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ORIGINAL ARTICLE

Vertical niche and trait associations in Central African amphibians

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Abstract

Tropical forests are vertically complex and offer unique niche opportunities in the form of resources, climate, and habitat gradients from the forest floor to the canopy. Rainforest amphibians have diversified within this vertical space, resulting in partitioned niches and corresponding morphological, behavioral, and reproductive traits. However, a lack of data regarding the vertical niche space used by amphibian species has prevented a nuanced analysis of the form-function relationship between traits and vertical height. We performed 74 ground-to-canopy surveys for amphibians in the tropical rainforest of Gabon and described the vertical stratification patterns of the assemblage in terms of richness, abundance, and species-specific vertical niches. We determined that the community shift in richness and abundance between the ground and understory was pronounced, while the community change from understory to canopy was gradual. We analyzed the relationships between amphibian traits with vertical height using linear mixed effects models, finding strong support (>60% variance explained) that frogs with bigger toes in relation to their length access greater height in the canopy. This relationship provides support for the form-function hypothesis: that morphology changes predictably to meet the functional demands of species along niche gradients. Furthermore, we documented differences in the vertical heights of species according to their reproductive modes, highlighting the potential impact of reproductive mode diversity on the vertical stratification patterns of amphibian assemblages.

KEYWORDS
Arboreality, canopy, ecology, frogs, Gabon, morphology, tropical rainforest, vertical stratification

1 | INTRODUCTION

Tropical rainforests are the most biodiverse and vertically complex terrestrial ecosystems on Earth. Here, abiotic conditions, including light, wind speed, temperature, and humidity, change from ground to canopy (Basham & Scheffers, 2020; Scheffers et al., 2013; Smith, 1973; Ulyshen, 2011), and most climatic variables shift from stable at the ground level to variable in the canopy due to the buffering effects of overlying vegetation (Klinges & Scheffers, 2021; Oliveira & Scheffers, 2019). As a result, species vertically stratify and partition their niches in accordance with the variety of challenges and resources encountered across vertical space (Ashton et al., 2016; Oliveira & Scheffers, 2019; Parker et al., 1995). This partitioning occurs in tandem with the evolution of traits, which play a crucial role in determining species' ability to fulfill functional niches (Butefish & Moen, 2016; Moen et al., 2016).

The form-function hypothesis in ecology posits that the form (e.g., morphology) of an organism is closely related to its function or the ecological role that it serves (Moen, 2019). Frogs are an excellent model for exploring the relationship between traits and the vertical niche, as they are highly diverse in tropical rainforests and have evolved specific morphological (e.g., toe disc width; Langowski et al., 2018), physiological (e.g., desiccation tolerance; Lion et al., 2019), behavioral (e.g., use of microhabitat refugia; Scheffers, Edwards, et al., 2014, Seidl et al., 2019), and biological (e.g., reproductive mode; Portik & Blackburn, 2016) adaptations, which correspond to their use of forest strata.

Scheffers and Williams (2018) propose the presence of an "arboreality syndrome" whereby adaptations and strategies for aboveground living yield syndromes of traits, that is a suite of arboreal-linked traits such as desiccation resistance, phytotelmata-linked reproduction, and large toes. Frog toe disc morphology is a key trait that has convergently evolved in many frog lineages to provide soft elastic pads which act to confer greater adhesion and therefore climbing ability (Langowski et al., 2018). Furthermore, frogs have permeable skin and are cold-blooded, which makes them sensitive to the environmental changes between ground and canopy, including shifts in water availability and exposure to extreme heat (Duellman & Trueb, 1994). However, studies on frog traits have relied on effective but broad categories to define the amphibian vertical niche; for example, Moen and Wiens (2017) utilize seven categories which incorporate vertical habitat use (Aquatic, Arboreal, Burrowing, Semi-aquatic, Semi-arboreal, Semi-burrowing, Terrestrial, Torrential). Such categorical analyses have proven highly effective in testing evolutionary theories across wide spatial and evolutionary scales despite the absence of available vertical niche data (Moen & Wiens, 2017). However, by using continuous vertical niche and trait data, we seek to increase sensitivity and statistical power for a more nuanced analysis of these specific ecological relationships.

Here, using frogs in the tropical rainforests of Gabon, we test the form-function hypothesis at fine ecological and spatial resolutions as it relates to morphology, reproduction, and vertical niche partitioning. Specifically, we characterize the vertical stratification of this tropical rainforest frog community from which we hypothesize that: (1) toe disc size will positively correlate with vertical niche height due to its importance for climbing performance, and (2) that direct developing and phytotelm breeding frogs will positively correlate with vertical niche height, as these strategies are not dependent on streams or ponds.

