urbanization, leads to habitat loss and fragmentation (Diniz et al., 2022), degradation (Menin et al., 2019; Lapola et al., 2023), and simplification of resource structures (Iglesias-Carrasco et al., 2022). Beyond the loss of niches and resources, fragmented landscapes expose anurans to smaller available habitats and edge effects, aggravate degradation (Lapola et al., 2023), and disrupt gene flow (Andersen et al., 2004; Cubides and Cardona, 2011; Ramalho et al., 2022), and induce habitat split, i.e., the disconnection between habitats used by different life stages of a species (Becker et al., 2007; Lion et al., 2014). Additionally, water and soil contamination from mining activities negatively affects anurans due to their susceptibility to environmental changes and limited dispersal abilities (Ficken and Byrne, 2013; Adlassnig et al., 2013). Moreover, the pathogenic chytrid fungus further exerts severe threats to anurans survival worldwide (Olson et al., 2013; Fisher and Garner, 2020). These disturbances have been found to induce changes in species composition (Ernst and Rödel, 2005; Menin et al., 2019; Iglesias-Carrasco et al., 2022) and declines in species abundance and richness (Becker et al., 2007; Wanger et al., 2010; Menin et al., 2019; Fulgence et al., 2022). Furthermore, the interactions between multiple disturbances drive anuran diversity towards rapid declines (Stuart et al., 2004; Hof et al., 2011), potentially leading to the loss of ecosystem functions provided by these communities (Whiles et al., 2006).

Most studies on anuran diversity have focused on taxonomic diversity, neglecting the insights phylogenetic diversity might offer (Zhao et al., 2018). Although taxonomic diversity provides an intuitive understanding of the diversity present in a community, it assumes all species are weighed equal and disregards evolutionary relatedness and functional differences (Naeem et al., 2012). Phylogenetic diversity, on the other hand, measures the evolutionary distinctiveness between clades (Faith, 1992), representing accumulations of adaptations and capturing trait evolution (Kraft et al., 2007). Further, it serves as a proxy for phylogenetically conserved traits, such as reproductive traits (da Silva et al., 2012) and thermal physiological traits (von May et al., 2019), which represent diversity in ecological functions (Srivastava et al., 2012; Cadotte et al., 2013; Tucker et al., 2018; Zhao et al., 2018). Measuring multiple facets of diversity, i.e., taxonomic and phylogenetic, provides insights into the evolutionary history of communities and the ecological factors driving them, offering a more mechanistic view of diversity patterns (Pyron and Wiens, 2013). Moreover, recent research has shown the phylogenetic diversity declines with anthropogenic disturbances (Dehling and Dehling, 2023) and climate change (Lourenço-de-Moraes et al., 2019; Oliveira et al., 2020; Rodriguez et al., 2022). These findings highlight the need to consider multiple facets of diversity under changing environments, as relying on a single facet risks overlooking losses in ecosystem functioning and evolutionary potential represented by the tree of life.

The Amazon basin is the largest and most diverse region in the world (Da Silva et al., 2005), and the primary source of Neotropical biodiversity (Antonelli et al., 2018). It hosts 577 anuran species (Godinho and da Silva 2018), 8.7 % of all anuran species worldwide described to date, and ongoing discoveries continue to raise this number (Vacher et al., 2020). The region's high anuran diversity can be partly attributed to historical processes involving high speciation in the tropics, higher extinctions in temperate regions, and limited dispersal out of the tropics compared to the amount of temperate clades that colonized tropical regions (Buckley and Jetz, 2007; Pyron and Wiens, 2013). Additionally, favorable climatic conditions, i.e., high temperatures and precipitation, contribute to the high anuran diversity (Duellman, 1988; Buckley and Jetz, 2007; Pyron and Wiens, 2013; Ochoa-Ochoa et al., 2019). Across diverse forest types in the Amazon basin, anuran communities may exhibit different patterns due to variations in vegetation structure and microhabitats, resulting in different species compositions and diversity (von May et al., 2009; Bernarde et al., 2013; Menin et al., 2019; González-Abella et al., 2021). Floodplain forests frequently have temporary water bodies, which are important reproductive and larval

habitats for most anurans (Wilbur, 1980; Griffiths, 1997; Liedtke et al., 2022). These forests have higher taxonomic anuran diversity, likely due to increased water availability being more important than other environmental drivers (von May et al., 2009). Yet, the influence of forest types, environmental conditions, and anthropogenic disturbances on anuran phylogenetic diversity in the Amazon basin remains a subject of ongoing research.

Here, we examine anuran taxonomic and phylogenetic diversity across sites and forest types (floodplain or terra firme forests) in Southeastern Peruvian Amazonia and assess how environmental conditions and anthropogenic disturbances drive these patterns. To this end, we use an extensive dataset of anuran communities to estimate diversity indices. We then use linear mixed models to analyze the effects of forest type and multiple environmental and anthropogenic drivers of anuran taxonomic and phylogenetic diversity. We expect that (1) environmental conditions, i.e., climatic and vegetation properties, related to higher humidity and tree cover positively affect anuran taxonomic and phylogenetic diversity, as most anurans are sensitive to desiccation and dependent on aquatic environments, and higher tree cover provides a more suitable habitat and more resources to anurans (e.g., via habitat diversity, microclimate, and shade) (Skelly et al., 2005; Werner et al., 2007; da Silva et al., 2012); (2) variables indicating higher anthropogenic influence have negative effects on anuran taxonomic and phylogenetic diversity because degradation and pollution of habitats results in filtering effects on anuran species (Ficken and Byrne, 2013; Iglesias-Carrasco et al., 2022); (3) forest types, i.e., floodplain and terra firme forests, act as proxies for the influence of different habitat features on anuran composition and are the strongest drivers of taxonomic and phylogenetic diversity, as different forest types provide distinct microhabitats for anurans (Healey et al., 1997; Montufar and Pintaud, 2006; González-Abella et al., 2021); and (4) floodplain forests exhibit higher anuran taxonomic and phylogenetic diversity due to the temporary water bodies, which are important reproductive and larval habitats for most anurans (Wilbur,

