










Patterns of species richness and turnover in endemic amphibians of the Guineo-Congolian rain forest

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Abstract

Aim: The African Guineo-Congolian (GC) region is a global biodiversity hotspot with high species endemism, bioclimatic heterogeneity, complex landscape features, and multiple biogeographic barriers. Bioclimatic and geographic variables influence global patterns of species richness and endemism, but their relative importance varies across taxa and regions and is poorly understood for many faunas. Here, we test the hypothesis that turnover in endemic amphibians of the GC biodiversity hotspot is influenced mainly by the geographic distance between grid cells and secondarily by rainfall- and temperature-related variables.

Location: West and Central Africa.

Major Taxa Studied: Amphibians.

Methods: We compiled species-occurrence records via field sampling, online databases, and taxonomic literature. Our study used 1205 unique georeferenced records of 222 amphibian species endemic to the GC region. Patterns of species richness were mapped onto a grid with a spatial resolution of $0.5^\circ \times 0.5^\circ$. We estimated weighted endemism and tested whether endemism was higher than the expected species richness (randomization test). We quantified species turnover using generalized dissimilarity modelling to evaluate the processes underlying observed patterns of species richness in GC endemic amphibians. We explored bioregionalization using agglomerative hierarchical clustering based on the unweighted pair group method with arithmetic averages.

Results: We identified seven areas within the lower GC region – forests in Cameroon, Gabon, Southern Nigeria, Equatorial Guinea, Republic of Congo, Democratic Republic of Congo, and Cote d'Ivoire – as having high species richness of endemic amphibians. The randomization test returned four major areas of significant weighted endemism: Nigeria-Cameroon mountains, forest regions of the Democratic Republic of Congo, Cote d'Ivoire, and Ghana. Our analysis revealed five bioregions for amphibian

Lotanna M. Nneji and Josué A. R. Azevedo share equal first co-authorship to the paper.

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endemism, four of which were located within the lower Guineo-Congolian forest. Species turnover was strongly related to the geographic distance between grid cells; contributing bioclimatic variables included precipitation of the warmest quarter, mean temperature of the wettest quarter, and mean diurnal temperature range.

Main Conclusions: Our results indicate that geographic distance between grid cells is the primary determinant of turnover in GC endemic amphibians, with secondary but significant effects of rainfall- and temperature-related variables. Our study identifies key areas of endemic amphibian richness that could be prioritized for conservation actions.

KEYWORDS

Africa, amphibians, endemic species richness, generalized dissimilarity modelling, species distribution models, β -diversity

1 | INTRODUCTION

Understanding broad-scale patterns of species richness, endemism and turnover is a fundamental goal in ecology, biogeography, and conservation biology (Currie et al., 2004; Hillebrand, 2004; Mittelbach et al., 2007; Storch et al., 2006). Although species richness has long been the most commonly investigated metric (Myers et al., 2000; Pearson & Cassola, 1992; Prendergast & Eversham, 1997; Schall & Pianka, 1978), it is not the only component of biological diversity. Endemism, the extent to which species are unique to a defined geographical location, is often used to demarcate biogeographic regions (Morrone, 2014), investigate species-environment interactions (Gámez et al., 2017), and set priority targets for conservation plans (Huang et al., 2010; Myers et al., 2000; Noroozi et al., 2018). Endemic species are typically restricted to small geographic ranges and contribute disproportionately to global biodiversity (Kier & Barthlott, 2001), making it important to understand patterns of endemic species richness and its correlates (Collen et al., 2014; Kier et al., 2009; Lamoreux et al., 2006; Orme et al., 2005). While these patterns have been intensively studied for many groups of organisms at various spatial and phylogenetic scales – including European butterflies (Dennis et al., 1998), Afrotropical birds (Williams et al., 1999), Amazonian plants (Tuomisto, Ruokolainen, & Yli-Halla, 2003), North American mammals (Rodríguez & Arita, 2004), temperate trees (Qian et al., 2005), and Himalayan aphids (Huang et al., 2008), among others – many other taxa and regions have been comparatively neglected and lack detailed data at biogeographic scales. For example, Afrotropical wet forests are inordinately important centres of biodiversity, yet their endemic species richness patterns remain poorly characterized (Anthony et al., 2015; McRae et al., 2017).

