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Environmental filtering and deforestation shape frog assemblages in Amazonia: An empirical approach assessing species abundances and functional traits

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Abstract

Biological assemblages are often predictable from knowledge of natural environmental heterogeneity and change in response to anthropogenic disturbances, such as deforestation, so understanding ecological mechanisms and processes mediating assemblages is essential to direct conservation actions. We sampled frogs along an edaphic and vegetation-structure gradient in the Brazilian Amazon to test the hypothesis that assemblages change in species composition and functional trait characteristics across landscapes due to environmental filtering. Our study area covered a gradient of forest fragmentation, and we hypothesized that assemblages would change in response to both natural gradients and deforestation. We found that frog assemblages are locally structured by species turnover along gradients in distance to water bodies, vegetation structure, soil sand and silt content, and proportion of the area deforested. Additionally, we found that small-bodied species and those with direct breeding (no larval stage) were no longer present in deforested areas. We conclude that frog assemblages are not randomly distributed across forests, but trait filtering has resulted in different species subsets from the regional pool, which change among sites with different environmental conditions and disturbance levels. Our findings highlight the importance of creating reserves to effectively protect forests and maintain connectivity among forest fragments resulting from deforestation.

Abstract in Portuguese is available with online material.

KEYWORDS
Alter do Chão, anthropogenic disturbance, community structure, functional diversity, Tapajós FLONA, taxonomic composition

1 | INTRODUCTION

Biological assemblages (*sensu* Stroud et al., 2015) are likely to be affected by multiple variables measured at interacting spatial scales, such as biogeographic barriers and climatic clines limiting dispersal (Forman, 1995; Rahel, 2007; Robillard et al., 2015; Travis et al., 2013). At local scales (e.g., few kilometers), even species widely distributed across landscapes may have their distributions limited by environmental filtering, competition, reduced or blocked dispersal, and physiological intolerance (Azevedo-Ramos & Magnusson, 1999;

Braga-Neto et al., 2008; Carr & Fahrig, 2001). Despite local environmental conditions being largely dependent on broader scales, investigating the role of environmental gradients shaping local assemblages may reveal biotic complementarities and redundancies among sites (Díaz & Cabido, 2001; McGill et al., 2006). This approach provides a basis for assessing the efficiency of reserves and environmental legislation at a scale compatible with most management decisions (Bueno et al., 2012; Fraga et al., 2011).

In Amazonian forests, local assemblage turnover along environmental gradients has been found for a wide variety of organisms (e.g., Costa et al., 2009, Braga-Neto et al., 2008, Fraga et al., 2011, Torralvo et al., 2020). Overall, these studies showed that assemblages differ between sites because environmental gradients select different species subsets from the regional pool. However, few studies have investigated how Amazonian assemblages respond to anthropogenic changes in habitat quality, such as deforestation leading to fragmentation (Benchimol & Peres, 2015; Cintra et al., 2013). Fragmentation is one of the main anthropogenic disturbances affecting ecosystem functioning and has eroded biodiversity globally (Haddad, 2015, Fahrig, 2017). A key difference between continuous and fragmented forests is that assemblage resilience to fragmentation depends on a balance between the size and degree of isolation of habitat patches, matrix quality, colonization capacity (Gustafson & Gardner, 1996; Laurance et al., 2011; Murcia, 1995; Ricketts, 2001), and level of forest dependence (Palmeirim et al., 2018). Additionally, since edge effects can penetrate habitat patches, especially if they are small, local assemblages are likely to be affected by environmental conditions within patches (Schlaepfer & Gavin, 2001).

Dispersal ability and physiological tolerance are key elements determining the effects of environmental gradients on assemblages. Thus, assemblages are likely to be affected by the ability of individual species to survive under local environmental conditions. Such ability is often defined by their morphological or physiological traits (functional traits) that directly influence performance via effects on growth, reproduction, and survival (Violle et al., 2007). The taxonomic and functional components of biodiversity may respond differently to anthropogenically altered habitats and, although these components may be partially related to each other, they cover different facets of biodiversity that need to be considered in biodiversity monitoring (Vandewalle et al., 2010). The role of traits in determining assemblages has been investigated through measures of functional diversity, although this term covers a variety of concepts and applications at both trophic and evolutionary levels (see Laureto et al., 2015; Rosado et al., 2016). Here, we adopt the assumption that assemblages are largely affected by how species use available resources (Elton, 1927) and that specific traits that are selected by the environment vary along gradients according to their contribution to fitness (Bradshaw et al., 2009; Violle et al., 2007). We use this background to assess the importance of trait diversity on the variation in frog assemblage composition along a gradient of continuous to fragmented forests in eastern Amazonia.

Amazonian frog assemblages vary along environmental gradients in both relatively pristine (Menin et al., 2007, 2011; Rojas-Ahumada et al., 2012) and human-modified landscapes (Díaz-Ricaurte et al., 2020; Tsuji-Nishikido & Menin, 2011). Assemblages can change spatially in response to changes in competition along environmental gradients, or to multiple evolutionary and ecological processes that have shaped species distributions at different spatial scales (Dias-Terceiro et al., 2015; Menin et al., 2008; Ramalho et al., 2018). Additionally, the wide variety of body sizes and other traits that allow frogs to explore different vertical and horizontal strata generate different levels of specificity in the use of habitats (Bolochio et al., 2020; Ernst & Rödel, 2006; Ganança et al., 2021). Fragmentation may affect the ability of species with certain traits to persist. For instance, small-bodied species may be unable to colonize isolated patches of forest, as crossing open corridors can lead to death from desiccation or exposure to predators, arboreal species obviously lose habitats if forests are cleared, and species with aquatic eggs or larvae are unlikely to thrive if fragmentation disrupts the connection between aquatic and terrestrial habitats. Therefore, quantifying species abundances and traits are potentially complementary approaches to understand the ecological processes shaping assemblages. However, these approaches may interact, such as when traits associated with dispersal and survival generate high local species abundances (Ganança et al., 2021).

We sampled 57 plots in eastern Amazonia to identify factors affecting frog assemblages. We used a generalized linear model to test the hypothesis that species abundances change along gradients of distance from water bodies, forest structure, soil sand and silt content, and proportional deforestation. This hypothesis is based on the premise that environmental gradients form habitat-quality mosaics, which can reduce local abundance, or even preclude the occurrence of poorly tolerant species, weak competitors, or those that cannot reach a location via dispersal. We hypothesized that the high degree of forest fragmentation concentrated in the north of our study area has driven assemblages to be predominantly composed of species that have evolved to occupy open areas or forest edges. We used a combination of RLQ and fourth-corner analysis (Dray et al., 2014) to quantify relationships between the occurrence of traits and environmental gradients. We expected local frog assemblages to change spatially as multiple traits are selected from segments of gradients, which defines the subsets of species with common traits that can share habitats. In both well-conserved and fragmented areas, assemblages are subject to filtering effects, competition, and dispersal limitation, but we expected traits to be associated with intolerance to edge effects to be infrequent or absent from highly fragmented areas.

2 | METHODS

2.1 | Study area

The Tapajós National Forest (FLONA) covers 527,319 ha of mainly old-growth dense rainforests near the Tapajós River (Figure 1). The climate is seasonal, with greater rainfall between January and May, and annual average precipitation of 1892 mm (ICMBio, 2019). The average annual temperature is around 25.6°C (INMET, 2020).

To the north of the study area is Alter do Chão (Figure 1), a village which is important for tourism and local economy. The region is mainly covered by secondary continuous or fragmented forests and savannah patches which forms mosaics that induce turnover in some animal assemblages (e.g., Borges-Matos et al., 2016).

2.2 | Sampling design

In the south of the study area, our sampling design followed the RAPELD method (Magnusson et al., 2005, 2013), which is based on 250-m-long plots up to 40 m wide. We sampled 33 plots organized in four modules (with 10, 6, 8, and 9 plots) composed of two 5-km parallel trails, with a minimum distance of 1 km between neighboring plots. In the northern portion of the study area, we sampled 24 plots; 19 in forest fragments and five in continuous forests. The plots did not follow the RAPELD design, though they were 250 m long, because they did not follow the terrain contours. However, this area was comparatively flat, so this caused negligible differences in within-plot variability. The minimum distance between neighboring plots was 723 m.