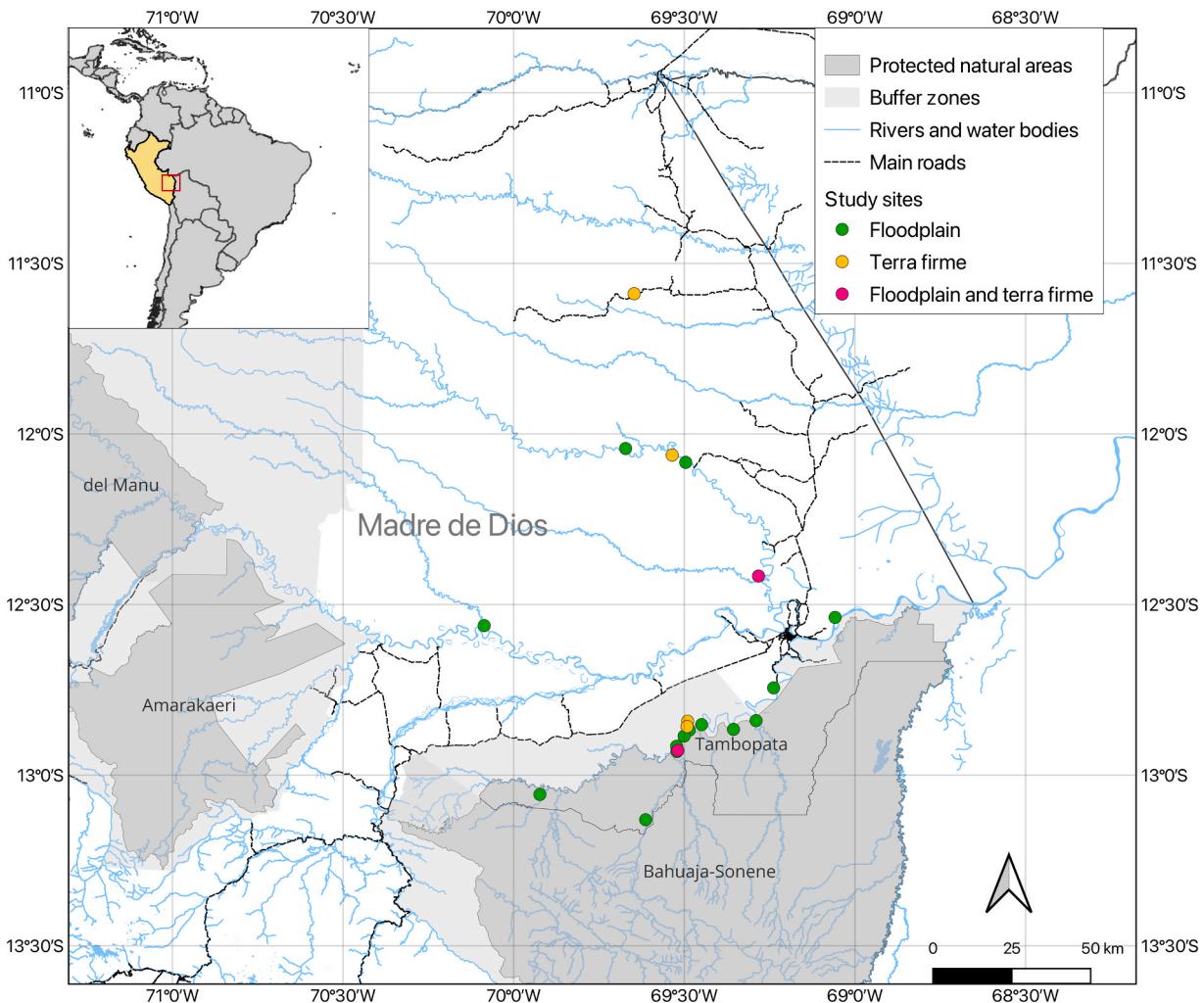


Fig. 1. Map of the Madre de Dios region (red rectangle in the upper left inset map) in Southeastern Peru (in yellow in the upper left inset map), Western Amazonia. The 20 study sites (colored dots) are located on lands with different protection levels: five sites are inside the Tambopata National Reserve (darker grey), eight sites are in its buffer zone (lighter grey), and seven sites are outside any protected area (white). Dot colors denote forest type at each site: floodplain forests (green), terra firme forests (yellow), or a mix (pink).

1980; Griffiths, 1997; Liedtke et al., 2022).

2. Methods

2.1. Study region and study design

This study was conducted in the southeastern Madre de Dios region (hereafter Madre de Dios), located in Southeastern Peru, Western Amazonia (Fig. 1). Forests in this region are classified as tropical moist forests (Holdridge et al., 1971), with mean annual temperature ranging between 24.4 and 25 °C and annual precipitation between 1822 and 2460 mm during the study years (CHELSA v2.1; Karger et al., 2021). There is a distinct dry season between May and September, during which mean monthly precipitation falls below 100 mm (Karger et al., 2021).

Data were collected at 20 sites recognized for their high conservation value, with land access permits and the presence of research stations that supported the surveys. These sites encompass high quality old-growth and secondary forests in the Tambopata National Reserve (hereafter Tambopata NR), its buffer zone, and adjacent areas of Madre de Dios. The study sites are dominated by two main forest types: terra firme and floodplain forests. These are two of the most common forest types in lowland Amazonia (Melack and Hess, 2011; Hess et al., 2015). Terra firme forests are located on higher terrain that is rarely flooded and are characterized by a tall and dense upper canopy and a relatively open and dark interior. Floodplain forests are found on low-lying, flat areas usually adjacent to rivers or streams which experience seasonal flooding and have open to closed canopies and rich understories (Kvist and Nebel, 2001; Bernarde et al., 2013). In floodplain forests, the frequent formation of temporary ponds from precipitation, surface water, and floodwater provides suitable breeding sites for pond-breeding anurans (Abrunhosa et al., 2006).

2.2. Plot design and survey method

Each study site consisted of one to ten 1-ha plots established in terra firme or floodplain forests, covering predominantly dry land areas. Plots were located within 1 km of the site center and positioned to represent the dominant habitats at each site. On each plot, anuran communities were sampled along 11×100 -m unbounded terrestrial transects using Visual Encounter Surveys (Doan, 2003).