2 | METHODS

2.1 | Study area

In southern Gabon, we surveyed a Dense Moist Forest (Verhegghen et al., 2012) located around Baposso Village, Ngounie Province, which borders the Monts Birougou Ramsar site (Lat 20°85′00″ N: Lon 12°13′50″; 650–800 m asl, Figure 1a,b). The area around Baposso is a matrix of old growth forest, secondary forest of mixed ages, and plantations, but we focused our sampling in old growth areas with mature trees and consistent canopy cover (mean canopy height of 74 surveyed trees = 28.6 ± 5.5 m).

2.2 | Vertical stratification of amphibians

We surveyed for frogs during the wet season of 2022 (October–November). We conducted vertical, ground-to-canopy surveys for amphibians, with each survey centered on a single canopy tree. We searched along trails in the forest for trees which were required to be a minimum of 20 m apart and had to meet safety standards for arborist single-rope climbing (Jepson, 2000). We did not limit our selection by tree species and were only limited in selection by safety concerns, thus attaining a representative mixed sample of trees across the area. We surveyed 74 trees at night for amphibians. At each tree we surveyed for 10 min at the ground, understory, sub-canopy (approx. half the maximum height climbed), and canopy (maximum height climbed), with a 20-min roaming survey between the strata totalling to 60 min. The 10-min ground survey consisted of searching through leaf litter and ground habitat in a 4 m diameter circle to standardize to the same search area available during climbing. Aboveground, we searched for arboreal amphibians in tree holes, moss, epiphytes and other microhabitat structures (Heyer et al., 1994), and measured the height above ground of each individual using a laser distance meter (Leica Geosystems, Leica Disto D2; http://www.leica-geosystems.ca).

Encountered amphibians were photographed and trait data collected. Morphological traits were selected as represent principal aspects of frog morphology, particularly as they related to locomotion. Frogs were weighed (Pesola spring scales: ± 0.1 g), and measured (mechanical calipers: ± 0.05 mm) for snout-vent length (SVL), mouth width (hereafter: mouth), tibia length (hereafter: tibia), and toe disc width (3rd digit from inside thumb; hereafter: toe). Amphibians were identified from photos by experts of the local amphibian fauna, GJ and ABK.

2.3 | Statistical analysis

All analyses were conducted using R v.4.3 (R Core Team, 2023). We used univariate kernel density and estimated the abundance distribution of frogs across vertical forest strata (Silverman, 1986; Venables & Ripley, 2013). Kernel density estimation generates a smoothed histogram of data, where the area under the histogram integrates to one. Following methods in Scheffers et al. (2013), we estimated the probability density of the height at which frogs were found, that is, the relative density of frogs with height. We estimated a kernel bandwidth (see Silverman, 1986) for our complete dataset and then used this bandwidth independently for each tree to perform kernel tree-specific density estimates to account for variation in tree height. We combined our tree-specific kernels by a weighted