Beta diversity, the dissimilarity in species composition arising from interactions between local and regional diversity, is important for understanding patterns of richness and endemism (Qian et al., 2005, 2009; Tang et al., 2012). Beta diversity comprises two components, nestedness (the extent to which species at one site

are a subset of those at another) and turnover (species replacement) (Baselga, 2010; Gaston & Blackburn, 2000), both of which are influenced by bioclimatic factors (mostly related to water and energy) and spatial factors (e.g. distance, geographic barriers) (Buckley & Jetz, 2008; Condit et al., 2002; Daru et al., 2017; Duivenvoorden et al., 2002; Ficetola et al., 2017; Gaston et al., 2007; Jansson, 2003; Leprieur et al., 2009; Linares-Palomino & Kessler, 2009; Qian et al., 2005, 2009; Qian & Ricklefs, 2007; Rosauer & Jetz, 2015; Sandel et al., 2011; Tuomisto, Poulsen, et al., 2003). However, the relative importance of these factors may vary in taxon- and scale-dependent ways (Qian et al., 2009; Steinitz et al., 2006), making it difficult to extrapolate from well studied to poorly studied systems. Elucidating the separate and combined effects of bioclimatic and spatial variables on the distribution and richness of endemic species in biodiverse yet understudied regions is thus important for a more comprehensive understanding of biodiversity and biogeography.

The West/Central African Guineo-Congolian (GC) region contains the world's second-largest tropical rain forest (Malhi et al., 2013) along with many threatened species with high endemism – characteristics of global biodiversity hotspots (Huntley et al., 2019; Linder, 2001; Myers et al., 2000). The GC region is notable for its high biodiversity, spatiotemporal heterogeneity, and complex landscape features that include several major biogeographic barriers (Bell et al., 2017; Penner et al., 2011; Portik et al., 2017; Figure 1). Despite its outsized importance to biodiversity, the GC region is one of the world's least studied hotspots owing to inaccessibility, political instability, and underdeveloped scientific infrastructure (Anthony et al., 2015; Daskin & Pringle, 2018; Plana, 2004). Patterns and correlates of species richness and endemism in this region have been explored for several terrestrial vertebrate taxa (e.g. birds and reptiles: Hawkins et al., 2003; Terribile et al., 2009) but remain coarsely characterized for amphibians.

Amphibians are among the most threatened vertebrates worldwide, and extinction risk is particularly acute for endemic species with narrow distributional range (Stuart et al., 2004; Vié et al., 2009;