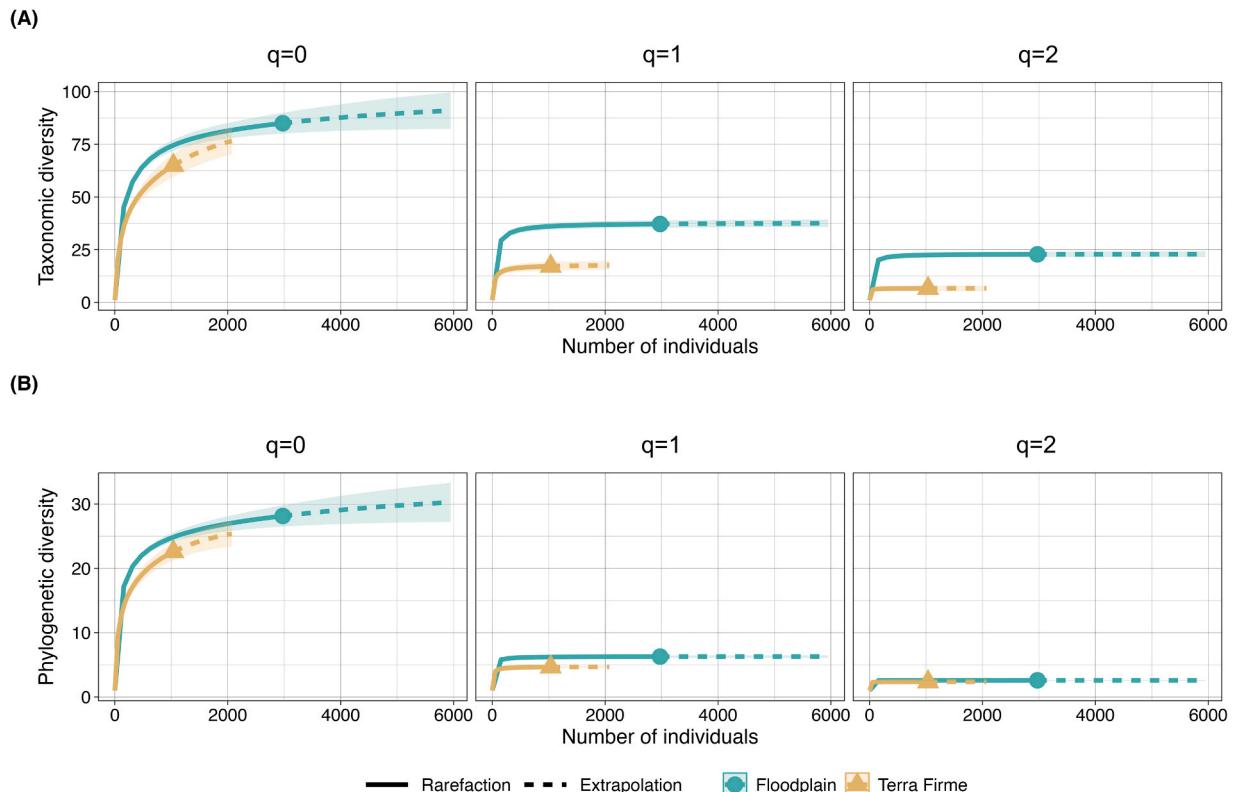


Fig. 2. Sample size-based rarefaction (solid lines) and extrapolation curves (dashed lines) for anuran taxonomic (A) and phylogenetic (B) diversity for Hill-Chao numbers 0, 1, and 2 in floodplain and terra firme forests in the Madre de Dios region, in Southeastern Peru, Western Amazonia. Shaded areas represent 95 % confidence intervals obtained from a bootstrap method with 100 replications. Reference time (Ref time; Fig. B) is the chosen age of the root of the phylogenetic tree spanned by all species in the assemblage.

During each survey, groups of 2–4 observers led by experienced herpetologists trained in the same methodology, ensuring searches were carried out at comparable speed and intensity. The observers walked in along the center of the transect on the ground and recorded all anuran individuals visually detected from the center of the transect. Each survey lasted 20–120 min depending on the number of encounters. Surveys were carried out both day and night, and in wet (October–April) and dry (May–September) seasons between 2004 and 2022. We acknowledge potential biases associated with uneven sampling size, variation in observer, and seasonal differences in anuran detectability and abundance. To address these, we applied (Chao and Jost, 2012; Roswell et al., 2021) to reduce sampling bias and included season as a variable in subsequent models. Additionally, recognizing possible changes in populations and environmental conditions over this period (e.g., the spread of chytridiomycosis), we treated sampling year as a random factor in model analyses to minimize the influence of temporal variation.

2.3. Data preparation

2.3.1. Taxonomic standardization

We standardized species names using the "nameMatch" function in the *U.Taxonstand* R package with the Catalogue of Life anuran database (Zhang and Qian, 2022; Pottier et al., 2022). After taxonomic standardization, the dataset contained 88 accepted species (from which 77 were identified to species level and 11 to genus level) that were used to carry out all subsequent analyses. For species identified only to the genus level in VES but distinguishable from other records, we treated them as unique species for taxonomic diversity while assigning them to the genus-level for phylogenetic analysis. Species identified to species level were linked to the Neotropical anuran trait database (Fontana et al., 2021) and IUCN assessments (2025) to obtain reproductive trait information (e.g., oviposition site, larval type, and development mode).

2.3.2. Sample coverage

To compare the diversity of plots with varying sampling efforts and sample sizes, we employed a coverage-based standardization method (Chao and Jost, 2012; Roswell et al., 2021). This approach uses rarefaction and interpolation to estimate diversity of samples with the same coverage representing the proportion of the total number of individuals in the entire assemblage that belongs to the detected species. Prior to the standardization process, we assessed the sample coverage for each study plot using the "Coverage" function in the *iNEXT.3D* R package (Hu and Chao, 2022). The plot-level sample coverage ranged between 0.25 and 0.99, and to prevent over-extrapolation during standardization, we excluded four plots with less than 0.5 sample coverage. This resulted in a final dataset of 72 plots. To assess the representativeness of data, we generated rank abundance curves (Fig. 2) and sample completeness curves for both forest types with the "ggiNEXT3D" function of the same package.

2.3.3. Phylogeny

We matched the taxonomic species list to a global anuran synthesis-based phylogeny developed by Jetz and Pyron (2018) as a backbone using the "phylo.maker" function of the *U.PhyloMaker* R package (Jin and Qian, 2022), and then we calculated plot-level metrics using the resulting pruned tree. This synthesis-based approach is commonly applied when molecular data are not available, and recent studies have shown that it produces highly correlated estimates of community-level phylogenetic diversity compared to phylogenies generated from gene sequence data (Li et al., 2019). We used the phylogenetic hypothesis based on scenario 3, where the tip for a new genus is attached to the midpoint of the family branch (Qian and Jin, 2016). In total, 61 species matched the megatree directly, while 16 were placed at the genus level and 11 at the family level when it was genus-level identification or when the megatree doesn't include the species or genera (Fig. S1).

2.3.4. Environmental and anthropogenic variables

To identify potential environmental drivers of anuran multifaceted diversity, we considered climatic variables, tree cover, and distance to water body. We selected mean annual temperature (°C; mean annual daily mean air temperatures averaged over one year), annual precipitation (mm/a; accumulated precipitation amount over one year), temperature seasonality (°C; standard deviation of the monthly mean temperatures), and precipitation seasonality (mm; standard deviation of the monthly precipitation) as climatic variables representing water and energy availability. All climatic variables were derived from the Climatologies at high resolution for the earth's land surface areas (CHELSA v2.1; Karger et al., 2021). We derived average tree cover (%) within a 1-km radius of the center of each site in the year 2000 from the Global Forest Change map (Hansen et al., 2013) and measured the distance between the center of each site and the nearest water body (m; hereafter distance to water body). We differentiated water bodies as permanent or seasonal based on the Water Dynamic Map (Pickens et al., 2020).