We sampled all plots using visual and acoustic search from afternoon to twilight (1630–1800 h) and at night (1900–2300 h). Acoustic search was particularly useful for small, diurnal, and litter species, which are usually difficult to detect (e.g., *Adenomera* spp. and *Allobates* spp.). Frogs detected within 20 m of either side of the plot center line were recorded. To reduce potential detectability effects on assemblage-level data, we sampled each plot three times. We surveyed all plots during the rainy season (January–March) in 2018 and 2019, covering the reproductive peak of most species. Our dataset consisted of counts of frogs found by two simultaneous observers per plot. The average observation time per plot per survey was 22.8 min (SD = 8.45) during the afternoon and twilight and 61.4 min at night (SD = 11.8).

We identified species based on the literature (e.g., Carvalho et al., 2021; Lima et al., 2006) and comparisons with specimens deposited in the herpetological collection of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus). We collected a maximum of five voucher specimens per species, following protocols for collecting and preserving specimens that were approved by ICMBio/SISBIO license nº 60193–2. No endangered species was collected.

2.3 | Environmental variables

We measured litter depth with a Marimon-Hay sampler (Marimon-Junior & Hay, 2008) because litter depth determines the availability of refuge, breeding, and foraging sites for terrestrial species (Fauth et al., 1989; Van Sluys et al., 2007). We measured this variable at six points separated by 50-m intervals in each plot and used mean values per plot in the analyses.

We measured several variables quantifying forest structure (see Torralvo et al., 2020) and used principal component analysis (PCA) to summarize them into a single variable that potentially affects the overall habitat availability and quality. This forest-structure variable is related to levels of vertical stratification, incidence of sunlight and moonlight, microclimate, and primary productivity (Parker et al., 2004). In addition, forest structure may affect frogs indirectly, because primary productivity affects the overall availability or turnover of invertebrate food resources (e.g., Death & Zimmermann, 2005). We used data collected by a portable light detection and ranging (LIDAR) device, which scans the environment with a laser for rapid measurement of multiple variables quantifying forest structure (Parker et al., 2004). We measured mean and maximum vegetation height, leaf density, and leaf area between 0 and 15 m high, and above 15 m, canopy opening and clearing fractions at 5, 10, and 15 m above ground. To represent forest structure in the inferential models, we summarized all LIDAR variables as the first axis of a principal component analysis (PCA), which captured 59% of the variance in the original variables (Table S1). We also tested the original variables with the harmonicmeanp R-package, a statistical technique used for addressing multiple-comparison questions that controls the probability of making one or more false discoveries, or type I errors, when performing multiple hypotheses tests (Wilson, 2019). In our case, the PCA axis had a stronger relationship with the response variables than using all the variables, which indicates that it captures most of the useful information about forest structure.

Temperature potentially limits frog species' abundances and trait occurrence because it affects metabolic and physiological processes linked to survival and reproduction (von May et al., 2017; Ståhlberg et al., 2001) of frogs or organisms that interact with them, such as predators (Greenwald, 1974) and prey (Gilbert & Raworth, 1996). We measured temperature at the beginning of day and night sampling using AK172-AKSO® data loggers and used mean values for each plot in the inferential models.

We measured distance from the nearest water body because it differentiates assemblages between riparian and non-riparian zones (Fraga et al., 2011; Rojas-Ahumada et al., 2012). We measured the distances from the coordinates of each plot to the nearest water body using the linear-distance matrix and Qchainage tools of the QGis 3.16.2 software (QGIS Development Team, 2020), applied over combined hydrography shapefiles from public repositories (MMA, 2006), following Venticinque et al. (2016).

We measured soil texture because this variable potentially affects frog diversity by determining moisture retention and availability of invertebrates that are part of the diet of most frogs (Menin et al., 2007; Nielsen et al., 2010). We used SoilGrids (Arrouays et al., 2014) to obtain sand and silt content 0–5 m deep, assuming that this layer is more likely to affect frogs than deeper strata. We extracted sand- and silt-content values from centroid coordinates of each plot using the raster R-package (Hijmans, 2020).

We measured deforestation because habitat loss and fragmentation due to the expansion of human occupation is one of the main causes of the local and global amphibian decline (Collins et al., 2009;

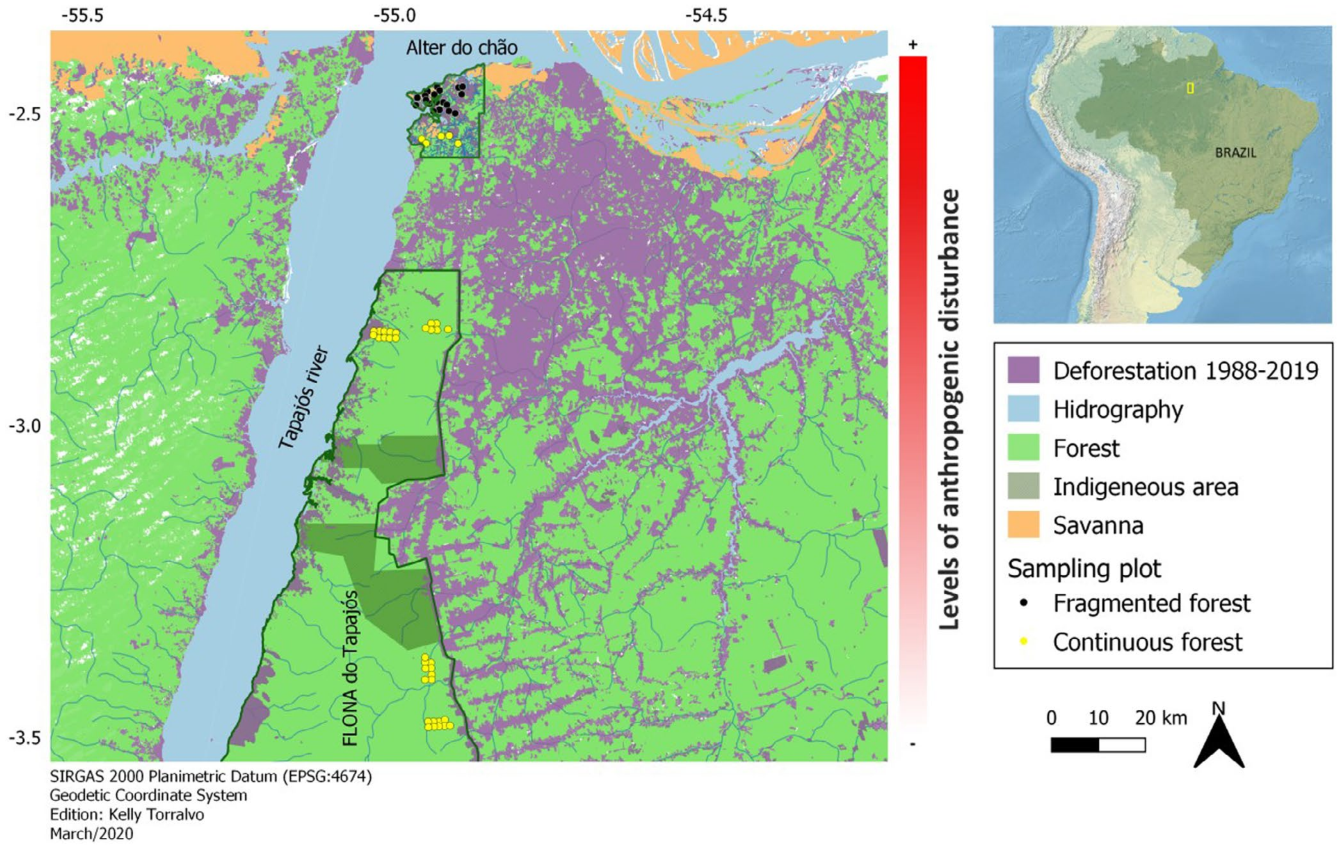


FIGURE 1 Study area in western Pará, eastern Amazonia, showing the location of 57 sampling plots, each 250 m long. Note that the gradient in anthropogenic deforestation generally increased in the south–north direction

Menin et al., 2019; Sodhi et al., 2008). Although our sampling was designed at a local scale, assemblage responses to environmental conditions are usually hierarchically dependent (Peixoto et al., 2020; Vellend, 2010). We used a 30 x 30 m^2 satellite-based layer summarizing deforestation until 2019 from the MapBiomas project (Souza et al., 2020, see full description in http://mapbiomas.org) to extract proportions of deforested areas in 500-m buffers using the raster R-package (Hijmans, 2020). The size of the buffers was defined to avoid overlap, so deforestation values are spatially independent.