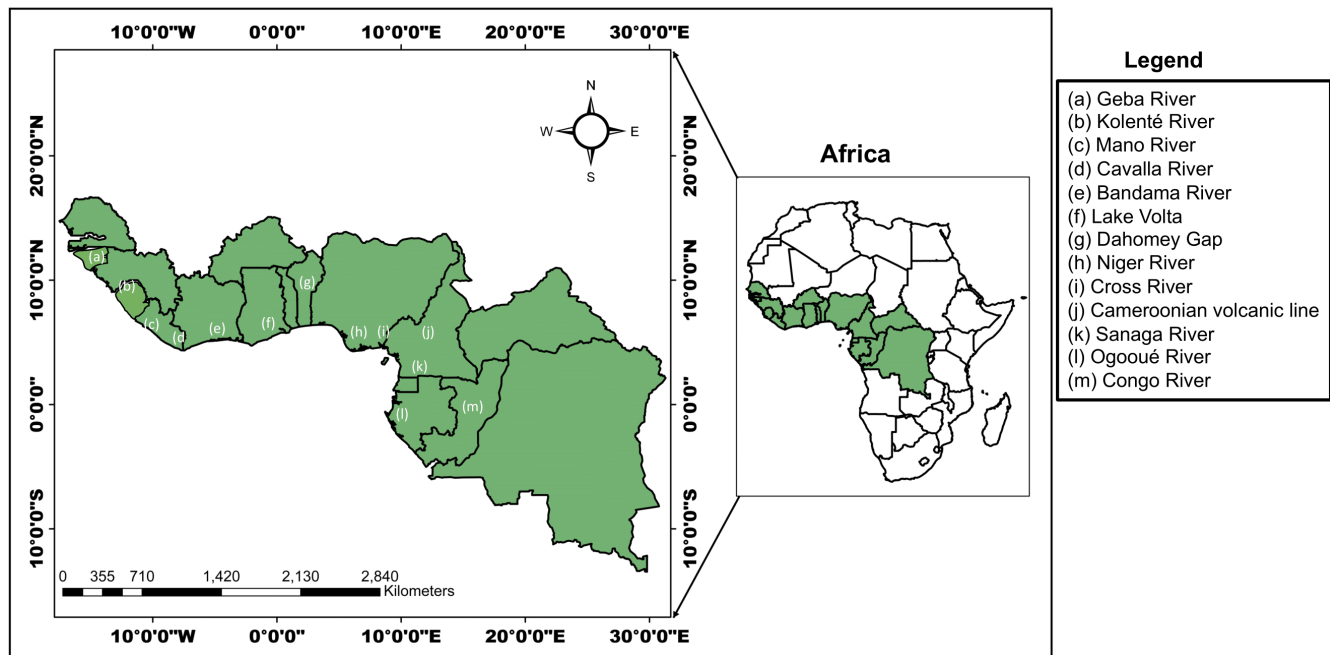


FIGURE 1 Map of Africa showing West and Central African Guineo-Congolian region. Letters in brackets show the approximate location of potentially important biogeographic barriers.

Wake & Vredenburg, 2008). Recent studies have documented increased threats to amphibians in the Afrotropics due to intensifying human activities (Aukema et al., 2017; Brooks et al., 2002; Ernst et al., 2012). In the GC region specifically, high rates of human activities and population increase often result in habitat degradation, elevating threats to forest ecosystems and wildlife (Aukema et al., 2017). Understanding the distribution and correlates of diversity in GC endemic amphibians is therefore important not just for plugging gaps in biogeographic knowledge but also for informing conservation and management policies.

Studies have shown that turnover accounts for the vast majority of beta diversity in tropical amphibians (Azevedo et al., 2021; Baselga et al., 2012; Jiménez-Robles et al., 2017). As water-dependent ectotherms, amphibians are highly sensitive to variation in temperature and rainfall (Angilletta et al., 2002; Duellman & Trueb, 1994; Hillman et al., 2009). These variables may influence turnover by affecting abundance, breeding phenology, immune function, and mating (Derivo et al., 2016; Ficetola & Maiorano, 2016 and references therein). In addition, the low dispersal ability and high dispersal limitation of amphibians could increase the degree of turnover (Qian, 2009). Thus, climatic and spatial factors may independently or jointly regulate turnover in amphibians. However, the magnitude and relative strength of these effects in causing turnover among GC endemic amphibians are unknown.

We tested the hypothesis that turnover in GC endemic amphibians is principally determined by the geographic distance between grid cells and secondarily by rainfall- and temperature-related variables. First, we characterized patterns of endemic amphibian species richness in the GC region. Second, we used generalized dissimilarity modelling to investigate how species

turnover is influenced by the geographic distance between grid cells and a suite of bioclimatic (water and temperature-related) variables. Specifically, we addressed two questions: (1) What are the biogeographic patterns of endemic amphibian species richness across the GC region? Burgess et al. (2004) identified at least 10 terrestrial bioregions in the broader GC region for near-endemic vertebrate species, but other studies have reported distinct bioregions of endemism among vertebrate groups due to species' differing ecophysiological requirements and regional zoogeographic barriers. For example, de Klerk et al. (2002) identified at least six bioregions for range-restricted terrestrial GC endemic birds, whereas Lewin et al. (2016) identified five and four bioregions for narrow endemic snakes and lizards, respectively. Because amphibians are particularly unlikely to be uniformly distributed owing to limited dispersal capacity, sensitivity to climate, and presence of biogeographic barriers in the GC region (Figure 1), we expected to find high variability in endemic amphibian richness across the GC region. (2) What are the most important variables influencing turnover in endemic amphibians of the GC region? Previous studies have shown that geographic distance is an important factor in the generation and persistence of unique faunas with narrow geographic ranges (Ota, 1998; Rosauer & Jetz, 2015). We predicted that turnover in GC endemic amphibians would be strongly associated with geographic distance between grid cells, again due to the limited dispersal capacity of amphibians coupled with the presence of major rivers, mountains and other zoogeographic barriers. Further, given amphibians' narrow thermal tolerance and performance breadths, seasonal breeding, and dependence on a humid environment (Qian, 2010; Qian et al., 2007; Rohr et al., 2018), we predicted that extreme or limiting bioclimatic factors (e.g.

precipitation of the wettest/warmest quarter) and seasonality (e.g. annual range in temperature) would be the predominant climatic correlates of turnover.