To assess the effect of anthropogenic disturbances on anuran communities, we included the distance to road (m), distance to reserve (m), forest loss (%), forest degradation (%), and human footprint to represent human activity levels. Roads were defined as main roads according to OpenStreetMap (2022). Reserves are nature-protected areas as defined by the National Agency for the Protection and Conservation of Natural Areas (SERNANP, 2023). Distance to roads or reserves is the linear distance from the center of each site to the nearest road or reserve, respectively. To quantify forest loss, we derived the percentage of forest loss area (i.e., areas that experienced a complete loss of trees between the years 2000–2021) within a 1-km radius from the center of each site from the Global Forest Change Map (Hansen et al., 2013). Forest degradation was derived from the percentage of vegetation-degraded areas, i.e., areas showing loss of the normalized difference vegetation index (NDVI) between the years 2000 and 2021, within a 1-km radius around the center of each site from the area of degradation map (MINAM, 2021). Finally, we derived average human footprint levels for the years 1993 and 2009 within a 1-km radius from the center of each site from the Global Human Footprint map, where one represents the lowest human

footprint (Venter et al., 2016).

2.4. Multifaceted diversity

We estimated taxonomic and phylogenetic diversity for each plot based on the framework by Chao et al. (2021), i.e., Hill-Chao numbers, in order to allow for direct comparisons between the two diversity facets, while accounting for the influence of species abundances. We measured diversity for three Hill-Chao numbers ($q=0, 1, 2$), where q indicates the sensitivity of the measure to the abundance of species. For taxonomic diversity, each species is considered as an equally distinct taxonomic entity, and diversity is quantified as the effective number of equally-abundant species (Jost, 2006). When the effective number of species is of order zero ($q=0$), it is equal to species richness and does not account for species abundances; when the effective number of species is of order one ($q=1$), species are weighted proportionally to their abundance, resulting in the effective number of common species; and when the effective number of species is of order two ($q=2$), common species are emphasized and rare species discounted, resulting in the effective number of dominant species (Chao et al., 2014, 2021). For phylogenetic diversity each unit-length branch segment is considered a phylogenetic entity, and diversity is quantified as the effective number of phylogenetic entities or effective total branch length divided by tree length. This results in the number of equally abundant and equally divergent lineages, i.e., mean phylogenetic diversity. When mean phylogenetic diversity is of order zero ($q=0$), the number of entities in the assemblage equals Faith's PD divided by tree depth; mean phylogenetic diversity of order one ($q=1$) is the effective number of common lineages; and mean phylogenetic diversity of order two ($q=2$) is the effective number of highly abundant lineages (Faith, 1992; Chao et al., 2010, 2021). To account for the variability in sampling effort or sampling size in the dataset, we computed coverage-based standardized taxonomic and phylogenetic diversity indices with the "estimate3D" function of the *iNEXT.3D* R package (Hu and Chao, 2022) which uses rarefaction and interpolation to standardize diversity in samples to the same sample coverage (Chao and Jost, 2012; Roswell et al., 2021). Based on recommendations by Chao (2020) for the maximum standardized sample coverage, we standardized diversity values to the minimum sample coverage among samples extrapolated to double size, which was 70 % sample coverage for each plot. We estimated mean, standard deviation, and confidence intervals of observed species richness and standardized diversity facets. In all cases, we differentiated between floodplain and terra firme forest plots.

2.5. Statistical analysis

We used linear mixed effects models to investigate the influence of forest type, and anthropogenic and environmental drivers on anuran taxonomic and phylogenetic diversity. Due to strongly skewed distributions, we log-transformed (\log_e) taxonomic and phylogenetic diversity indices, tree cover, distance to water body, distance to reserve, and distance to road; and square-root transformed forest loss (Fig. S2). To ensure compatibility of model coefficients, all variables were standardized using a z-transformation. This involved centering the variables by subtracting their means and scaling them by dividing them by their standard deviations (Schielzeth, 2010). Highly correlated variables were identified using the Pearson correlation test (absolute values of coefficients > 0.7). Annual precipitation, mean annual temperature, human footprint, and distance to reserve were removed from the analysis as they were highly correlated (Fig. S3).

We fitted linear mixed effects models using the "lmer" function from the *lme4* R package for each diversity facet and each q -order (six indices in total). We included tree cover, distance to water body, distance to road, forest loss, temperature seasonality, precipitation seasonality, forest degradation, and the interactions between forest type and all other variables, season and distance to water body, forest loss and distance to road, and forest degradation and distance to road as fixed effects in the initial model. Sampling year was included as a random effect (Bates et al., 2015). For model selection, we used the "dredge" function from the *MuMin* R package, which tests all possible combinations of variables and ranks the models by their performance (Bartoń 2023). We selected models based on their delta Akaike's Information Criterion (ΔAIC), where models with ΔAIC smaller than four were selected (Burnham and Anderson, 2004). We verified model assumptions using the "check_model" function from the *performance* R package (Lüdecke et al., 2021). Further, we assessed multicollinearity with the Variance Inflation Factor (VIF) for each model. We then examined spatial autocorrelation using Moran's I test and found no evidence of spatial autocorrelation in the model's residuals (Moran's I < 0.3 ; $p > 0.05$). We visualized the marginal effects for selected models using the R package *ggeffects* (Lüdecke, 2018). We used the "sw" function in the *MuMin* R package to analyse the sum weight of each variable in the models (Bartoń 2023). We conducted Type III Wald F tests to analyze the significance of the fixed effects using the "Anova" function in the R package *car* (Fox and Weisberg, 2019).

All analyses were conducted in R version 4.3.0 (R Core Team, 2023) using the following R-packages: *ape* (Paradis and Schliep, 2019), *cowplot* (Wilke, 2020), *dplyr* (Wickham et al., 2023), *ggcorplot* (Kassambara, 2022), *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2023), *grDevices* (Wilke, 2022), *jtools* (Long, 2022), *kableExtra* (Zhu, 2021), *lubridate* (Grolemund and Wickham, 2011), *modelsummary* (Arel-Bundock, 2022), *patchwork* (Pedersen, 2022), *raster* (Hijmans, 2022), *readxl* (Wickham and Bryan, 2023), *rgdal* (Bivand et al., 2023), *rgeos* (Bivand and Rundel, 2023), *scales* (Wickham and Seidel, 2022), *sf* (Pebesma, 2018), *spdep* (Pebesma Bivand, 2023), *stringr* (Wickham, 2022), and *tidyverse* (Wickham et al., 2019).