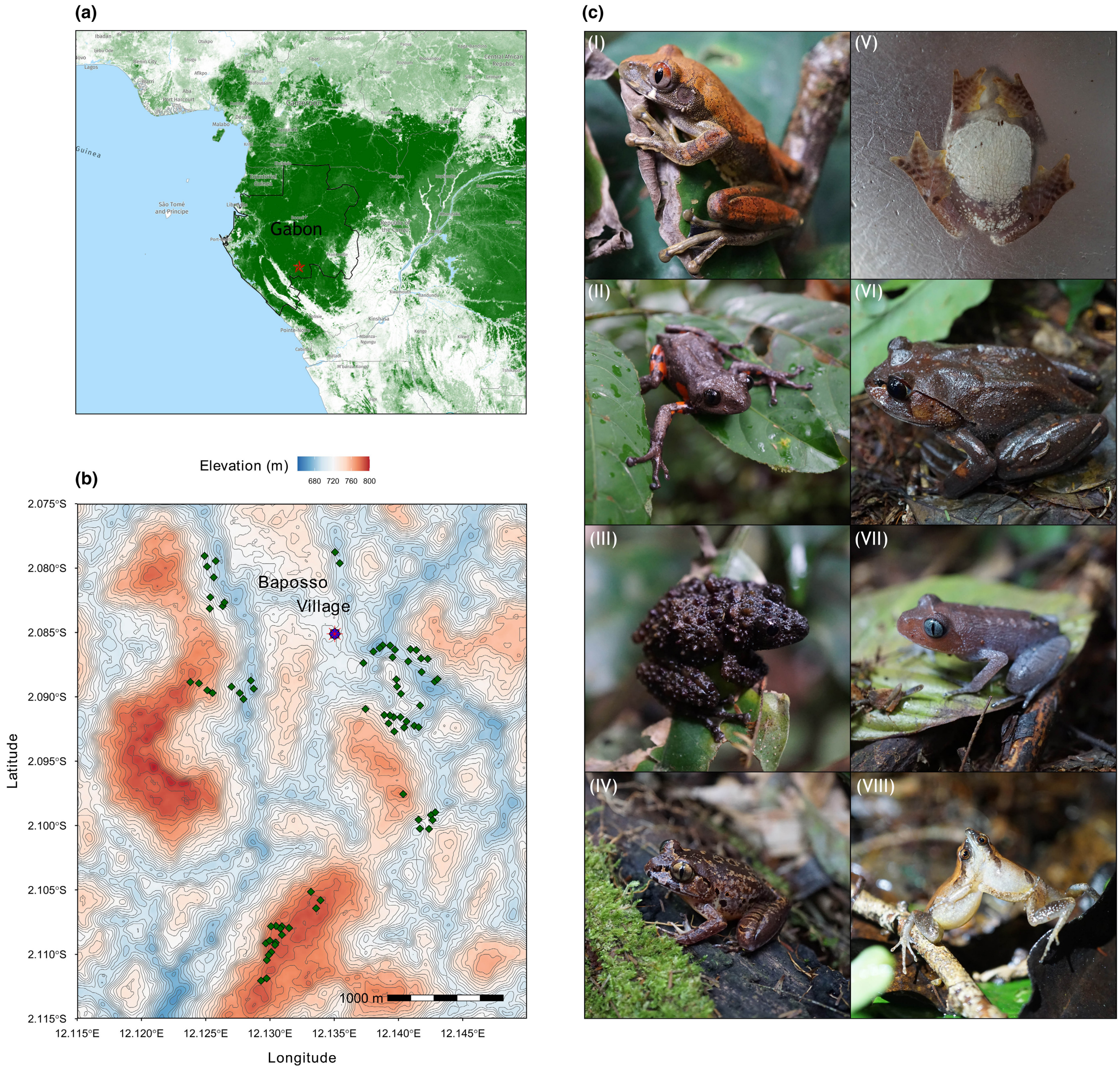


FIGURE 1 (a) Map of forest height (dark green = 30 m, white = 0 m) in Gabon and central Africa with the study site represented by a red star. Data utilized is a Global Forest Watch product. (b) Topographical map of the study site at Baposso Village, Ngounie Province, Gabon. Green diamonds represent each sampled tree. The research station is represented by the blue and red symbol. (c) Panel of frogs encountered at Baposso demonstrating the variety of morphologies found in the community: (I) *Leptopelis boulengeri*, (II), *Phlyctimantis leonardi affin*, (III) *Acanthixalus spinosus*, (IV), *Astylosternus batesi*, (V) *Nectophryne batesii*, (VI) *Trichobatrachus robustus*, (VII) *Nyctibates corrugatus*, (VIII) *Arthroleptis sylvaticus affin*. Photos © Edmund Basham.

mean, with each tree weighted according to the kernel describing the distribution of tree heights. Lastly, as frogs were not observed at negative height, we used a modified version of the "density" function (R Package 'stats') to generate left-bounded univariate kernel-density estimates, which reflect the density falling below zero back into the positive domain of the estimated kernel.

Following methods in Basham and Scheffers (2020), community vertical stratification was assessed using a site (height intervals of 1 m) by species matrix. The first height category was for individuals captured at 0 m (i.e., site 1), then >0 & ≤1 m (site 2), >1 & ≤2 m (site 3) and so on to 30 m (site 31). Singletons were removed (to reduce the impact of rare species whose vertical range was not fully sampled), the data transformed to presence/absence (to isolate composition without abundance), and gaps between the lowest and highest recording for each species filled (the range where the species would be expected to occur). We then partitioned the nestedness (species loss) and turnover (species replacement) components of community similarity between sites (height intervals) using the Jaccard dissimilarity index (1 = similar, 0 = dissimilar) calculated by the *beta. pair* function in the "betapart" package (Baselga, 2010). For each pairwise comparison between height intervals, we calculated the distance in meters and fitted linear models of this distance against the corresponding pairwise values of nestedness and turnover. To identify the heights at which the greatest changes in composition occurred we applied linear models using only pairwise comparisons from adjacent height intervals (0–1, 1–2, 2–3, etc), and only where any composition change occurred.

For a trait-based analysis we first compiled a dataset of five morphological traits: snout-vent-length (SVL; mm), mass (g), mouth-width (mm), tibia-length (mm), and toe-width (mm). Then, each combination of these traits was taken to form 10 additional ratio trait variables (e.g., the ratio of SVL to mouth). We scaled each continuous variable to a mean of zero and unit variance by subtracting the mean and dividing by the standard deviation. Lastly, a categorical reproductive mode trait was included, modified from Portik and Blackburn (2016) to include phytotelm breeding separately: Aquatic eggs and aquatic larvae (AQAQ), terrestrial eggs and aquatic larvae (TEAQ), arboreal eggs and aquatic larvae (ARAQ), phytotelm breeding (PHAQ), and direct development (DD).