2.4 | Taxonomic composition

We applied generalized linear models to high-dimensional data to test the effects of environmental variables on frog abundances. We used the manyglm function of the mvabund R-package (Wang et al., 2020). This analysis allows for hypothesis testing and, unlike distance-based methods, does not confound node and link effects due to the misspecification of the mean–variance relationship (Warton et al., 2012). We evaluated levels of multicollinearity among environmental variables based on the variance inflation factor (VIF), which we calculated using the car R-package (Fox et al., 2012). This approach indicated that there was little redundancy in the predictor variables (VIF < 1.91 in all cases). We assessed the significance of the final model using Wald's test and PIT-trap resampling with 999 iterations (anova.manyglm function) and plotted diagnostic residual distributions in Figure S1. To visualize the variation in species abundance along the environmental gradients and deforestation, we sorted the plots in ascending order of values relative to the gradients and plotted their positions with symbol sizes encoding abundances (Figure S2).

2.5 | Functional composition

We measured species traits which are potentially mediators of environmental filtering, based on the assumption that traits poorly fitted to local environmental conditions tend to generate low abundance or absence of species. Relating these traits to the predictive variables of taxonomic diversity can provide a link between spatial variation in species and trait selection due to environmental heterogeneity. We selected traits that could potentially be selected by the environment as they determine species fitness and dispersal ability under local environmental conditions (Table 1).

We measured snout–vent length (SVL) and leg length relative to SVL in five adult males and used mean values per plot in the analyses. For those species for which no specimens were collected, we obtained mean SVL and leg length values for adult males from the

TABLE 1 Species traits and underlying ecological processes potentially mediating relationships between frog functional composition and environmental gradients

Trait	Abbr	Type of data	Underlying ecological process	References
SVL	SVL	Continuous	Ability to disperse, forage and escape predators	Altwegg & Reyer, 2003, Buckley et al., 2005
SVL relative to leg length	legs	Continuous	Ability to disperse, forage and escape predators	Altwegg & Reyer, 2003, Buckley et al., 2005
Arboreal or terrestrial habit	arbo; ter	Binary	Direct interactions between frogs and habitats	Duellman & Trueb, 1994
Direct or larval breeding	breed_dir; breed_lar	Binary	Mediates reproductive-migration behavior	Lutz, 1948, Sinsch, 1990
Terrestrial or water eggs and terrestrial or larval tadpoles	eggs_ter; eggs_ter; tad_ter; tad_wat ac	Binary	Exposure of eggs and metamorphs to predation	Magnusson & Hero, 1991, Azevedo-Ramos & Magnusson, 1999
Diurnal, crepuscular or nocturnal activity	act_diur; act_crep; act_noc	Binary	Circadian patterns of foraging, reproduction and resting-site occupancy	Duellman & Trueb, 1994

Note: Trait abbreviations (Abbr) are used in some of the graphs shown in the results.

literature (e.g., Carvalho et al., 2021; Lima et al., 2006; Oliveira et al., 2017). This does not include species identified as aff. (*affinis*) or gr. (group), for which traits were measured or observed in the field. Additionally, we evaluated the effects of environmental variables on thirteen binary traits (presence or absence). We evaluated the effects of terrestrial and arboreal habits, expecting that plots where the forest structure is relatively open and little vertically stratified, or the vegetation density is relatively low because of high deforestation, would have less availability of foraging and reproduction sites for arboreal species. Consequently, the occurrence frequency of arboreal species should be higher in plots with denser and taller vegetation and plots with less deforestation.

We hypothesized that species with direct breeding should be able to occur at greater distances from the water, and in sites with greater litter depth in the case of species that build foam nests. Additionally, proportion of deforestation may affect breeding mode by selecting against species sensitive to edge effects. We expected that species with terrestrial eggs and tadpoles would be affected by litter depth and soil water-retention capacity associated with sand content. These variables may be altered by deforestation, so we expected effects of deforestation on the type of substrate for eggs and tadpoles. Diurnal, crepuscular, and nocturnal activity is also likely to be affected by deforestation, because forest fragmentation increases light incidence and temperature in the hottest hours of the day, which potentially leads to dehydration.

To test the effects of environmental gradients and deforestation on species traits, we used a combination of RLQ and fourth-corner analysis (Dray et al., 2014). This approach performs a double-inertia analysis of environmental data (R) and functional traits (Q) with a link expressed by a contingency table composed of species relative abundances (L). We undertook RLQ using the ade4 R-package (Dray & Dufour, 2007), which applies a correspondence analysis (CA) on the L array and evaluates covariance between the R and Q arrays through Hill-Smith PCA (principal component analysis), respectively. We set up the model with environmental variables scaled to have mean zero and standard deviation one and species abundances standardized by the maximum abundance. We tested a combination of null hypotheses assuming that (i) the distribution of species with fixed traits (site-independent) is not influenced by environmental variables, and (ii) the distribution of species along fixed environmental conditions is not influenced by traits (trait-independent). This configuration corresponds to the model 6 available in the ade4 R-package, for which we assessed coefficients based on 49999 permutations (following Farneda et al., 2015; Núñez et al., 2019). The predictive power of this combination of null hypotheses depends on well-adjusted relationships between the RLQ arrays, but an exploratory analysis showed that to achieve this relationship two outlier species (*Adenomera* gr. *hylaedactyla* and *Leptodactylus* gr. *petersii*) had to be removed (Figure S3).

The fourth-corner analysis tests correlations between environmental variables and species traits, and we combined it with the first two axes produced by the RLQ, summarizing environmental variables and species traits. This approach was advantageous for producing correlation matrices, which is a simplified way of showing the results.

2.6 | Spatial autocorrelation

Considering that plots in highly deforested areas were concentrated in the north of our study area, spatial autocorrelation effects could confound the results of both the linear model to predict species abundance, and the RLQ + fourth-corner analysis. To quantify the effects of spatial autocorrelation, we applied Moran's *I* tests to the summed residuals derived from the linear model and the scores produced by the RLQ analysis. We used the ape R-package (Paradis et al., 2004) for global spatial autocorrelation and the pgirmess R-package (Giraudoux, 2018) for spatial autocorrelation in seven distance classes. Additionally, we partitioned the variances explained by the RLQ + fourth-corner between the RLQ axis 1 and 2 separately and the geographic distance, which we represented by the axis of a Principal Coordinates of the Neighborhood Matrix (PCNM) applied to the Euclidean distances among paired plots that was more positively correlated with the RLQ axis (Borcard & Legendre, 2002; see Figure S4). Our dataset can be fully accessed at https://doi.org/10.5061/dryad.gb5mkkwqv.

3 | RESULTS

3.1 | Sampling overview

We found 1221 individuals belonging to 26 species and seven families (Table 2). Some of them were in unsolved species complexes or undescribed species. For those, we assigned gr., aff. or sp. The leptodactylids *Leptodactylus paraensis* and *Adenomera amicorum* found in 84.2% and 64.9% of the plots, respectively, were the most frequently sampled species. In contrast, *Leptodactylus* gr. *petersii* (Leptodactylidae) and *Boana* gr. *geographica* (Hylidae) were recorded in only 3.5% and 1.7% of the plots, respectively.

3.2 | Taxonomic and functional assemblage composition

Assemblage composition was significantly (p = .001) affected by deforestation (Wald = 6.96, p = .002), distance from nearest water body (Wald = 7.11, p = .003), forest structure (Wald = 6.78, p = .005), soil sand (Wald = 7.32, p = .001) and silt (Wald = 6.76, p = .004) contents. These results suggest that distinct local assemblages were generated by multiple environmental variables filtering species across landscapes. Furthermore, they show that deforestation has altered frog assemblage composition by causing changes in the occurrence or abundance of some species, particularly in the north of the study area, where forests have been more intensely fragmented (see Figure 1).

Most of the sampled species had locally restricted distributions or noticeably higher abundances at one of the ends of the environmental gradients, while smaller proportions of species occurred with approximately homogeneous abundances throughout the gradients (Figure S2). Overall, these findings suggest that frog assemblages are structured by species turnover along environmental gradients, since random assemblage composition would be shown in these graphs by a rectangular pattern of multiple species distribution (most species occurring along large portions of the gradients), and nested assemblages would form triangles (most species more common at one extreme of the gradient). Furthermore, 46% of the sampled species (e.g., *Adelphobates castaneoticus*, *Allobates magnussoni*, *Pristimantis ockendeni*, and *Osteocephalus* aff. *oophagus*) occurred exclusively in plots with no deforestation, while 19% of the species (e.g., *Boana wavrini*, *Rhinella major*, and *Adenomera* gr. *hylaedactyla*) occurred exclusively or with higher abundances in plots with high proportional deforestation. The other species occurred with similar abundances throughout the deforestation gradient. Similar patterns occurred for the soil silt-content gradient.