3. Results

3.1. Anuran species and family composition in Madre de Dios

A total of 4010 anuran individuals belonging to 88 species, from 29 genera and 10 families were found across all 20 sites and 72

plots. Sixty-eight species occurred within the Tambopata NR sites, 64 species in the buffer zone sites, and 75 species in the sites outside the protected area (Table S1, Fig. S4). Floodplain forests showed higher total species richness with 85 species in 27 genera, compared to the 65 species in 24 genera in terra firme forests. The most abundant species in the study region was *Pristimantis reichlei* (541 individuals; 14 sites), and the most frequent and second abundant species was *Adenomera andreae* (444 individuals; 19 sites). *Pristimantis* emerged as the most species-rich genus (13 species), followed by *Dendropsophus* (11 species), and *Leptodactylus* (9 species). The most species-rich family was Hylidae, i.e., tree frogs, with 33 species, followed by Craugastoridae and Leptodactylidae with 15 species each. Similarly, in floodplain forests, the most abundant family was Hylidae (967 individuals), followed by Leptodactylidae (783 individuals), and Strabomantidae (542 individuals). While in terra firme forest the most abundant family was Strabomantidae (643 individuals), followed by Hylidae (218 individuals), and Leptodactylidae (124 individuals). Within the 77 anuran species identified to species level, 14 are direct-developing species, accounting for 18 % of observed abundance in floodplain forests and 38 % in terra firme forests; 57 species breed or their larvae develop in water bodies, accounting for 68 % of observed abundance in floodplain forests and 38 % in terra firme forests.

3.2. Anuran diversity in Madre de Dios

Rarefaction and extrapolation curves showed that at landscape scale, floodplain forest exhibited higher taxonomic and phylogenetic diversity than terra firme forests for all q-orders ($q=0, q=1, q=2$; Fig. 2 and S5). Besides, the difference between the two forest types was stronger for taxonomic diversity than for phylogenetic diversity. Rarefaction and extrapolation curves did not display a tendency towards saturation for taxonomic and phylogenetic diversity when emphasizing rare species ($q=0$), indicating undiscovered species in both forest types (Figs. 2 and S5). However, when abundances were taken into account ($q=1$) and common species emphasized ($q=2$), stabilized in the sample size-based rarefaction curves (Fig. 2). Rank abundance curves for both forest types exhibited a rapid decline in species abundance at higher ranks, with the curve for terra firme forests displaying a steeper decline, indicating lower species evenness in this forest type (Fig. S6).

Observed and standardized taxonomic and phylogenetic diversity are consistently higher in floodplain forests than in terra firme forests across all diversity facets and q-orders (Fig. 3 and Table S2), with an average increase of $\sim 35\%$. Taxonomic diversity was always higher than phylogenetic diversity in each plot, and diversity values decreased when q-orders increased, i.e., species

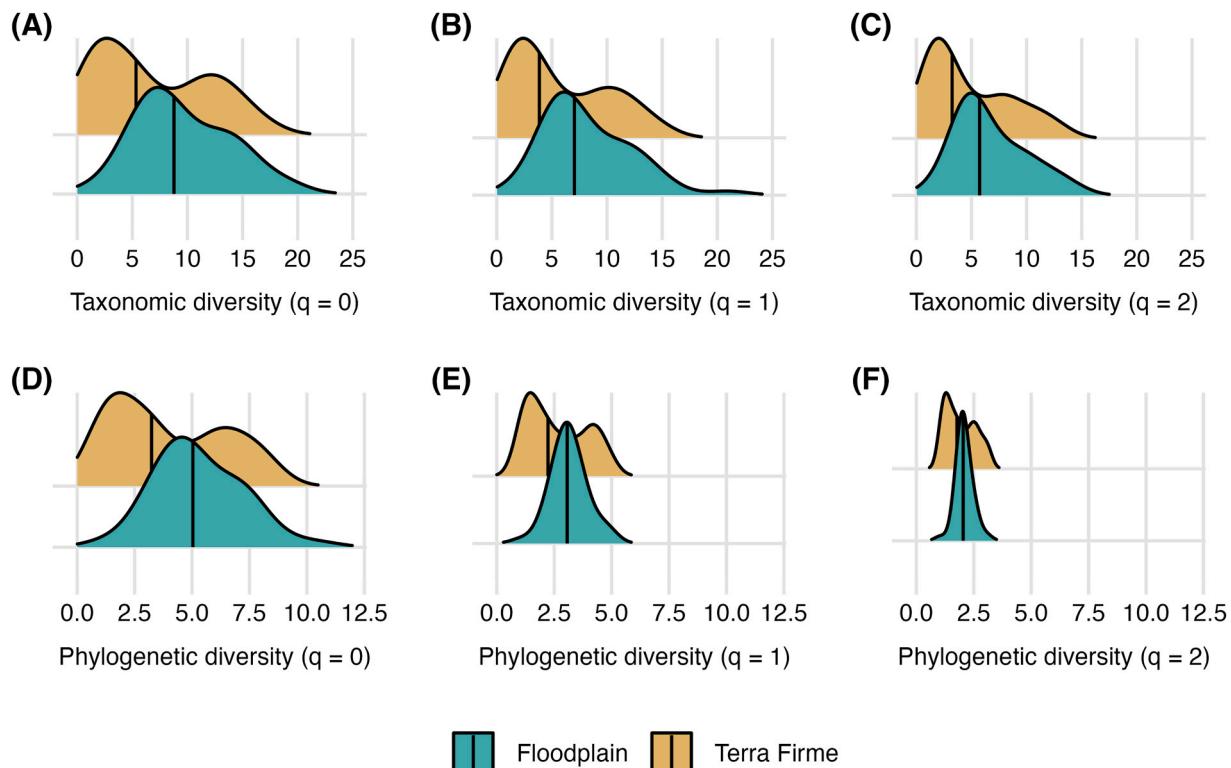


Fig. 3. Plot-level distribution of coverage-based standardized anuran taxonomic (A, B and C) and phylogenetic (D, E and F) diversity for Hill-Chao numbers 0 (A and D), 1 (B and E), and 2 (C and F) in floodplain (51 plots) and terra firme (21 plots) forests in the Madre de Dios region, in Southeastern Peru, Western Amazonia. Samples were standardized to a coverage of 0.7. Taxonomic and phylogenetic diversity are integrated under a common framework and therefore directly comparable (Hill-Chao numbers; Chao et al., 2021). Black vertical lines denote the median values of each diversity distribution.

abundances were taken into account and given more emphasis.

3.3. Environmental and anthropogenic drivers of anuran diversity

Linear mixed effects models analyzing drivers of plot-level variation in anuran diversity reveal that forest type, tree cover, and the interactive effect of forest type and tree cover were the most influential predictors of anuran taxonomic and phylogenetic diversity across Hill-Chao numbers (Tables 1, 2, and S3). These two variables and their interaction were consistently selected in all models (Tables 1 and 2) and had the highest model weights for all diversity facets and Hill-Chao numbers (weights: 1.0; Table S3). Additionally, season (weights: 0.16–0.19), forest degradation (weights: 0.1–0.6), the interactive effect of forest degradation and forest type (weight: 0.28 for phylogenetic diversity $q=2$), and distance to road (weight: 0.8 for phylogenetic diversity $q=0$) were selected in at least one model (Tables 1, 2, and S3). However, F tests showed significant effects only for forest type, the interactive effect of forest type and tree cover, and forest degradation (Table S4 and S5; $p < 0.05$). All models demonstrated substantial explanatory power, with marginal R^2 values, i.e., accounting for only fixed effects, ranging between 0.48 and 0.55 and conditional R^2 values, i.e., accounting for fixed and random effects, between 0.54 and 0.68 (Tables 1 and 2). The variances explained by fixed effects were higher in phylogenetic diversity compared to taxonomic diversity, and the variances explained by fixed effects increased with Hill-Chao numbers for phylogenetic diversity.