To assess the relationship between traits in the community, we applied a Principal Components Analysis (PCA) for all individuals through the *prcomp* function in the base R 'stats' package and a collinearity analysis using the pairwise nonparametric Spearman correlations function *corr.test* from the R package 'psych' (Revelle, 2015). To determine how frog traits were related to the vertical niche, we calculated the mean of each variable for all species, separately. We then used linear models via the *lm* function in the base R package 'stats'. Finding that many variables were collinear, we built a candidate model set to determine the influence of each trait independently. The response variable, vertical height (m), was log $(x+1)$ transformed for the analysis to help models meet the assumptions of normality because data were right-skewed. The candidate model set was built by specifying each trait as an explanatory variable. Lastly, models were duplicated with a polynomial term to test for non-linear relationships. We employed an information theoretic approach with Akaike's Information Criteria (AIC) as our operative criterion for determining relative explanatory power (Burnham & Anderson, 2004). Model weights indicated the level of support across the candidate model set and were calculated using the *aictab* function within the 'AICcmodavg' package (Mazerolle, 2023). Reproductive mode, as the sole categorical variable, was assessed by applying a Tukey Test (R package 'stats') for significant differences in mean height.

3 | RESULTS

3.1 | Richness and abundance

Vertical sampling uncovered a total of 141 frogs of 29 species, representing 14 genera and six families (Table S1). The most abundant species were *Arthroleptis sylvaticus* and *Leptopelis aubryioides*. The species most consistently encountered in the upper canopy was the tree-hole-breeding Bate's Tree Toad (*Nectophryne batesii*; family *Bufonidae*). Both richness and abundance were greater towards the ground; however, abundance was greatest on the forest floor and declined steeply with increasing height in the first 10 m (0 m; Figure 2a). Richness, however, peaked at 13 species between 3 and 4 m in the understory shrub layer (Figure 2b), declined to around seven species in the midstory (10–20 m), then was followed by a depleted community in the canopy where we encountered 2–3 species (20–30 m; Figure 2b). Composition did not change evenly across vertical height, with turnover by species replacement predominant from the ground to the lower understory, though this relationship was not significant due to lack of data points ($p = .087$, $R^2 = .17$; Figure 2c), whereas nestedness increased from the understory into the canopy ($p = .014$, $R^2 = .39$; Figure 2c). Utilizing all pairwise comparisons between height intervals, both turnover (species replacement; $p < .001$, $R^2 = .29$) and nestedness (species loss; $p < .001$, $R^2 = .04$) increased significantly with vertical distance, evidencing a vertical distance decay relationship (Figure S1).

3.2 | Trait analyses

PCA analysis demonstrated clear groupings of individuals within species and species within genera, with a strong delineation along axis PC2 between arboreal (e.g., *Hyperolius* and *Leptopelis*) and terrestrial genera (e.g., *Arthroleptis* and *Phrynobatrachus*; Figure 3a). Collinearity testing showed strong patterns of trait collinearity among variables (Figure 3b), thus supporting the use of separate models when testing the relationships between traits and vertical height.

Our mixed-effect models indicated the polynomial model of SVL:Toe ratio was the best predictor of frog vertical height (Table 1, Figure 4a,c,d); explaining over 60% of variance. There was, however, competing support from the model of SVL:Toe ratio and the polynomial model of Mouth:Toe ratio. The top three models cumulatively explained approximately 86% of the overall variance in our analysis of morphological traits and vertical height (Tables 1; S2). All but one top model contained Toe, indicating the importance of this variable for predicting the vertical niche of amphibian species.

The vertical height of species across different reproductive modes varied, but multiple differences were not significant due to a lack of data (Figure 4b). Nonetheless, TEAQ (7 species), ARAQ (8 species), and PHAQ (3 species) were all associated with greater height, whereas AQAQ (6 species) and DD (5 species) modes were associated with lower vertical height (Figure 4b).

4 | DISCUSSION

This study represents the first ground-to-canopy survey of amphibians in Central Africa. By examining morphological traits and reproductive modes, we identified highly resolved form-function relationships that span the vertical domain. As the community shifts away from the ground, we observed three patterns: (1) increased