2 | METHODS

2.1 | Study area

The study area approximately corresponds to the GC rain forest defined by White (1979 & 1983) as a phytogeographic centre of endemism, with more than 8000 plant species, of which 80% are endemic. The GC forest is subdivided into three sub-centres (Figure 2) based on phytogeography as follows: Upper Guinean Forest (West-African rain forest from Sierra Leone to Ghana), Lower Guinean Forest (the western part of the Central African rain forest, from southern Nigeria to the southwestern part of the Republic of Congo and the Democratic Republic of Congo), and Congo Forest (eastern part of the Central African rain forest and the Congo River basin).

The GC forest comprises several terrestrial ecoregions (Olson et al., 2001). The *upper Guinean forest* encompasses the Eastern Guinean forest, Guinean montane forest, and Western Guinean lowland forest ecoregions. The *lower Guinean forest* hosts diverse terrestrial ecoregions ranging from Nigerian lowland forests, Niger Delta

swamp forests, Cross-Sanaga-Bioko coastal forest, Cameroonian Highland Forest, Cross-Niger transition forest, Guinean Mangroves, and Mount Cameroon and Bioko montane forest ecoregions. High species richness and endemism have been reported in the Cameroon Highlands and attributed to a high diversity of habitats in a restricted geographic area (Penner et al., 2011). The *Congo forest* spans six ecoregions, including the Atlantic Equatorial coastal forest, Northwestern Congolian lowland forest, Western Congolian swamp forest, Eastern Congolian swamp forest, Central Congolian lowland forest and Northeastern Congolian lowland forest ecoregions (Olson et al., 2001).

The biota in GC forests has an uneven distribution, with some species restricted to only one sub-centre, while others co-occur in multiple sub-centres or beyond (Hardy et al., 2013; Linder et al., 2012). The upper and lower Guinean forests are separated by an approximately 200-km-wide savanna corridor in Benin, known as the Dahomey Gap (Hardy et al., 2013). The floodplain of the Ubangi River and a portion of the Congo River, primarily composed of swamp woods, separate the lower Guinean and Congo forests (Hardy et al., 2013).

In this study, we considered 16 countries across the GC forest: Benin, Burkina Faso, Cameroon, Central African Republic, Republic of Congo, Democratic Republic of Congo, Cote d'Ivoire, Equatorial Guinea, Gabon, Ghana, Guinea, Liberia, Nigeria, Senegal, Sierra Leone and Togo.