The first two RLQ axes, which indicate the inertia derived from the relationship between species traits and environmental variables, captured an accumulated variance of 96.81% (92.56% axis 1 and 4.25% axis 2). The Hill-Smith PCA summarizing the R table captured 32.9% of the variance in environmental variables along axis 1. Deforestation plus soil silt content and forest structure plus distance from water body were at opposite ends of the first PCA axis (Figure 2a). PCA axis 2 captured 22.4% of the variance in environmental variables and was associated with litter depth, soil sand content, and temperature. The correspondence analysis (CA) summarizing table L captured 19.4% of the variance in species abundance along axis 1 and 9.1% along axis 2. This analysis graphically revealed at least four clusters, which are composed of (i) Hylid treefrogs that live close to water bodies (e.g., *Boana wavrini*, *Boana* gr. *geographica*, and *Leptodactylus pentadactylus*), (ii) large-bodied species plus *Rhinella major*, which typically occupy open areas and forest edges, (iii) forest-dweller species such as Phyllomedusid treefrogs (e.g., *Phyllomedusa vaillanti* and *Phyllomedusa hypochondrialis*) and small-bodied litter frogs (e.g., *Allobates femoralis*, *Adenomera amicorum*, and *Adelphobates castaneoticus*), and (iv) direct-breeding Craugastorid species (Figure 2b). The PCA summarizing the Q table captured 38.4% of the variance in species traits along axis 1, which mainly separated into opposite ends spawning and larval-breeding site, and period of activity. Axis 2 captured 27.1% of the variance in the traits and separated species with larvae from those with direct development of juveniles (Figure 2c). Complete results from the RLQ can be found in Table 3.

Combining RLQ with fourth-corner (Figure 3) revealed that the axis relative to the species traits (table Q) was significantly affected by deforestation (p = .002), distance from the nearest water body (p = .02), temperature (p = .03), soil silt content ($p < .001$), and forest structure (p = .01). Overall, these findings were consistent with the linear model predicting species abundances, suggesting that spatial variation in abundances is mediated by the environment selecting species traits. These variables negatively affected SVL (p = .008) and the occurrence of species which lay eggs on land (p = .04), while positively affecting the occurrence of species which lay eggs in water ($p = .04$). The distribution of values related to environmental gradients measured along the axes derived from the Hill-Smith PCA (Figure S5) indicates that (i) small-bodied species have been filtered from plots located in heavily deforested areas, with silt-rich soils and low and sparse vegetation. Additionally, small-bodied species have been filtered from plots close to water bodies, but this finding reflects the fact that mean distances to water bodies were higher in the north of the study area (ANOVA $F_{1-51} = 15.08$, $p < .0001$), where deforestation levels are lower. The medium-sized toad *Rhinella major* (55 mm on average) clustered with large-bodied species under the same environmental conditions, but this species typically occupies open areas and forest edges and is unlikely to be found in the interior of forests; (ii) species that lay eggs on land or have direct juvenile development (without larval stage) have been filtered from plots in heavily deforested sites. *Leptodactylus paraensis* is not water-dependent for breeding because it lays eggs in foam nests on land, suggesting that the greater availability of breeding sites in the north of the study area is not the only factor mediating the local species distribution via trait selection.

4 | DISCUSSION

We showed that a combination of variables naturally changing over space and deforestation determine the local frog composition in an eastern Amazonian region. Overall, forests are not homogeneously suitable for all species, but habitat-suitability mosaics have spatially structured assemblages through species turnover. This is consistent with the premises of environmental filtering, which predict that local species subsets from the regional pool will differ across heterogeneous landscapes because species have different environmental requirements (Chase & Myers, 2011; Leibold & McPeek, 2006). Additionally, forest structure was one of the main predictors of the variation in the species abundances and trait occurrence, indicating that it has driven local assemblage composition across the study area. Deforestation negatively affects forest-dwelling species, favors the establishment of generalist species (Furlani et al., 2009), and potentially increases the risk of lethal disease spread (Becker et al., 2016). Deforestation was associated with assemblage turnover along the south–north axis of the study area, with the north being mainly occupied by species relatively more tolerant to open areas and edge effects.

We found evidence that abundance-based frog assemblages are spatially heterogeneous across the study area because species are filtered from deforested areas through relationships mediated by some of their functional traits. Assemblages occupying heavily deforested areas were dominated by large-bodied species, such as *Leptodactylus paraensis* and *Rhinella marina* (Figure S2), probably because small-bodied species are more dependent on forest corridors to disperse, or have a higher risk of death when crossing open environments to reach nearby forest fragments (Carr & Fahrig, 2001; Gibbs, 1998). The medium-sized *Rhinella major* shares habitats with large-bodied species in deforested sites, but it is part of

TABLE 2 Frog species found in 57 sampling plots in the Tapajós National Forest (southern portion of the study area) and around the village of Alter do Chão (northern portion of the study area), western Pará, Brazil

Taxa	Abbr	Frequency
Aromobatidae		
Allobates femoralis (Boulenger, 1884)	A.fem	42.10
Allobates magnussoni (Lima, Simões & Kaefer, 2014)	A.mag	5.26
Bufonidae		
Rhinella castaneotica (Caldwell, 1991)	R.cas	15.78
Rhinella magnussoni (Lima, Menin & Araújo, 2007)	R.mag	35.08
Rhinella major (Muller & Helmich, 1936)	R.maj	8.77
Rhinella marina (Linnaeus, 1758)	R.mar	35.08
Craugastoridae		
Pristimantis aff. *fenestratus* (Steindachner, 1864)	P.fen	7.01
Pristimantis latro (Oliveira et al., 2017)	P.lat	59.64
Pristimantis ockendeni (Boulenger, 1912)	P.ock	15.78
Dendrobatidae		
Adelphobates castaneoticus (Caldwell & Myers, 1990)	A.cas	7.01
Hylidae		
Boana gr. *geographica* (Spix, 1824)	B.geo	1.75
Boana wavrini (Parker, 1936)	B.wav	8.77
Osteocephalus aff. *oophagus* (Jungfer & Schiesari, 1995)	O.oop	33.33
Osteocephalus aff. *taurinus* (Steindachner, 1862)	O.tau	33.33
Trachycephalus helioi (Nunes, Suárez, Gordo, and Pombal, 2013)	T.hel	8.77
Trachycephalus typhonius (Linnaeus, 1758)	T.typ	7.01
Trachycephalus resinifictrix (Goeldi, 1907)	T.res	57.89
Leptodactylidae		
Adenomera gr. *andreae* (Müller, 1923)	A.and	63.15
Adenomera gr. *hylaedactyla* (Cope, 1868)	A.hyl	49.12
Adenomera amicorum (Carvalho et al., 2021)	A.ami	64.91
Leptodactylus gr. *petersii* (Steindachner, 1864)	L.pet	3.50
Leptodactylus mystaceus (Spix, 1824)	L.mys	12.28
Leptodactylus paraensis (Heyer, 2005)	L.par	84.21
Leptodactylus pentadactylus (Laurenti, 1768)	L.pen	12.28
Phyllomedusidae		
Phyllomedusa vaillantii (Boulenger, 1882)	P.vai	5.26
Pithecopus hypochondrialis (Daudin, 1800)	P.hyp	7.01

Note: Species abbreviations (Abbr) are used in some of the graphs shown in the results. Occurrence frequencies are relative to the number of plots in which the species was recorded.

a clade dominated by open-habitat dwellers that reproduce near forest edges and river beaches without vegetation cover (Silva et al., 2017). Also, the thick skins of bufonid toads provide high resistance to cutaneous dehydration, which likely enables them to occupy warm, dry habitats (Young et al., 2005). Therefore, our results suggest that frog assemblages in areas fragmented by deforestation are structured by environmental conditions limiting local species distribution through a combination of dispersal capacity and dehydration tolerance.

We found that species with direct breeding and terrestrial oviposition were less abundant in deforested sites. The availability of egg-deposition and tadpole-development sites seems to be a limiting factor for regional frog diversity, which has been considerably reduced in fragmented forests. These findings may reflect the general expectation that forests tend to have more frog species that do not depend on water to reproduce than non-forest habitats (Duellman, 1992; Höld, 1990). However, these findings may also be biased by the inequity in the distribution of water bodies throughout the study area. Although our analyses did not detect effects of spatial autocorrelation in the predictive models, the higher concentration of water bodies in the most deforested sites does not allow us to precisely distinguish whether species that lay eggs on land have been filtered from these sites by competition with species that lay eggs in water (e.g., by space or food), or if they do not tolerate the edge effects caused by forest fragmentation. Future studies should focus on the role of distance from water bodies on frog assemblages through sampling in the south of the FLONA, where the density of streams and ponds is higher.