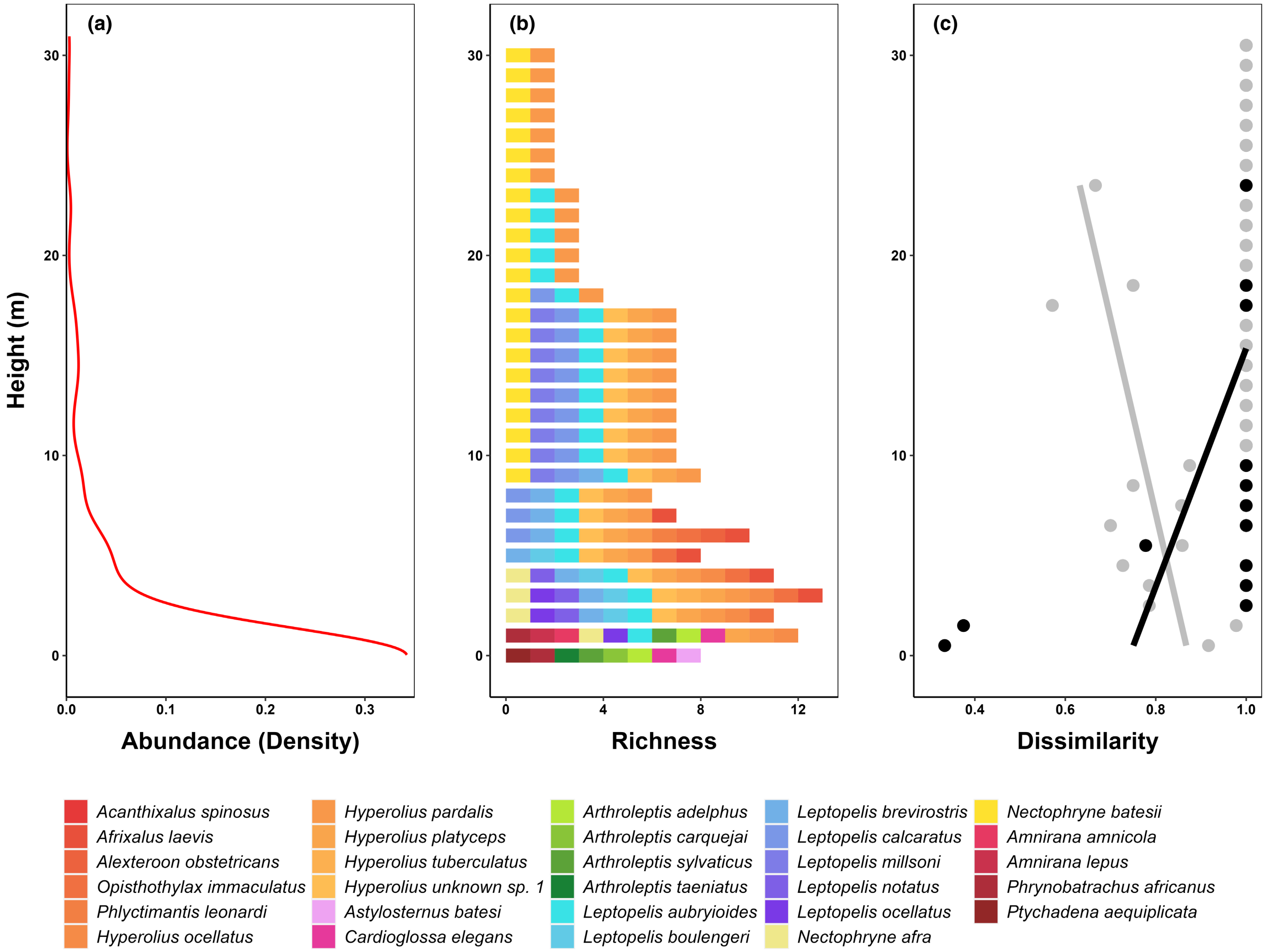
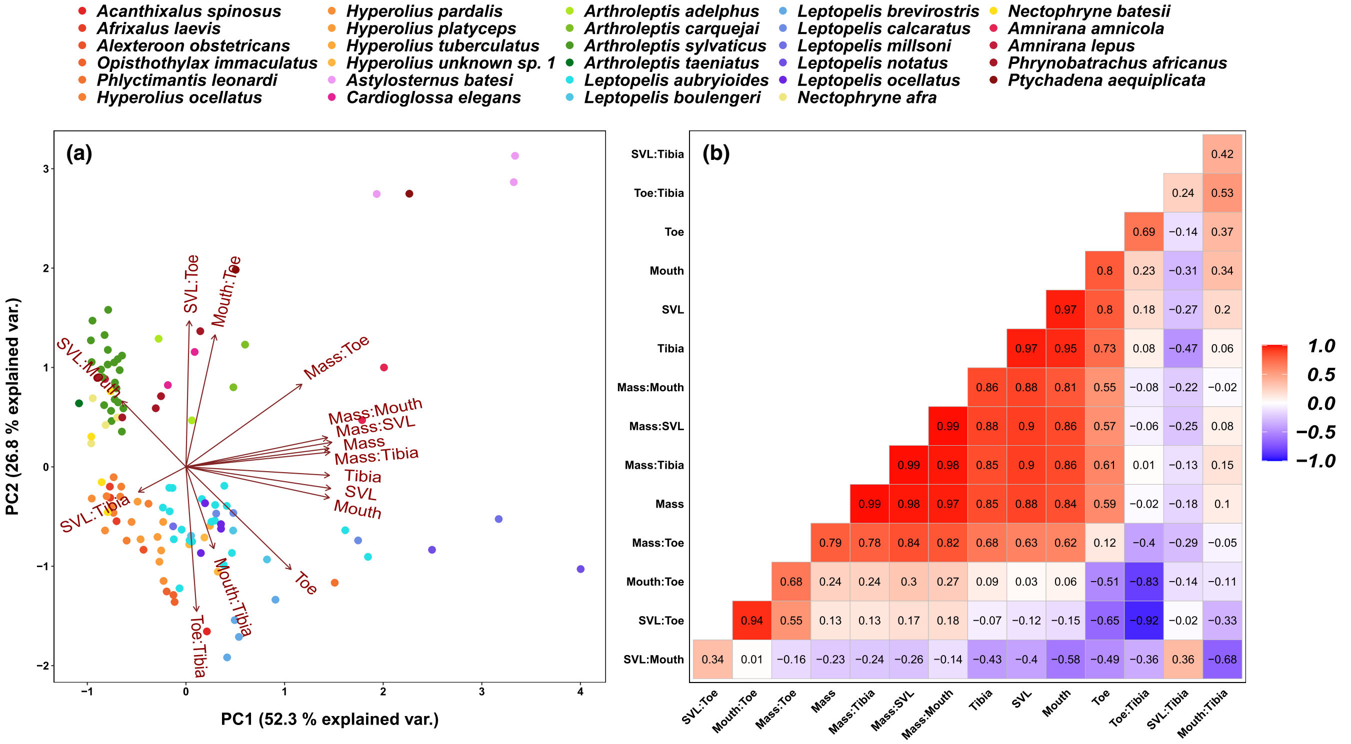