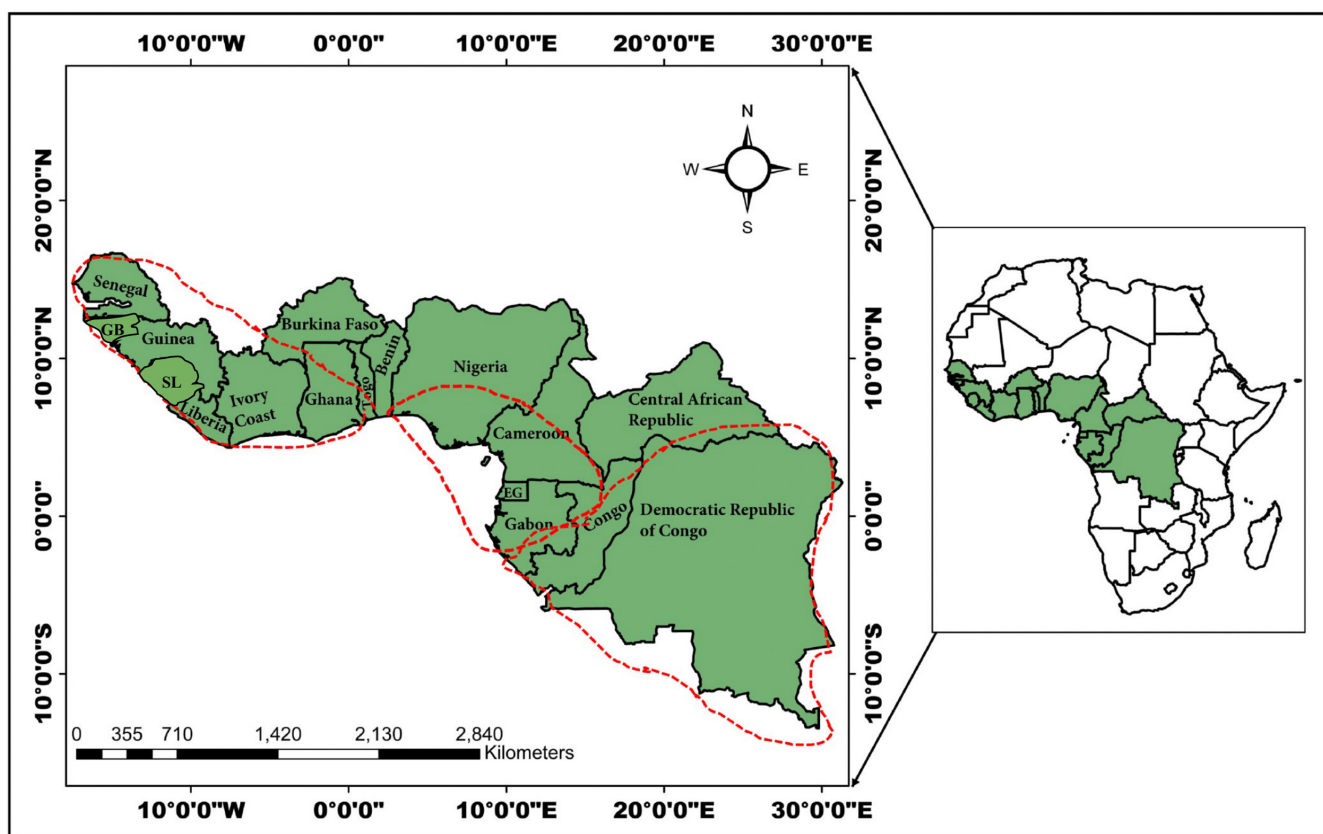


FIGURE 2 Map of West and Central African Guineo-Congolian region showing the three floristically defined blocks of forest (red dashed). The approximate delineation of the forest blocks was modified from Huntley et al. (2019). Abbreviations on the map stand for: SL=Sierra Leone; GB=Guinea Bissau.

2.2 | Distributional data

To generate a comprehensive checklist of endemic amphibians of the GC forest, we searched the Amphibiaweb (<https://amphiaweb.org/>; last accessed date: 1 April 2021) and the Amphibian Species of the World databases (<https://amphibiansoftheworld.amnh.org/>; last accessed date: 1 April 2021) to confirm the geographic distribution and taxonomic citations of amphibian species. We further searched the International Union for Conservation of Nature (IUCN) Red List database (<https://www.iucnredlist.org>) to cross-validate each species' geographic range and IUCN Red List status. We considered extant (resident) species in the GC forest for this study. Records with inaccurate and/or incomplete geographical location points were eliminated. Each species record was double-checked to match the currently recognized species distributions to produce an endemic amphibian species inventory for GC (Table S1).

After this process, our initial data comprised 310 endemic amphibian species belonging to 41 genera and 17 families (Table S1). Of these, 305 species were anurans and 5 were caecilians (Table S1). The most species-rich anuran families were Arthroleptidae (86 species), Hyperoliidae (81 species), Phrynobatrachidae (49 species), Bufonidae (28 species) and Pipidae (16 species; Figure S1). Other families were represented by ≤ 9 species. According to the IUCN Red List, 122 (39%) of the endemic species are considered Least Concern, 78 (25%) are Data Deficient (Figure S1), and 110 (36%) are threatened to varying degrees: Near Threatened (6%), Vulnerable (8%), Endangered (14%), or Critically Endangered (8%) (Figure S1).

For the geographic occurrence of each species, we consulted the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>; last accessed date: 17 April 2021). We manually performed quality evaluation of the dataset to identify uncertainty and mistakes in the geographic or taxonomic information before further analyses. Each record was reviewed for species identification; we included only individuals with 'accepted' status in the 'taxonomicstatus' field in GBIF and excluded those with 'doubtful' taxonomic status. We also eliminated records with inaccurate geographic information, records that could not be georeferenced, duplicate records, and records outside the GC region. We assembled other species records from published literature and online portals (the University of California's Museum of Vertebrate Zoology; <https://mvz.berkeley.edu>; last accessed date: 21 April 2021). We restricted records to those collected between 1980 and the date of access. Lastly, we conducted field surveys to cover an underrepresented area in Nigeria. Methods used for the field survey in Nigeria can be found in Appendix S1.