Information on species turnover along natural environmental gradients is useful for biodiversity conservation because it indicates biotic complementarities among sites, which can be used as a criterion to define priority areas (Cabeza & Moilanen, 2001; Margules et al., 1994; Rodrigues et al., 2000) or to assess the efficiency of conservation policies (Bueno et al., 2012; Fraga et al., 2011). Although our models identified species turnover mainly associated with deforestation, we also detected turnover along gradients that do not necessarily reflect human activities, such as distance from nearest water body and soil sand content. Distance from water is commonly associated with variation in frog assemblages in the Amazon, as it determines the presence or the absence of species with specialized reproductive modes (Menin et al., 2011; Ribeiro et al., 2012; Rojas-Ahumada et al., 2012). Soil texture determines its potential to retain moisture (e.g., Menin et al., 2007; Woinarski et al., 1999) and the composition of soil fauna (Anderson, 1977; Nielsen et al., 2008, 2010) that are prey for frogs. The most deforested areas were also the areas with the highest silt concentrations (Figure S2). This may be an effect of deforestation, or human activities may have been directed toward areas with more silt. The species most common to these areas were terrestrial species known to be associated with deforestation in other areas in the Amazon (Menin et al., 2019; Tsuji-Nishikido & Menin, 2011), so it is unlikely that they were more common there only because of the greater silt availability. Additionally, some species that did not occur in these areas are found in areas with high silt content (e.g., *Allobates femoralis*, Ferreira et al., 2018), so it is unlikely that their absence from the most disturbed areas was because of excess silt. Future studies should focus

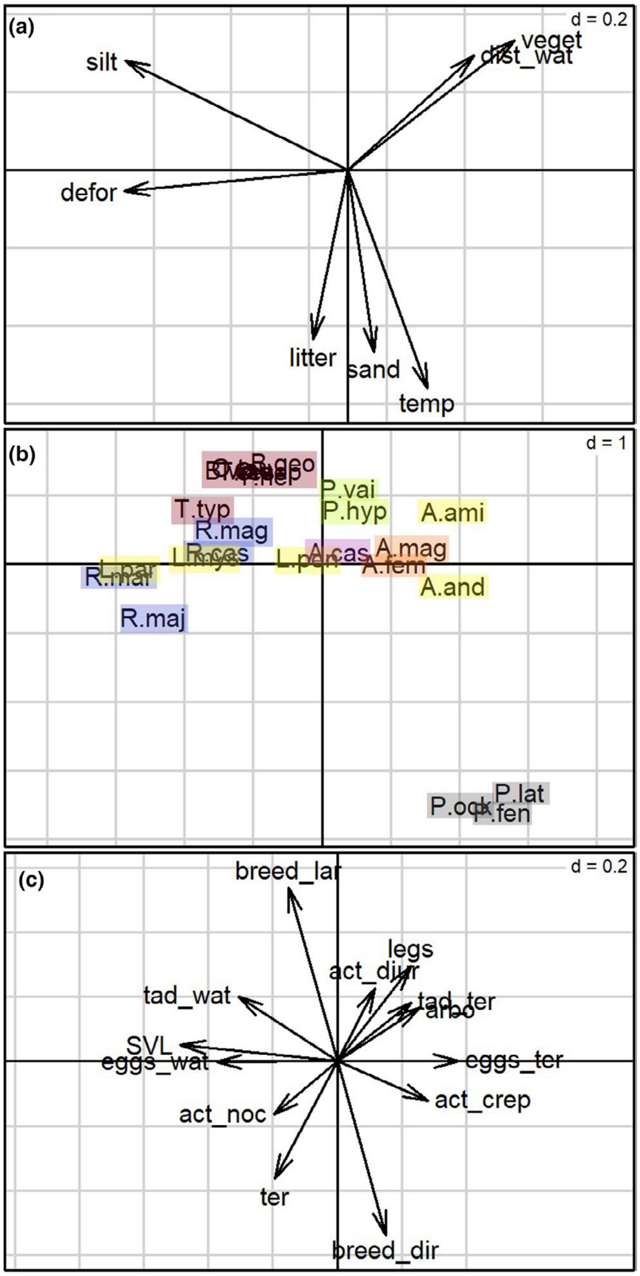


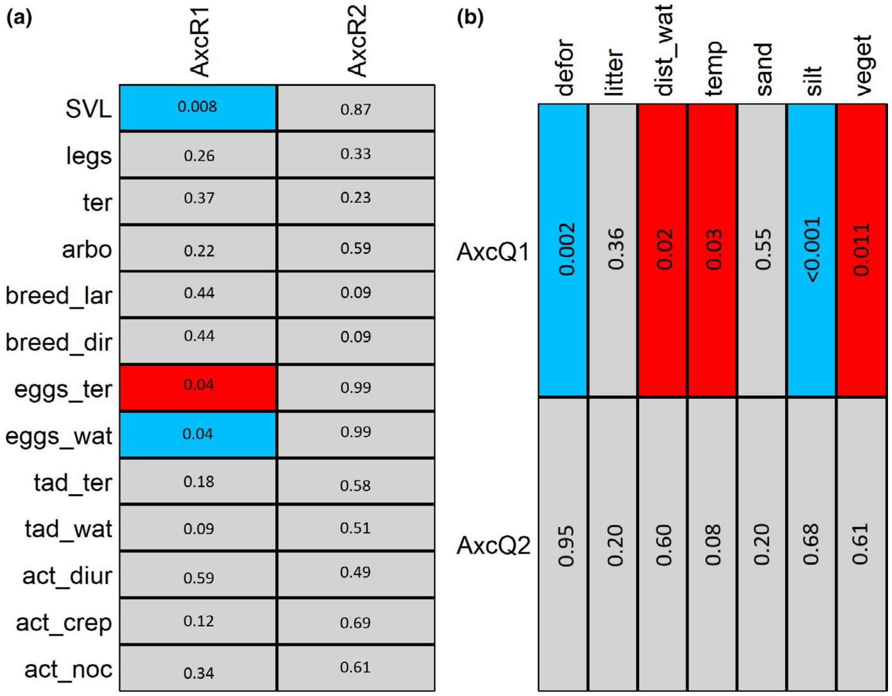
FIGURE 2 Biplots derived from a RLQ analysis applied to estimate the effects of environmental variables on frog species traits. (a) Hill-Smith PCA (principal component analysis) summarizing environmental gradients, where vectors denote distances and directions from the centroid, (b) row CA scores summarizing species, where colors distinguish frog families (dark red—Hylidae, blue—Bufonidae, yellow–Leptodactylidae, orange—Aromobatidae, green—Phyllomedusidae, purple—Dendrobatidae, and gray—Craugastoridae. (c) PCA loadings summarizing species traits. Environmental variables are abbreviated as defor—deforestation, litter—litter depth, dist_wat—distance from nearest water body. temp—temperature, sand—soil sand content, silt—soil silt content, and veget—forest structure). For species and trait abbreviations, see Tables 1 and 2, respectively

TABLE 3 Summary of a RLQ analysis applied to estimate the effects of environmental variables on frog species traits

	RLQ 1		RLQ 2	
	Eigenvalues	%	Eigenvalues	%
RLQ ordination	1.57	92.56	0.07	4.25
Correlation: L	0.45	56	0.15	28
Covariance	1.25	-	0.26	-
Projected variance: Q	3.59	72	5.5	64
Projected variance: R	2.15	93	3.76	97
R table (Hill-Smith PCA)	2.3	32.98	1.56	22.4
L table (CA)	0.63	19.41	0.3	9.15
Q table (PCA)	4.99	38.4	3.53	27.15

Note: Percentages denote total co-inertias explained by the first two RLQ axes. The R table summarizes environmental variables, the L table summarizes species abundances, and the Q table summarizes species traits. Traces are shown when a coefficient does not apply to RLQ-derived attributes.

Abbreviations: CA, correspondence analysis; PCA, principal component analysis.