FIGURE 2 (a) Vertical stratification of amphibian abundance. The curve is derived from kernel- density estimation (see methods) and can be understood as the relative density of amphibians with height. (b) Stacked plot of species occurrence across 1 m intervals of vertical height. Heights between maximum and minimum heights are filled and singletons are excluded. (c) Pairwise dissimilarity (similar = 1, dissimilar = 0), between 1 m binned communities in a sequence where only communities immediately adjacent were compared (0–1, 1–2, 2–3 ...). Black points represent turnover (species replacement; $p = .087$), and gray denotes the nestedness (species loss; $p = .014$).

toepad size relative to body length, (2) a decline in abundance and richness, and (3) a shift in compositional change from species replacement to species loss. Our results highlight the importance of toepad evolution in facilitating vertical niche packing in tropical frog communities. Prior studies often categorically delineate the vertical niche (e.g., Moen & Wiens, 2017; Portik & Blackburn, 2016), and may be effective in describing broad patterns and trait syndromes (Scheffers & Williams, 2018). For example, here, PCA analysis strongly indicates the presence of arboreal and terrestrial clustering in morphological trait-space (Figure 3a). Yet, by using precise height data we show that this niche placement occurs along a continuous gradient whereby fine adjustments in morphology correspond to predictable adjustments in the vertical niche.

In species-rich communities, where there are more species competing for similar resources, we expect a higher degree of character displacement that corresponds with the partitioning of niches. Of the traits considered in our study, toe morphology had the most pronounced association with a species' vertical niche, although contrary to hypothesis (1) it was the ratio of toe disc to SVL which was the best predictor for vertical height, not toe disc width alone. The functional value of large toe discs and small body size is linked to the efficiency of toe pad adhesion which does not scale linearly with mass or SVL (J. M. Smith et al., 2006). Indeed, we found strong competing support for other models of the ratio of toe disc with mouth width and tibia length (Table 1), thereby highlighting the overall importance of the toe disc to frog 'size' ratio in predicting vertical height.

At our study site, amphibian abundance and richness is weighted towards the ground, which broadly matches patterns observed in other tropical forest systems (Basham & Scheffers, 2020; Basham et al., 2019; Scheffers et al., 2013). Indeed, as observed in Panama (Basham & Scheffers, 2020), rapid turnover in Gabonese frogs occurs between the ground and understory at 1–2 m (Figure 2c), where purely terrestrial species are replaced by semi-arboreal and arboreal species, followed by a pattern of species loss without



	SVL:Toe	Mouth:Toe	Mass:Toe	Mass	Mass:Tibia	Mass:SVL	Mass:Mouth	Tibia	SVL	Mouth	Toe	Toe:Tibia	SVL:Tibia	Mouth:Tibia
SVL:Tibia														0.42
Toe:Tibia													0.24	0.53
Toe												0.69	−0.14	0.37
Mouth											0.8	0.23	−0.31	0.34
SVL										0.97	0.8	0.18	−0.27	0.2
Tibia									0.97	0.95	0.73	0.08	−0.47	0.06
Mass:Mouth								0.86	0.88	0.81	0.55	−0.08	−0.22	−0.02
Mass:SVL							0.99	0.88	0.9	0.86	0.57	−0.06	−0.25	0.08
Mass:Tibia						0.99	0.98	0.85	0.9	0.86	0.61	0.01	−0.13	0.15
Mass					0.99	0.98	0.97	0.85	0.88	0.84	0.59	−0.02	−0.18	0.1
Mass:Toe				0.79	0.78	0.84	0.82	0.68	0.63	0.62	0.12	−0.4	−0.29	−0.05
Mouth:Toe			0.68	0.24	0.24	0.3	0.27	0.09	0.03	0.06	−0.51	−0.83	−0.14	−0.11
SVL:Toe		0.94	0.55	0.13	0.13	0.17	0.18	−0.07	−0.12	−0.15	−0.65	−0.92	−0.02	−0.33
SVL:Mouth	0.34	0.01	−0.16	−0.23	−0.24	−0.26	−0.14	−0.43	−0.4	−0.58	−0.49	−0.36	0.36	−0.68

FIGURE 3 (a) Principal component analysis of morphological traits ($n=5$) and ratio traits ($n=10$) for all individuals. All traits were scaled and centred. (b) Correlation plot of scaled traits. Color strength indicates a stronger correlation, while cell color indicates directionality (red = positive correlation and blue = negative correlation.