Our initial dataset included 7536 valid georeferenced records (Table S2). We could not obtain georeferenced records for 88 species due to a lack of records in either online databases or published primary literature, which reduced our dataset to 222 species, representing 72% of the endemic amphibian species currently known from the GC region (Table S2). Of the 7536 valid records, 7476 were from searched databases and primary literature, and 60 additional

georeferenced records were from our field surveys in an underrepresented area in Nigeria (Table S2). Our initial datasets included >500 georeferenced records each from Cameroon, Gabon, Republic of Congo, Ghana, Equatorial Guinea, and Democratic Republic of Congo (Table S2). We obtained 11–499 occurrence records each from Liberia, Nigeria, Guinea, Cote d'Ivoire, Benin, and Sierra Leone (Table S2). Burkina Faso, Guinea, Central African Republic, and Togo each had <10 georeferenced records for endemic amphibians (Table S2).

We performed data cleaning and quality control of the records using the R package *CoordinateCleaner* (Zizka et al., 2019). This package automatically filters common erroneous coordinates in public databases, such as those assigned to the sea, capital cities, or biodiversity institutions (Maldonado et al., 2015). To avoid potential spatial autocorrelation among occurrence records or uneven sampling, we thinned the records (Table S3) by removing localities within a 15 km radius of one another using the package *spThin* (Aiello-Lammens et al., 2015), allowing only a single record per pixel (grid cell size of $0.5^\circ \times 0.5^\circ$). This helps to reduce biased selection of variables or model coefficients (Cruz et al., 2014). After removing duplicates of georeferenced records, we retained 1205 unique records of 222 endemic species for further analysis (Table S3). Figure 3 shows the distribution map of some GC endemic amphibian species.

2.3 | Environmental data

We downloaded 19 bioclimatic variables (Table S4) from the CHELSA project (Climatologies at High Resolution for the Earth's Land Surface Areas; <http://chelsa-climate.org/>; Karger et al., 2017) at 30 arc-seconds resolution corresponding to a spatial resolution of 1 km at the equator. We also downloaded a digital elevation model (DEM) from <https://opentopography.org/about> (Krishnan et al., 2011). We then aggregated all rasters to a $0.1^\circ \times 0.1^\circ$ resolution and resampled the DEM to match the spatial resolution of the bioclimatic rasters. We also calculated slope from the DEM. The largest difference in elevation between each site and its eight nearest neighbours was used to calculate relief roughness (also referred to as terrain ruggedness; Riley et al., 1999). All variables were cropped to a 1-degree buffer around all species records to ensure that the background of the environmental data for the species distribution modelling was not restricted to the inferred species range but also encompassed potentially relevant points lying outside the set of species distribution records. We prepared all data using the R package *raster*.

We estimated the Variance Inflation Factor (VIF) to measure the degree of multicollinearity among all variables. We removed variables exceeding a VIF threshold of 10 using the packages *USDM* (Naimi et al., 2014) and retained those without multicollinearity for further analyses (Table 1). The retained variables included relief roughness and eight bioclimatic variables (Mean Diurnal Range; Maximum Temperature of Warmest Month; Mean Temperature of Wettest and Coldest Quarters; Precipitation of Wettest, Driest, and Warmest Quarters; and Precipitation Seasonality).