(a)

	AxcR1	AxcR2
SVL	0.008	0.87
legs	0.26	0.33
ter	0.37	0.23
arbo	0.22	0.59
breed_lar	0.44	0.09
breed_dir	0.44	0.09
eggs_ter	0.04	0.99
eggs_wat	0.04	0.99
tad_ter	0.18	0.58
tad_wat	0.09	0.51
act_diur	0.59	0.49
act_crep	0.12	0.69
act_noc	0.34	0.61

(b)

	defor	litter	dist_wat	temp	sand	silt	veget
AxcQ1	0.002	0.36	0.02	0.03	0.55	<0.001	0.011
AxcQ2	0.95	0.20	0.60	0.08	0.20	0.68	0.61

FIGURE 3 Summarized coefficients derived from a combined RLQ and fourth-corner analysis used to infer the effects of environmental variables on frog species traits. (a) correlations between the first two RLQ axes summarizing environmental variables (AxcR1 and AxcR2) and species traits. (b) Correlations between the first two RLQ axes summarizing species traits (AxcQ1 and AxcQ2) and environmental variables. Red cells are positive correlations, blue cells are negative correlations, and gray cells show statistically nonsignificant correlations ($p > .05$). Environmental variables are abbreviated as defor—deforestation, litter—litter depth, dist_wat—distance from nearest water body, temp—temperature, sand—soil sand content, silt—soil silt content, and veget—forest structure). For trait abbreviations, see Table 1

on investigating the effects of deforestation on soil structure, especially in regard to silt content, which has been little discussed in studies of Amazonian frogs.

We conclude that frog assemblages in an eastern Amazonian region are not randomly distributed across forests but represent local species subsets from a regional pool. Many of the species we sampled are widely distributed across eastern Amazonia or cover large extents of the Amazon (Frost, 2019; Moraes et al., 2016). However, these species have found barriers to dispersal and survival, which have limited their distribution on a local scale. Specifically, small-bodied species and those that lay eggs on land have been filtered from deforested sites, probably because they do not tolerate edge effects, while species that do not depend on water for reproduction and those with direct development of juveniles have shared habitats in continuous forests. Therefore, the barriers to the local species distribution are mainly derived from the deforestation around Alter do Chão, a particularly sensitive site for biodiversity conservation in the region we sampled. Although this area is classified as an environmental protection area (APA in Portuguese), it has been under strong pressure from real-estate speculation because, in practice, APAs have little legal protection in Brazil (ICMBio, 2009).

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CONFLICT OF INTERESTS

The corresponding author confirms on behalf of the authors that there have been no involvements that might raise the question of bias in the work, conclusions, implications, or opinions here stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gb5mkkwqv (Torralvo et al., 2021).

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REFERENCES

Altwegg, R., & Reyer, H. U. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution*, *57*, 872–882. https://doi.org/10.1111/j.0014-3820.2003.tb00298.x

Anderson, J. M. (1977). The organization of soil animal communities. *Components of Ecosystems Ecological Bulletins*, *25*, 15–23.

Arrouays, D., Grundy, M. G., Hartemink, A. E., Hempel, J. W., Heuvelink, G. B., Hong, S. Y., Lagacherie, P., Lelyk, G., McBratney, A. B., McKenzie, N. J., Mendonca-Santos, M. L., Minasny, B., Montanarella, L., Odeh, I. O. A., Sanchez, P. A., Thompson, J. A., & Zhang, G. L. (2014). GlobalSoilMap: Toward a fine-resolution global grid of soil properties. *Advances in Agronomy*, *125*, 93–134.

Azevedo-Ramos, C., & Magnusson, W. E. (1999). Tropical tadpole vulnerability to predation: Association between laboratory results and prey distribution in an Amazonian savanna. *Copeia*, *1999*(1), 58–67. https://doi.org/10.2307/1447385

Becker, C. G., Rodriguez, D., Longo, A. V., Toledo, L. F., Lambertini, C., Leite, D. S., Haddad, C. F. B., & Zamudio, K. R. (2016). Deforestation, host community structure, and amphibian disease risk. *Basic and Applied Ecology*, *17*(1), 72–80. https://doi.org/10.1016/j.baae.2015.08.004

Benchimol, M., & Peres, C. A. (2015). Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of Ecology*, *103*, 408–420.

Bolochio, B. E., Lescano, J. N., Cordier, J. M., Loyola, R., & Nori, J. (2020). A functional perspective for global amphibian conservation. *Biological Conservation*, *245*, 108572–https://doi.org/10.1016/j.biocon.2020.108572

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*, 51–68. https://doi.org/10.1016/S0304-3800(01)00501-4

Borges-Matos, C., Aragón, S., da Silva, M. N. F., Fortin, M., & Magnusson, W. E. (2016). Importance of the matrix in determining small-mammal assemblages in an Amazonian forest-savanna mosaic. *Biological Conservation*, *204*, 417–425. https://doi.org/10.1016/j.biocon.2016.10.037

Bradshaw, C. J. A., Sodhi, N. S., & Brook, B. W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, *7*, 79–87. https://doi.org/10.1890/070193

Braga-Neto, R., Luizão, R. C. C., Magnusson, W. E., Zuquim, G., & De Castilho, C. V. (2008). Leaf litter fungi in a Central Amazonian forest: The influence of rainfall, soil and topography on the distribution of fruiting bodies. *Biodiversity and Conservation*, *17*, 2701–2712.

Buckley, C. R., Michael, S. F., & Irschick, D. J. (2005). Early hatching decreases jumping performance in a direct-developing frog, *Eleutherodactylus coqui*. *Functional Ecology*, *19*, 67–72.

Bueno, A. S., Bruno, R. S., Pimentel, T. P., Sanaiotti, T. M., & Magnusson, W. E. (2012). The width of riparian habitats for understory birds in an Amazonian forest. *Ecological Applications*, *22*, 722–734. https://doi.org/10.1890/11-0789.1

Cabeza, M., & Moilanen, A. (2001). Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution*, *16*, 242–248. https://doi.org/10.1016/S0169-5347(01)02125-5

Carr, L. W., & Fahrig, L. (2001). Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology*, *15*, 1071–1078. https://doi.org/10.1046/j.1523-1739.2001.0150041071.x

Carvalho, T. R., Moraes, L. J., Lima, A. P., Fouquet, A., Peloso, P. L., Pavan, D., Drummond, L. O., Rodrigues, M. T., Giaretta, A. A., Gordo, M., Neckel-Oliveira, S., & Haddad, C. F. B. (2021). Systematics and historical biogeography of Neotropical foam-nesting frogs of the Adenomera heyeri clade (Leptodactylidae), with the description of six new Amazonian species. *Zoological Journal of the Linnean Society*, *191*, 395–433. https://doi.org/10.1093/zoolinnean/zlaa051/5880331

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Cintra, R., Magnusson, W. E., & Albernaz, A. (2013). Spatial and temporal changes in bird assemblages in forest fragments in an eastern Amazonian savannah. *Ecology and Evolution*, *3*, 3249–3262. https://doi.org/10.1002/ece3.700

Collins, J. P., Crump, M. L., & Lovejoy, T. E. III (2009). *Extinction in our times: Global amphibian decline*. Oxford University Press.

Costa, F. R., Guillaumet, J. L., Lima, A. P., & Pereira, O. S. (2009). Gradients within gradients: The mesoscale distribution patterns of palms in a central amazonian forest. *Journal of Vegetation Science*, *20*, 69–78. https://doi.org/10.3170/2008-8-18478

da Silva, M. I., Schiesari, L. C., & Menin, M. (2017). The egg clutch and tadpole of Rhinella merianae (Gallardo, 1965) (Anura: Bufonidae) from Central Amazonia, Brazil. *Zootaxa*, *4294*, 145. https://doi.org/10.11646/zootaxa.4294.1.12

de Fraga, R., Lima, A. P., & Magnusson, W. E. (2011). Mesoscale spatial ecology of a tropical snake assemblage: The width of riparian corridors in central Amazonia. *Herpetological Journal*, *21*, 51–57.

de Oliveira, E. A., Rodrigues, L. R., Kaefer, I. L., Pinto, K. C., & Hernández-Ruz, E. J. (2017). A new species of Pristimantis from eastern Brazilian Amazonia (Anura, Craugastoridae). *ZooKeys*, *2017*, 101–129. https://doi.org/10.3897/zookeys.687.13221

Death, R. G., & Zimmermann, E. M. (2005). Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos*, *111*, 392–402. https://doi.org/10.1111/j.0030-1299.2005.13799.x

Dias-Terceiro, R. G., Kaefer, I. L., de Fraga, R., de Araújo, M. C., Simões, P. I., & Lima, A. P. (2015). A matter of scale: Historical and environmental factors structure anuran assemblages from the Upper Madeira River, Amazonia. *Biotropica*, *47*, 259–266. https://doi.org/10.1111/btp.12197

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Díaz-Ricaurte, J. C., Arriaga Villegas, N. C., López Coronado, J. D., Macias Garzón, G. X., & Fiorillo, B. F. (2020). Effects of agricultural systems on the anuran diversity in the Colombian Amazon. *Studies on Neotropical Fauna and Environment*. https://doi.org/10.1080/01650521.2020.1809334

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & Ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, *95*, 14–21. https://doi.org/10.1890/13-0196.1

Dray, S., & Dufour, A.-B. (2007). The ade4 Package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Duellman, W. E. (1992). Reproductive strategies of frogs. *Scientific American*, *267*, 80–87. https://doi.org/10.1038/scientificamerican0792-80

Duellman, W. E., & Trueb, L. (1994). *Biology of amphibians*. JHU Press.