TABLE 1 Top 10 model results of vertical height ~ trait variables ranked by AICc.

Model	K	ΔAICc	ω_i	$\sum\omega_i$	R squared
Svl:Toe ^{2}	4	0.000	0.396	0.396	.613
Svl:Toe	3	0.173	0.363	0.760	.570
Mouth:Toe ^{2}	4	2.613	0.107	0.867	.575
Toe:Tibia ^{2}	4	2.807	0.097	0.964	.572
Toe:Tibia	3	5.395	0.027	0.991	.482
Mouth:Toe	3	7.756	0.008	0.999	.437
Toe ^{2}	4	14.363	0.000	1.000	.353
Toe	3	15.088	0.000	1.000	.268
Mass:Toe	3	19.901	0.000	1.000	.131
Svl:Mouth	3	21.146	0.000	1.000	.091

Note: See Table S2 for full model list. Polynomial models are denoted by ^{2}.

replacement into the canopy. That said, we observed relatively high species richness up to 17 m, contrary to the rapid decline of frog abundance from 0 to 10 m. The decline of abundance with height likely corresponds with decreasing vegetation density and dramatic shifts in climate, which is well documented in tropical forests (Chmel et al., 2016; Jayson & Mathew, 2003; Kays & Allison, 2001; Parker et al., 1995). Indeed, adaptation to the harsh canopy goes beyond the morphological, and further work will be required to elucidate the relative importance of traits likely to influence the vertical niche, thermal tolerances (Leahy et al., 2022; Spicer et al., 2017; Xing et al., 2023), desiccation resistance (Thorson, 1955; Tracy et al., 2010; Watling & Braga, 2015; Wygoda, 1984), and microhabitat use (Scheffers, Edwards, Diesmos, Williams, & Evans, 2014; Scheffers, Phillips, & Shoo, 2014).

The reproductive mode of amphibians also significantly influences their habitat preferences and the vertical distribution patterns of species richness and abundance. We theorize that a lack of direct developing frogs and aboveground breeding resources at our site may help to explain the lack of richness and abundance in the canopy. We found a single individual of the PHAQ tree-hole breeding specialist *Acanthixalus spinosus* and 4 individuals each of the diminutive tree-hole-breeding toads *Nectophryne Afra* and *N. batesii*. The *Nectophryne* species were found high aboveground, in agreement with hypothesis (2), which predicted that PHAQ species would occur higher in the canopy because they are not constrained to ground-based reproductive resources. Nonetheless, in the Neotropics at least 99 frog species have the PHAQ reproductive mode in specific relation with epiphytic bromeliads (Sabagh et al., 2017). However, the Afrotropics lack bromeliads or any other abundant phytotelmata-forming epiphyte (Dauby et al., 2008; van Rooyen et al., 2019), and thus there may be a comparatively smaller amphibian niche space in Afrotropical than Neotropical rainforest canopies. Compounding this is a relative lack of species with direct development— where embryos can develop within the egg without a water body, allowing species to potentially live and reproduce perpetually in the canopy of forests (Basham & Scheffers, 2020). At a site in Panama, Basham and Scheffers (2020) recorded 15 of 34