Floodplain forests exhibited significantly higher anuran taxonomic and phylogenetic diversity for all Hill-Chao numbers compared to terra firme forests ($p < 0.05$; Fig. 4A,D and S7; Tables 1 and 2). When considering the interactive effect of forest type and tree cover, model predictions showed that terra firme forests with higher tree cover exhibit higher anuran diversity for both diversity facets and all Hill-Chao numbers (Figs. 4B,E and S8; Tables 1 and 2). On the other hand, anuran taxonomic and phylogenetic diversity were only slightly positively related with increasing tree cover levels in floodplain forests for all Hill-Chao numbers (Figs. 4B,E and S8; Tables 1 and 2; $p < 0.001$).

Wet season exhibited higher taxonomic and phylogenetic diversity than dry season for all Hill-Chao numbers (taxonomic diversity) and for Hill-Chao numbers $q=0$ and $q=1$ (phylogenetic diversity) (Fig. S9; Tables 1 and 2). Forest degradation negatively influenced anuran diversity for all Hill-Chao numbers (taxonomic diversity) and for Hill-Chao numbers $q=1$ and $q=2$ (phylogenetic diversity) (Fig. 4C,F and S10). This effect was significant and showed a higher weight on phylogenetic diversity $q=2$ (weight: 0.6; Table 2, S3, and S5), but not for the other diversity indices (weights: 0.10–0.11; Tables S3, S4 and S5). Additionally, there was an interactive effect of forest degradation and forest type on anuran phylogenetic diversity $q=2$, showing that the influence of forest degradation was stronger in terra firme forests (Fig. S10F). Distance to road positively influenced anuran phylogenetic diversity $q=0$ (Fig. S11), but we did not find an influence of distance to road on taxonomic diversity.

4. Discussion

Our results reveal that environmental conditions and microhabitat-related variables drive anuran taxonomic and phylogenetic diversity across Madre de Dios, largely through the effects of forest type (floodplain or terra firme forests), tree cover, and their interactions. We show that floodplain forests hold higher anuran diversity than terra firme forests, and that taxonomic diversity is always higher than phylogenetic diversity across sites. Yet, increased tree cover levels are key for anuran diversity in terra firme forests, unlike floodplain forests where this effect is minimal. Moreover, we find anthropogenic disturbances also influence anuran multifaceted diversity via forest degradation. These findings emphasize the importance of a multifaceted approach and a careful selection of diversity drivers when assessing diversity patterns and impacts for indicator taxa such as anurans in highly threatened and diverse ecosystems.

Table 1

Summary table of linear mixed effects models examining the influence of forest type, and environmental and anthropogenic drivers on coverage-based standardized anuran taxonomic diversity (TD) for Hill-Chao numbers 0, 1, and 2 in the Madre de Dios region, in Southeastern Peru, Western Amazonia. Three models were selected for each response variable (each diversity index) based on AIC ($\Delta\text{AIC} < 4$). Explanatory variables in the models include forest type (terra firme or floodplain forests), tree cover, the interaction between forest type and tree cover, season (dry or wet), and forest degradation. The table shows the coefficients of intercepts and explanatory variables, the model performance for marginal R^2 values (R^2 Marg.), conditional R^2 values (R^2 Cond.), and Akaike information criterion (AIC). Stars denote the significance of coefficients (** $p < 0.001$).

Response variable	Intercept (coefficient)	Explanatory variable (coefficient)					Model performance		
		Tree cover	Forest Type	Tree cover X Forest Type	Season	Forest degradation	R^2 Marg.	R^2 Cond.	ΔAIC
TD ($q = 0$)	0.26	0.03	−0.95 ***	1.18 ***	−	−	0.426	0.653	0
	0.15	0.04	−0.96 ***	1.16 ***	0.18	−	0.440	0.671	3
	0.25	0.00	−0.95 ***	1.16 ***	−	−0.11	0.436	0.653	3.8
TD ($q = 1$)	0.25	0.05	−0.95 ***	1.17 ***	−	−	0.434	0.660	0
	0.14	0.50	−0.96 ***	1.14 ***	0.20	−	0.449	0.682	2.3
	0.25	0.02	−0.95 ***	1.15 ***	−	−0.11	0.443	0.660	3.7
TD ($q = 2$)	0.24	0.06	−0.93 ***	1.14 ***	−	−	0.425	0.651	0
	0.12	0.07	−0.95 ***	1.11 ***	0.22	−	0.442	0.677	2.1
	0.24	0.04	−0.94 ***	1.12 ***	−	−0.10	0.434	0.650	3.8

Table 2

Summary table of linear mixed effects models examining the influence of forest type, and environmental and anthropogenic drivers on coverage-based standardized anuran phylogenetic diversity (PD) for Hill-Chao numbers 0, 1, and 2 in the Madre de Dios region, in Southeastern Peru, Western Amazonia. Three models were selected for each response variable (each diversity index) based on AIC ($\Delta\text{AIC} < 4$). Explanatory variables in the models include forest type (terra firme or floodplain forests), tree cover, the interaction between forest type and tree cover, season (dry or wet), forest degradation, interaction between forest types and forest degradation, and distance to road. The table shows the coefficients of intercepts and explanatory variables, the model performance for marginal R^2 values (R^2 Marg.), conditional R^2 values (R^2 Cond.), and Akaike information criterion (AIC). Stars denote the significance of coefficients (** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.1$).