Elton, C. (1927). *Animal ecology*, *1927* (p. 56). Sidgwick Jackson, LTD.

Ernst, R., & Rödel, M. (2006). Community assembly and structure of tropical leaf-litter Anurans. *Ecotropica*, *12*, 113–129.

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology Evolution and Systematics*, *48*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D., & Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, *52*, 1381–1391. https://doi.org/10.1111/1365-2664.12490

Fauth, J. E., Crother, B. I., & Slowinski, J. B. (1989). Elevational patterns of species richness, evenness, and abundance of the costa rican leaf-litter Herpetofauna. *Biotropica*, *21*, 178. https://doi.org/10.2307/2388708

Ferreira, A. S., Jehle, R., Stow, A. J., & Lima, A. P. (2018). Soil and forest structure predicts large-scale patterns of occurrence and local abundance of a widespread Amazonian frog. *PeerJ*, *6*, 1–26. https://doi.org/10.7717/peerj.5424

Forman, R. T. T. (1995). Some general principles of landscape and regional ecology. *Landscape Ecology*, *10*, 133–142. https://doi.org/10.1007/BF00133027

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., & Graves, S. (2012). *Package 'car'*. R Found. Stat. Comput.

Frost, D. R. (2019). *Amphibian Species of the World: an Online Reference*. Electron. Database Access. Am. Museum Nat. Hist. New York, USA. Version 6: 1–23. http://research.amnh.org/herpetology/amphibia/index.html

Furlani, D., Francesco Ficetola, G., Colombo, G., Ugurlucan, M., & De Bernardi, F. (2009). Deforestation and the Structure of Frog Communities in the Humedale Terraba-Sierpe, Costa Rica. *Zoological Science*, *26*, 197–202. https://doi.org/10.2108/zsj.26.197

Ganança, P. H. S., Santos, A. P., Kawashita-Ribeiro, R. A., de Vasconcelos Neto, L. B., dos Santos Júnior, I. A., Guedes, D. S., & Fraga, R. (2021). Habitats determining local frog assemblages within aquatic macrophyte meadows in Amazonia, through species traits filtering. *Austral Ecology*, *46*, 574–587.

Gibbs, J. P. (1998). Amphibian movements in response to forest edges, roads, and streambeds in Southern New England. *Journal of Wildlife Management*, *62*, 584.

Gilbert, N., & Raworth, D. A. (1996). Forum: Insects and temperature—a general theory. *Canadian Entomologist*, *128*, 1–14. https://doi.org/10.4039/Ent1281-1

Giraudoux, P. (2018). pgirmess: Spatial Analysis and Data Mining for Field Ecologists. R package version 1.6.9. https://CRAN.R-project.org/package=pgirmess

Greenwald, O. E. (1974). Thermal dependence of striking and prey capture by Gopher Snakes. *Copeia*, *1974*, 141. https://doi.org/10.2307/1443016

Gustafson, E. J., & Gardner, R. H. (1996). The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, *77*, 94–107. https://doi.org/10.2307/2265659

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*, 1–10. https://doi.org/10.1126/sciadv.1500052

Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling. R package version 3.4-5*, 1–249. https://CRAN.R-project.org/package=raster

Höld, W. (1990). Reproductive diversity in Amazonian lowland frogs. *Fortschritte Der Zoologie*, *38*, 40–60.

ICMBio. (2009). *Legislação ICMBio - Sistema Nacional De Unidades De Conservação*, 1, 69. http://www.icmbio.gov.br/portal/images/stories/comunicacao/legislacaoambientalvolume1.pdf

ICMBio. (2019). *Plano De Manejo - Floresta Nacional do Tapajós. Volume I - Diagnóstico I*, 2–165. http://www.icmbio.gov.br/portal/images/stories/plano-de-manejo/plano_de_manejo_flona_do_tapajós_2019_vol1.pdf

INMET (2020). *Instituto Nacional de Meteorologia-Monitoramento da Estação Meteorológica de Belterra-PA*. https://portal.inmet.gov.br/

Laurance, W. F., Camargo, J. L. C., Luizão, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Bruce Williamson, G., Benítez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A., & Lovejoy, T. E. (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation*, *144*(1), 56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Laureto, L. M. O., Cianciaruso, M. V., & Samia, D. S. M. (2015). Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, *13*(2), 112–116. https://doi.org/10.1016/j.ncon.2015.11.001

Leibold, M. A., & McPeek, M. A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, *87*, 1399–1410. https://doi.org/10.1890/0012-9658(2006)87[1399:COTNA N]2.0.CO;2

Lima, A., Magnusson, W., Menin, M., Erdtmann, L., Rodrigues, D., Keller, C., & Hodl, W. (2006). *Guide to the frogs of Reserva Adolpho Ducke. Central Amazonia*. https://repositorio.inpa.gov.br/handle/1/36309

Lutz, B. (1948). Ontogenetic evolution in frogs. *Evolution*, *2*, 29–39. https://doi.org/10.1111/j.1558-5646.1948.tb02729.x

Magnusson, W., Braga-Neto, R., Pezzini, F., Baccaro, F., Bergallo, H., Penha, J., Rodrigues, D., Verdade, L. M., Lima, A., Albernaz, A. L., Hero, J.-M., Lawson, B., Castilho, C., Drucker, D., Franklin, E., Mendonça, F., Costa, F., Galdino, G., Castley, G., … Pontes, A. R. M. (2013). *Biodiversidade e Monitoramento Ambiental Integrado PPBio INPA*. https://repositorio.inpa.gov.br/bitstream/1/36304/1/Biodiversidade_e_monitoramento_ambiental_integrado.pdf

Magnusson, W. E., & Hero, J. M. (1991). Predation and the evolution of complex oviposition behaviour in Amazon rainforest frogs. *Oecologia*, *86*, 310–318. https://doi.org/10.1007/BF00317595

Magnusson, W. E., Lima, A. P., Luizão, R., Luizão, F., Costa, F. R. C., de Castilho, C. V., & Kinupp, V. F. (2005). RAPELD: A modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica*, *5*, 21–26. https://doi.org/10.1590/S1676-06032005000300002

Margules, C. R., Nicholls, A. O., & Usher, M. B. (1994). Apparent species turnover, probability of extinction and the selection of nature reserves: A case study of the Ingleborough limestone pavements. *Conservation Biology*, *8*, 398–409.

Marimon-Junior, B. H., & Hay, J. D. (2008). A new instrument for measurement and collection of quantitative samples of the litter layer in forests. *Forest Ecology and Management*, *255*, 2244–2250. https://doi.org/10.1016/j.foreco.2008.01.037

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Menin, M., Ferreira, R. F. B., Melo, I. B., Gordo, M., Hattori, G. Y., & Sant'anna, B. S. (2019). Anuran diversity in urban and rural zones of the Itacoatiara municipality, central Amazonia, Brazil. *Acta Amazonica*, *49*, 122–130. https://doi.org/10.1590/1809-4392201800284

Menin, M., Lima, A. P., Magnusson, W. E., & Waldez, F. (2007). Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: Mesoscale spatial patterns. *Journal of Tropical Ecology*, *23*(5), 539–547. https://doi.org/10.1017/S0266467407004269

Menin, M., Waldez, F., & Lima, A. P. (2008). Temporal variation in the abundance and number of species of frogs in 10,000 ha of a forest in central Amazonia, Brazil. *South American Journal of Herpetology*, *3*, 68–81. https://doi.org/10.2994/1808-9798(2008)3[68:TVITA]2.0.CO;2

Menin, M., Waldez, F., & Lima, A. P. (2011). Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia. *Herpetology Journal*, *21*, 255–261.

MMA (2006). *Mapas de Cobertura Vegetal dos Biomas Brasileiros*. Minist. do Meio Ambient. Retrieved from: http://mapas.mma.gov.br/mapas/aplic/probio/datadownload.htm?/ [Accessed November 14, 2016].