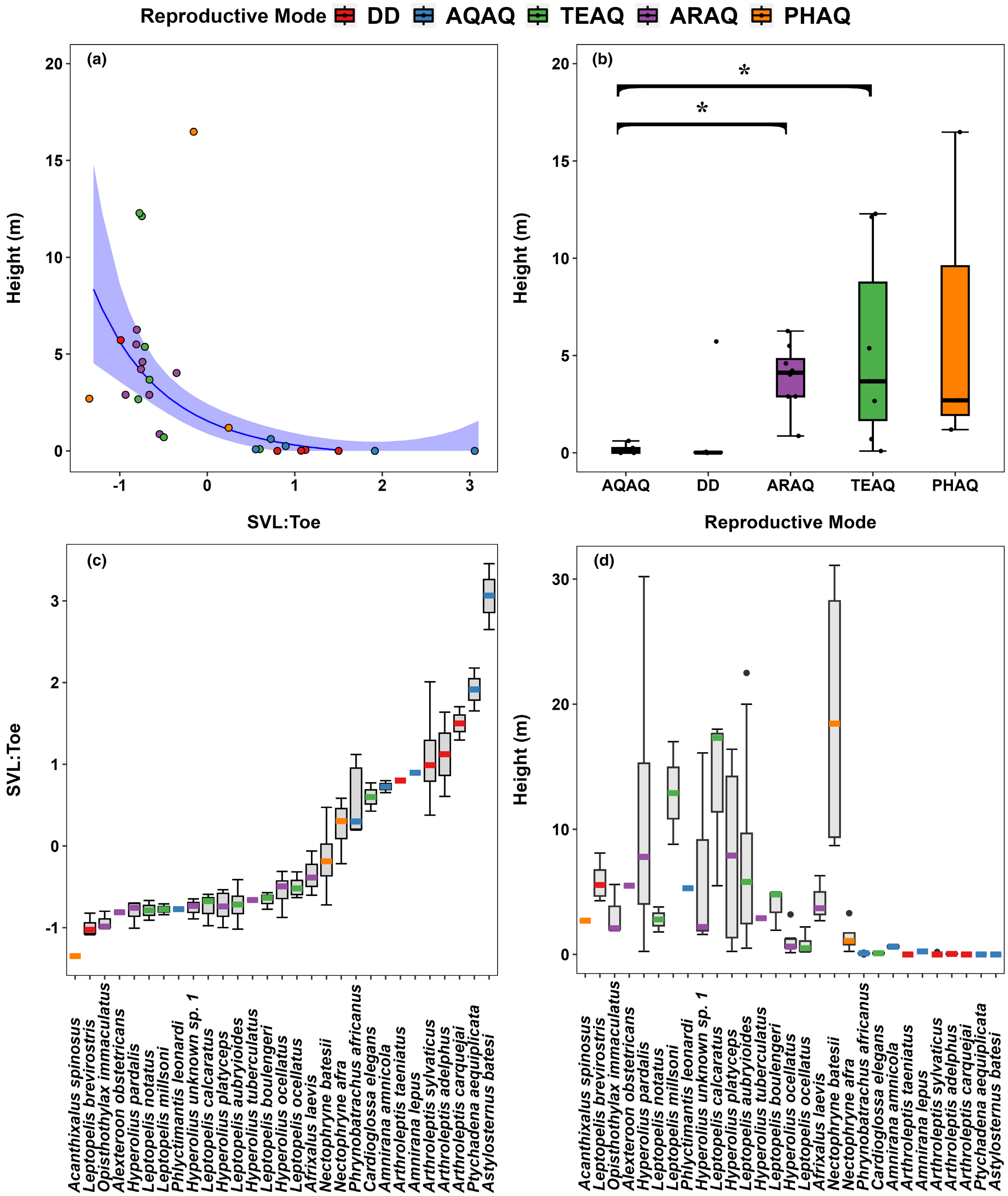


FIGURE 4 (a) Model predictions of vertical height (m) (log (x + 1)) as a function of SVL: Toe ratio. The solid blue line and shaded areas represent a predictive line of best fit and 95% confidence interval, respectively. Black circles represent raw (scaled) data, not predictions. Data were back transformed from log (x + 1) to show height in meters. (b) Boxplots of species mean vertical height (m) by reproductive mode. Black circles represent raw (scaled) data of all individuals. Reproductive modes: DD (direct development), AQAQ (aquatic eggs, aquatic larvae), TEAQ (terrestrial eggs, aquatic larvae), ARAQ (arboreal eggs, aquatic larvae), and PHAQ (phytotelm breeding). * Symbols denote significant TUKEY comparison at $p < .05$ (c) Boxplots of SVL:Toe ratio (scaled) by species in ascending order. (d) Boxplots of vertical height (m) by species in ascending order of SVL:Toe ratio.

(44%) species were direct developers, many of which were highly arboreal and laid eggs under moss and within arboreal soils (e.g., *Pristimantis cruentus*). Conversely, in Gabon, we found 17% of species (5 of 29 species) were direct developers, including 4 *Arthroleptis* species which all had a vertical niche between 0 and 1 m in height, in disagreement with hypothesis (2) (Figure 2b). These contrasts across biogeographic region hint at the impact of speciation and convergent evolution as it relates to reproductive mode and vertical niche use on the vertical stratification of communities.

In summary, studies that categorize vertical niches as either ground or arboreal miss important dimensionality in character evolution—microhabitat partitioning at fine spatial scales yields fine partitioning in morphological traits. Specifically, we confirm the clear importance of toe disc width relative to frog size in predicting vertical niche space use in this community. Finally, we underscore the significance of collecting aboveground data in rainforests, where a considerable realm of hidden amphibian diversity exists. Accessing this unique habitat is crucial for a comprehensive study of amphibian communities in all three spatial dimensions. Further data collection of vertical distributions, morphological traits, and reproductive modes across other frog lineages and locations will continue to refine these evolutionary relationships. We hope this paper captures the attention of other amphibian biologists working across the tropics and helps build traction for further research on the subject.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: http://doi.org/10.5061/dryad.0cfxpnw7k

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