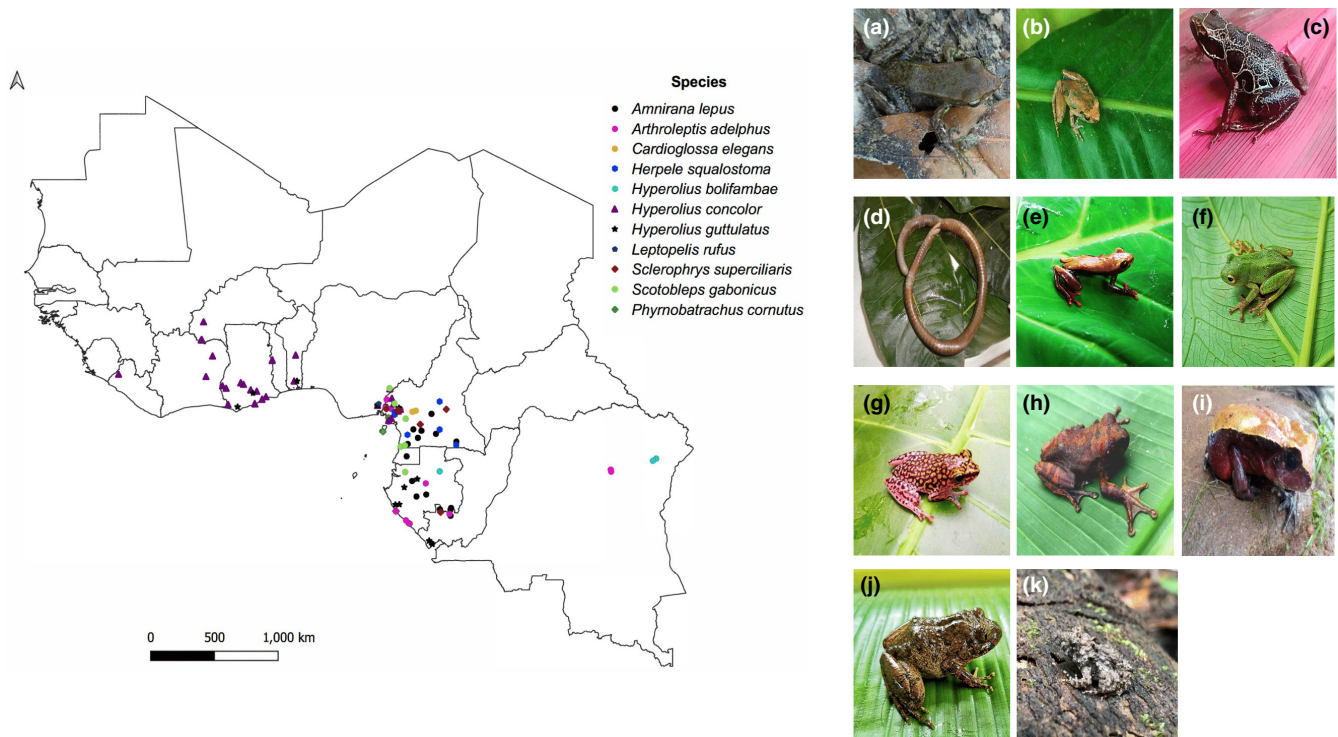


FIGURE 3 Distribution map of some GC endemic amphibian species (a) *Amnirana lepus* (Photo credit: Arnaud Marius Tchasse Fokoua); (b) *Arthroleptis adelphus* (Photo credit: LMN); (c) *Cardioglossa elegans* (Photo credit: LMN); (d) *Herpele squalostoma* (Photo credit: Arnaud Marius Tchasse Fokoua); (e) *Hyperolius bolifambe* (Photo credit: LMN); (f) *Hyperolius concolor* (Photo credit: LMN); (g) *Hyperolius guttulatus* (Photo credit: LMN); (h) *Leptopelis rufus* (Photo credit: LMN); (i) *Sclerophrys superciliaris* (Photo credit: LMN); (j) *Scotobleps gabonicus* (Photo credit: LMN); (k) *Phrynobatrachus cornutus* (Photo credit: Arnaud Marius Tchasse Fokoua). Geographic occurrences were based on our assembled datasets.

2.4 | Species ranges

Given the recommended minimum sample size of 3 for species range estimation and modelling (van Proosdij et al., 2016), we excluded 58 species with fewer than three unique records, leaving 164 species. Although we acknowledge that a minimum sample size of three is small, we consider it justifiable because (a) it makes our analyses more inclusive and representative of the endemic amphibian fauna; (b) endemic species often occur at low abundance in restricted ranges with specific habitat requirements; (c) 71% of retained species had >10 records and 29% had >3 records; and (d) previous studies show that range-size estimation based on a minimum of 3 samples can nonetheless provide valuable predictions (Bharti et al., 2021; Deb et al., 2017; Hernandez et al., 2006; Pearson et al., 2006; van Proosdij et al., 2016; Ye et al., 2021; Zizka et al., 2020). For the 164 species with ≥ 3 records, we used a two-tier approach to estimate range sizes depending on the total number of records per species. For species with 3–10 unique records ($n=47$), which are likely to be rare and range-restricted, we used the minimum convex polygon (MCP) method (Bekoff & Mech, 1984; Mohr, 1947) to estimate range sizes using a half-degree buffer to limit over-prediction (Whitfield, 1984). We used MCP because previous studies (Kazmaier et al., 2002; Row & Blouin-Demers, 2006) have supported the use of this method for estimating the range size of reptiles and amphibians in general and range-restricted

amphibians in particular (Blomquist & Hunter, 2009; Boenke, 2011; Miaud & Sanuy, 2005; Watson et al., 2003). For species with >10 unique records ($n=117$), which are likely to be widespread, we estimated MCPs using a one-degree buffer to ensure that ecologically relevant background points (pseudo-absences) are included in the species distribution modelling. Thereafter, we removed unsuitable areas within polygons following Förderer et al. (2018). To do this, we used species distribution modelling to overlay the MCPs and estimate the final species ranges.