Response variable	Intercept (coefficient)	Explanatory variable (coefficient)							Model performance		
		Tree cover	Forest Type	Tree cover X Forest Type	Season	Forest degradation	Distance to road	Forest degradation X Forest Type	R^2 Marg.	R^2 Cond.	ΔAIC
PD (q = 0)	0.23	0.02	-0.87 ***	1.26 ***	-	-	-	-	0.440	0.624	0
	0.12	0.03	-0.88 ***	1.23 ***	0.19	-	-	-	0.452	0.642	2.4
	0.23	0.00	-0.84 ***	1.21 ***	-	-	0.09	-	0.449	0.631	3.9
PD (q = 1)	0.21	0.07	-0.77 ***	1.38 ***	-	-	-	-	0.486	0.599	0
	0.09	0.08	-0.77 ***	1.35 ***	0.21	-0.12	-	-	0.495	0.617	2.2
	0.21	0.04	-0.79 ***	1.35 ***	-	-	-	-	0.499	0.601	2.4
PD (q = 2)	0.16	0.12	-0.59 **	1.45 ***	-	-	-	-	0.500	0.536	0
	0.17	0.07	-0.64 **	1.38 ***	-	-0.20*	-	-	0.535	0.548	0.2
	0.17	0.08	-0.75 ***	1.08 ***	-	-0.16 +	-	-0.54	0.548	0.569	0.2

4.1. The contribution of common and rare species to anuran multifaceted diversity

By examining taxonomic and phylogenetic diversity within the same framework, our study found taxonomic diversity to be highly correlated to phylogenetic diversity, changing in similar patterns across sites, but not fully equivalent. Further, from the observation that steep declines in rank abundance curves, our result highlighted the significant contribution of rare species to the anuran communities in the Madre de Dios region. This pattern also demonstrates a high proportion of rare anuran species in both forest types in this region, a common occurrence in Amazonian forests (Zimmerman, 1991). Since less abundant species might contribute less to the functioning of overall ecosystems functions (Dangles and Malmqvist, 2004; Gaston and Fuller, 2008; Winfree et al., 2015), this suggests that diversity indices that do not account for species abundances, e.g., species richness and Faith's phylogenetic diversity (PD), could overestimate the contribution of biodiversity to the functioning of ecosystems functions in this region. Yet, it is important to recognize that numerous cryptic anuran species might be still undiscovered or misclassified as rare species (Funk et al., 2012; Vacher et al., 2020), and the species that might play crucial but currently unknown roles in the ecosystems (Bickford et al., 2007; Vacher et al., 2020). We acknowledge that uneven detectability among anuran species may have influenced our results. Incorporating acoustic monitoring in future studies could provide a more comprehensive picture of community composition, although potential biases from interspecific differences in acoustic detectability should also be considered.

4.2. Environmental drivers of anuran multifaceted diversity

We find forest type and tree cover to be the main drivers of anuran taxonomic and phylogenetic diversity, partially supporting our first and third hypotheses, stating that environmental conditions affect anuran diversity, and that anuran diversity varies across forest type (as a proxy for different habitat features). Climate variables showed no significant effect in our study, likely because the relatively small spatial extent of our study area resulted in limited climatic variation. Our results show higher taxonomic and phylogenetic anuran diversity in floodplain forests than in terra firme forests, supporting our fourth hypothesis. This result is consistent with findings from previous research conducted at Los Amigos, in Madre de Dios (von May et al., 2009), where floodplain forests exhibited higher local taxonomic diversity compared to other forest types. The temporary water bodies found in floodplain forests are key features used for reproduction and larval stages by many anuran species, the reason for which floodplain forests contribute suitable habitats that are able to host higher anuran diversity (Griffiths, 1997; Tavares-Junior et al., 2020). Also, abundant understory vegetation increases habitat heterogeneity in floodplain forests, which could further explain why they display higher multifaceted anuran diversity and likely more functional types (Henning and Remsberg, 2009). However, contrasting results have been reported at Juruá River in the northern part of Western Amazonia (Gascon et al., 2000), where terra firme forests showed higher anuran species richness. One possible reason for this might be the array of anuran species composition across the Amazon basin due to factors such as spatial distance, geological barriers, and historical processes, e.g., dispersal across regions and speciation in each region

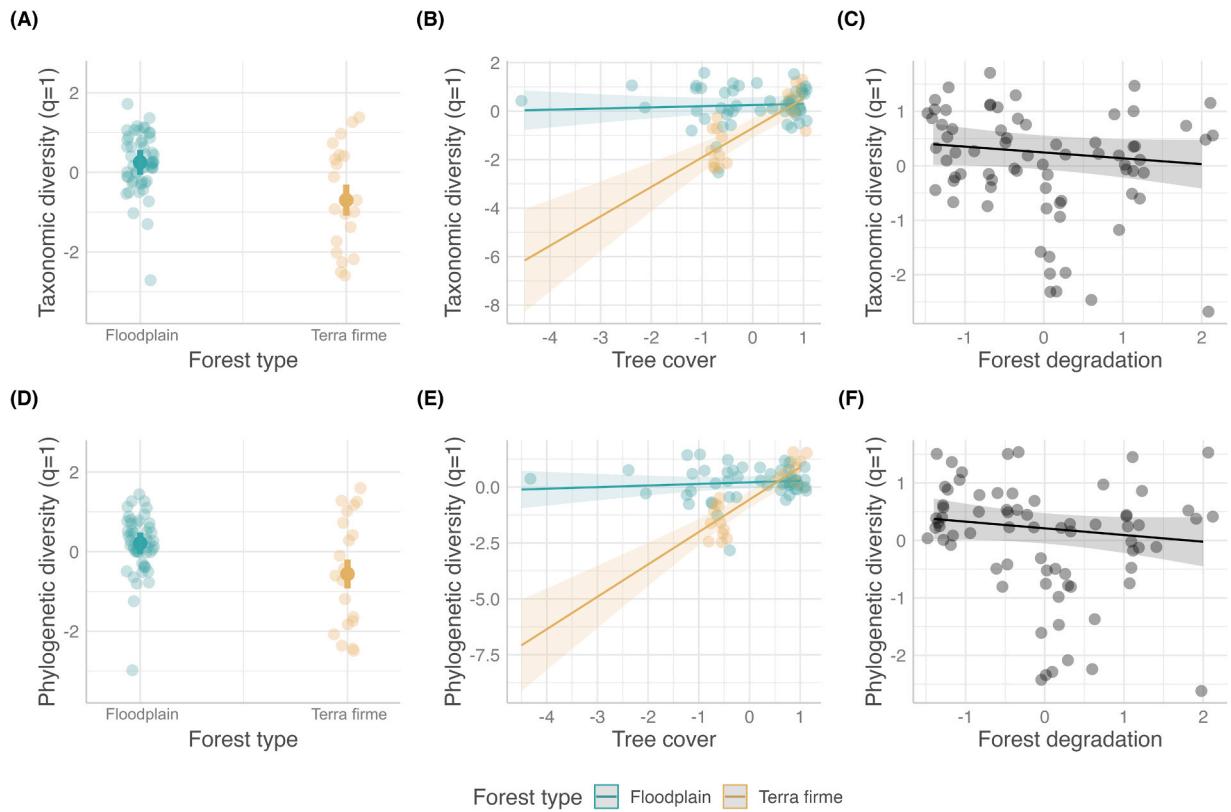


Fig. 4. Effects of forest type (floodplain and terra firme forests; A and D), the interaction of tree cover and forest type (B and E), and forest degradation (C and F) on anuran taxonomic (A, B and C) and phylogenetic (D, E and F) diversity for Hill-Chao number 1 in the Madre de Dios region, in Southeastern Peru, Western Amazonia. Shaded points show coverage-based standardized diversity at the plot-level. Error bars (A and D) or shaded areas (B, C, E and F) denote 95 % confidence intervals. Diversity indices were log- and z-transformed. Solid lines represent marginal effects.