Moraes, L. J. C. L., Pavan, D., Barros, M. C., & Ribas, C. C. (2016). The combined influence of riverine barriers and flooding gradients on biogeographical patterns for amphibians and squamates in southeastern Amazonia. *Journal of Biogeography*, *43*, 2113–2124. https://doi.org/10.1111/jbi.12756

Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology & Evolution*, *10*, 58–62. https://doi.org/10.1016/S0169-5347(00)88977-6

Nielsen, U. N., Osler, G. H. R., Campbell, C. D., Neilson, R., Burslem, D. F. R. P., & van der Wal, R. (2010). The enigma of soil animal species diversity revisited: The role of small-scale heterogeneity. *PLoS One*, *5*, 26–28. https://doi.org/10.1371/journal.pone.0011567

Nielsen, U. N., Osler, G. H. R., van der Wal, R., Campbell, C. D., & Burslem, D. F. R. P. (2008). Soil pore volume and the abundance of soil mites in two contrasting habitats. *Soil Biology & Biochemistry*, *40*, 1538–1541. https://doi.org/10.1016/j.soilbio.2007.12.029

Núñez, S. F., López-Baucells, A., Rocha, R., Farneda, F. Z., Bobrowiec, P. E. D., Palmeirim, J. M., & Meyer, C. F. J. (2019). Echolocation and stratum preference: Key trait correlates of vulnerability of insectivorous bats to tropical forest fragmentation. *Frontiers in Ecology and Evolution*, *7*, 1–12. https://doi.org/10.3389/fevo.2019.00373

Palmeirim, A. F., Benchimol, M., Vieira, M. V., & Peres, C. A. (2018). Small mammal responses to Amazonian forest islands are modulated by their forest dependence. *Oecologia*, *187*(1), 191–204. https://doi.org/10.1007/s00442-018-4114-6

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Parker, G. G., Harding, D. J., & Berger, M. L. (2004). A portable LIDAR system for rapid determination of forest canopy structure. *Journal of Applied Ecology*, *41*, 755–767. https://doi.org/10.1111/j.0021-8901.2004.00925.x

Peixoto, G. M., de Fraga, R., Araújo, M. C., Kaefer, I. L., & Lima, A. P. (2020). Hierarchical effects of historical and environmental factors on lizard assemblages in the upper Madeira River, Brazilian Amazonia. *PLoS One*, *15*, 1–19.

QGIS Development Team (2020). *QGIS Geographic Information System*. Proj: Open Source Geospatial Found. http://qgis.osgeo.org

Rahel, F. J. (2007). Biogeographic barriers, connectivity and homogenization of freshwater faunas: It's a small world after all. *Freshwater Biology*, *52*, 696–710.

Ramalho, W. P., Machado, I. F., & Vieira, L. J. S. (2018). Do flood pulses structure amphibian communities in floodplain environments? *Biotropica*, *50*, 338–345. https://doi.org/10.1111/btp.12523

Ribeiro, J. W., Lima, A. P., & Magnusson, W. E. (2012). The effect of Riparian Zones on species diversity of frogs in Amazonian forests. *Copeia*, *2012*, 375–381. https://doi.org/10.1643/CE-11-117

Ricketts, T. H. (2001). The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist*, *158*, 87. https://doi.org/10.1086/320863

Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, *29*, 1586–1595. https://doi.org/10.1111/cobi.12556

Rodrigues, A. S. L. L., Gregory, R. D., & Gaston, K. J. (2000). Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society B-Biological Sciences*, *267*, 49–55. https://doi.org/10.1098/rspb.2000.0965

Rojas-Ahumada, D. P., Landeiro, V. L., & Menin, M. (2012). Role of environmental and spatial processes in structuring anuran communities across a tropical rain forest. *Austral Ecology*, *37*, 865–873. https://doi.org/10.1111/j.1442-9993.2011.02330.x

Rosado, B. H. P., Figueiredo, M. S. L., de Mattos, E. A., & Grelle, C. E. V. (2016). Eltonian shortfall due to the Grinnellian view: functional ecology between the mismatch of niche concepts. *Ecography*, *39*, 1034–1041. https://doi.org/10.1111/ecog.01678

Schlaepfer, M. A., & Gavin, T. A. (2001). Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology*, *15*, 1079–1090. https://doi.org/10.1046/j.1523-1739.2001.0150041079.x

Sinsch, U. (1990). Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution*, *2*, 65–79. https://doi.org/10.1080/08927014.1990.9525494

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H., & Bradshaw, C. J. A. (2008). Measuring the meltdown: Drivers of global amphibian extinction and decline. *PLoS One*, *3*, 1–8. https://doi.org/10.1371/journal.pone.0001636

Souza, C. M., Z. Shimbo, J., Rosa, M. R., Parente, L. L., A. Alencar, A., Rudorff, B. F. T., Hasenack, H., Matsumoto, M., G. Ferreira, L., Souza-Filho, P. W. M., de Oliveira, S. W., Rocha, W. F., Fonseca, A. V., Marques, C. B., Diniz, C. G., Costa, D., Monteiro, D., Rosa, E. R., Vélez-Martin, E., … Azevedo, T. (2020). Reconstructing three decades of land use and land cover changes in Brazilian biomes with landsat archive and earth engine. *Remote Sensing*, *12*, 2735. https://doi.org/10.3390/rs12172735

Ståhlberg, F., Olsson, M., & Uller, T. (2001). Population divergence of developmental thermal optima in Swedish common frogs, *Rana temporaria*. *Journal of Evolutionary Biology*, *14*, 755–762.

Stroud, J. T., Bush, M. R., Ladd, M. C., Nowicki, R. J., Shantz, A. A., & Sweatman, J. (2015). Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecology and Evolution*, *5*, 4757–4765. https://doi.org/10.1002/ece3.1651

Torralvo, K., de Fraga, R., Lima, A. P., Dayrell, J., & Magnusson, W. E. (2021). Data from: Environmental filtering and deforestation shape frog assemblages in Amazonia: an empirical approach assessing species abundances and functional traits. Dryad Digital Repository, https://doi.org/10.5061/dryad.gb5mkkwqv

Torralvo, K., Lima, A., Rosa, C. A., & Magnusson, W. (2020). *Dados de estrutura da vegetação obtidos com LIDAR portátil de chão em parcelas permanentes de módulos RAPELD na Floresta Nacional (FLONA) do Tapajós- PA*. PPBio Repos. -ID PPBioAmOc.577.2. https://search.dataone.org/view/PPBioAmOc.577.2

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*, 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

Tsuji-Nishikido, B. M., & Menin, M. (2011). Distribution of frogs in riparian areas of an urban forest fragment in Central Amazonia. *Biota Neotropica*, *11*, 63–70. https://doi.org/10.1590/S1676-06032011000200007

Van Sluys, M., Vrcibradic, D., Alves, M. A. S., Bergallo, H. G., & Rocha, C. F. D. (2007). Ecological parameters of the leaf-litter frog community of an Atlantic Rainforest area at Ilha Grande, Rio de Janeiro state, Brazil. *Austral Ecology*, *32*, 254–260.

Vandewalle, M., de Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., Feld, C. K., Harrington, R., Harrison, P. A., Lavorel, S., da Silva, P. M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J. P., Sykes, M. T., Vanbergen, A. J., & Woodcock, B. A. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, *19*, 2921–2947. https://doi.org/10.1007/s10531-010-9798-9

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*, 183–206. https://doi.org/10.1086/652373

Venticinque, E., Forsberg, B., Barthem, R., Petry, P., Hess, L., Mercado, A., Cañas, C., Montoya, M., Durigan, C., & Goulding, M. (2016). An explicit GIS-based river basin framework for aquatic ecosystem conservation in the Amazon. *Earth System Science Data*, *8*, 651–661. https://doi.org/10.5194/essd-8-651-2016

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

von May, R., Catenazzi, A., Corl, A., Santa-Cruz, R., Carnaval, A. C., & Moritz, C. (2017). Divergence of thermal physiological traits in terrestrial breeding frogs along a tropical elevational gradient. *Ecology and Evolution*, *7*, 3257–3267. https://doi.org/10.1002/ece3.2929

Wang, Y., Naumann, U., Eddelbuettel, D., Wilshire, J., & Warton, D. (2020). mvabund: Statistical Methods for Analysing Multivariate Abundance Data. R package version 4.1.3. https://CRAN.Rproject.org/package=mvabund

Warton, D. I., Wright, S. T., & Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, *3*, 89–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x

Wilson, D. J. (2019). The harmonic mean p-value for combining dependent tests. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 1195–1200.

Woinarski, J. C. Z., Fisher, A., & Milne, D. (1999). Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia. *Journal of Tropical Ecology*, *15*, 381–398. https://doi.org/10.1017/S0266467499000905

Young, J. E., Christian, K. A., Donnellan, S., Tracy, C. R., & Parry, D. (2005). Comparative analysis of cutaneous evaporative water loss in frogs demonstrates correlation with ecological habits. *Physiological and Biochemical Zoology*, *78*, 847–856. https://doi.org/10.1086/432152

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