(Rojas-Ahumada et al., 2012; Godinho and da Silva, 2018). With dominant anuran species varying across regions and possibly having different environmental and habitat preferences, anuran species may interact differently with forest types, leading to contrasting diversity patterns.

Tree cover was found to have an overall positive influence on anuran taxonomic and phylogenetic diversity, yet it displayed a stronger influence in terra firme forests. This might be explained by differences in anuran species composition and their ecological preferences across forest types. In our observed data, we found a higher percentage of species abundance in floodplain forests dependent on water bodies for breeding or larval developing sites. However, a higher percentage of direct developing anuran species, such as species in Strabomantidae family, that develop without larva stage, occurred in terra firme forest. This finding suggests that floodplain forests may favor higher abundances of water-dependent anuran species, whereas the environmental conditions of terra firme forests may favor species that rely more on continuous vegetation cover and tall trees. Corresponding to previous studies showing that forest loss and fragmentation impact more vegetation-associated and direct-developing anurans (Torralvo et al., 2022), our finding indicates that a higher proportion of anuran species in terra firme forests might be sensitive to changes in tree cover.

4.3. Seasons and their impact on multifaceted anuran diversity

Our results demonstrated lower anuran diversity in dry season, likely due to a decrease in breeding activity and abundance during dry season (Vonesh, 2001; Adams and Frissell, 2001; Jansen et al., 2009), leading to decreased diversity. However, season also influences diversity facets that do not account for abundance ($q=0$), suggesting that reduction in anuran calls (Saenz et al., 2006; Ximenez and Tozetti, 2015) decreased detectability and may have introduced bias. Although we employed diversity standardization to mitigate the influence of sample size variation (Chao et al., 2020), the unequal reduction in detectability among anuran species might still not be fully addressed (de Solla et al., 2005; Cook et al., 2011), potentially affecting the results. This underlines the significance of accounting for seasonal effects when conducting investigations of anuran diversity in regions with distinct seasonal precipitation patterns.

4.4. Anthropogenic disturbances negatively affect anuran multifaceted diversity

We found a negative effect of forest degradation on anuran multifaceted diversity, supporting our second hypothesis, with forest degradation showing a stronger impact on phylogenetic diversity when emphasizing common species ($q=2$), indicating that forest degradation primarily affects the decline of certain common anuran lineages. Moreover, the interactive effect of forest degradation and forest type on anuran phylogenetic diversity further demonstrates that forest degradation was stronger in terra firme forests, aligning with our finding that tree cover is more influential to anuran diversity in terra firme forests. Additionally, we identified a positive effect of distance to road on anuran phylogenetic diversity supporting other studies revealing that distance to road is negatively correlated with deforestation rates in the Brazilian Amazon (Barber et al., 2014) and positively correlated with forest recovery in Tambopata (Requena Suarez et al., 2023). This suggests that higher forest accessibility negatively affects anuran habitats, potentially threatening their diversity.

Homogeneous environments and low levels of anthropogenic disturbance may explain the lack of effects of other environmental (e.g., precipitation seasonality and distance to water body) and anthropogenic variables (e.g., human footprint and forest loss) on anuran multifaceted diversity. The majority of study sites were located in well-preserved forests, away from human settlements, near rivers, and with similar climate conditions. While climatic variables affect anurans at macroecological scales (Buckley and Jetz, 2007), their subtle differences across sites at local scales might not influence anuran diversity significantly. Moreover, even though degraded forests were observed around study sites (MINAM, 2021), possibly resulting from selective logging, the extent of disturbances related to deforestation and the factors influential to human footprint (e.g., human population density) may be relatively limited within the scope of this study. Additionally, the use of remote sensing data as explanatory variables provided limited details and variance among the study sites. Therefore, it would be useful for future studies to explore the influence of site-related variables like vegetation structure and diversity, soil moisture, and water quality. This could reveal more nuanced environmental and anthropogenic drivers. Furthermore, including a land-use gradient could shed light on how anthropogenic disturbances and climate change may affect anuran diversity in the region.

4.5. Non-protected areas as conservation heavens

This study recorded high anuran species richness in Madre de Dios, with 88 species comprising 13 % of all anuran species in Peru (IUCN, 2025). A high proportion (95 %) of the recorded species were found on lands adjacent to protected areas, i.e., the Tambopata NR buffer zone, or privately owned forests. This highlights the importance of incorporating conservation efforts such as Other Effective Area-Based Conservation Measures (OECMs) into conservation planning, by increasing the areas where long-term, effective in-situ biodiversity conservation can be achieved (CBD, 2018). As Peru actively works to identify and recognize OECMs as part of its commitment to the 30×30 target of the Kunming-Montreal Global Biodiversity Framework (WWF, 2024), they may enhance the ecological representativeness of conservation areas, support local conservation initiatives, strengthen connectivity between protected areas, and safeguard biodiversity while complementing state-led conservation efforts (Alves-Pinto et al., 2021; Gurney et al., 2021).

5. Conclusions

In Western Amazonia, a region of exceptional biodiversity increasingly threatened by environmental change and anthropogenic pressures, our study identified distribution of anuran taxonomic and phylogenetic diversity. We highlight the critical role of environmental factors, particularly forest type and tree cover, in shaping both the taxonomic and phylogenetic diversity of anurans. Our results suggest that preserving floodplain forests and maintaining high tree cover in terra firme forests are essential for sustaining anuran diversity. At the same time, the negative effects of forest degradation and road proximity underscore the need to mitigate anthropogenic disturbances. These factors must be taken into account when formulating conservation strategies to safeguard anurans from climate change and human induced disturbances in this highly threatened ecosystem. Future research could incorporate functional diversity and microclimatic influences in the two habitats to better link anuran diversity with ecosystem functioning, thereby identifying more effective approaches to habitat conservation.

CRediT authorship contribution statement

I Chou: Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Gustavo Brant Paterno:** Writing – review & editing, Methodology, Conceptualization. **Holger Kreft:** Writing – review & editing, Methodology, Conceptualization. **Christopher Ketola:** Writing – review & editing, Resources, Investigation, Data curation, Conceptualization. **Christopher Kirkby:** Writing – review & editing, Resources, Investigation, Data curation. **Maria Laura Tolmos:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03910](https://doi.org/10.1016/j.gecco.2025.e03910).

Data availability

We have shared the link to data in "Data Availability" section. The data will be publicly available after acceptance. R codes and data used for analyses will be publicly available in Figshare upon acceptance (<https://doi.org/10.6084/m9.figshare.26806807>)

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