We used the Maxent algorithm for species distribution modelling (Phillips et al., 2006). Using the ENMevaluate function from the R package *ENMeval* (Muscarella et al., 2014), we performed model selection with testing parameters such as feature class combinations (linear, quadratic, product, and threshold). Regularization multipliers were selected in Maxent using ENMevaluate. Using cross-validation ($k=10$), we evaluated models and selected those with second-order Akaike Information Criterion difference ($\Delta AICc$) < 2 and Area Under the Receiver Operator Curve (AUC; a measure of the diagnostic test accuracy) > 0.75. We considered AUC values > 0.75 to be useful for modelling based on the recommendations of Elith (2002) and the results of previous studies on amphibians (e.g. Barrett et al., 2014; García et al., 2014; Milanovich et al., 2010; Urbina-Cardona & Loyola, 2008). To delineate the extent of the projected data within the polygons for each species, we generated ~1000 background points. To select background

TABLE 1 The variables (code, name, units and Variance Inflation Factor) used to predict the environmental correlates of richness patterns in GC endemic amphibians after multi-collinearity analysis.

Code	Variable name	Unit	Variance inflation factor
Bio2	Mean Diurnal temperature Range (Mean of monthly (max temp – min temp))	°C	4.3910
Bio3	Isothermality		2.5646
Bio8	Mean Temperature of Wettest Quarter	°C	3.8174
Bio11	Mean Temperature of Coldest Quarter	°C	2.8289
Bio13	Precipitation of Wettest Quarter	mm	2.0421
Bio14	Precipitation of Driest Quarter	mm	2.4028
Bio18	Precipitation of Warmest Quarter	mm	3.7220
Bio19	Precipitation of Coldest Quarter	mm	2.2361
RR	Relief Roughness	m	1.1610

points in each grid cell, we generated a sampling-bias layer based on historical sampling for African amphibians estimated by Farooq et al. (2021) (Figure S2). In this way, more ecologically relevant background points were selected for the SDM, thus fairly reflecting the ecological variability and sampling history of the study region. Finally, we used a threshold based on maximum specificity and sensitivity to produce binary predictions (presence-absence), which we converted into range maps for each species (Nenzen & Araujo, 2011).

2.5 | Species richness and endemism

To evaluate biogeographic patterns of endemic amphibian species richness across the GC region (question 1), we quantified species richness and endemism using two approaches of Crisp et al. (2001) and Linder (2001). Species richness was calculated as the number of endemic species in a grid cell ($0.5^\circ \times 0.5^\circ$) and also estimated the number of GC endemic species in each country. We mapped species richness at a coarse resolution to reduce potential bias in sampling effort and enable a better understanding and visualization of richness patterns (Graham & Hijmans, 2006). Endemism was measured as weighted endemism, where the proportion of endemics is inversely weighted by range size. The endemism value for a cell equals the sum of these weights for all species in the cell. To test whether weighted endemism was higher than the expected species richness, we produced replicate random draws from the species pool based on the observed species richness (i.e. the same number of species) and the actual species frequencies (the more frequent a species, the more likely it is to be drawn). For estimations of weighted endemism,

we used the functions 'weighted endemism' and 'endemism.null.test' from the R package *biomapME* (Guerin et al., 2015). The distribution of the resulting set of null endemism scores was compared to the observed endemism. Subsequently, grid cells were mapped as higher or lower than expected (based on significance testing and comparison to null quantiles) to produce a binary-weighted endemism map and we estimated the values of weighted endemism for each country. Finally, we performed sensitivity analyses in relation to the mapping strategy and for the presence of species with <3 unique records per grid cell. To do this, we calculated species richness and endemism with the following datasets: (1) without SDMs to remove unsuitable habitats and (2) without species with <3 unique records per grid cell.

2.6 | Generalized dissimilarity modelling (GDM)

To evaluate how much of the species turnover can be attributed to the independent and combined influences of geographic distance and bioclimatic variables (question 2), we used Generalized Dissimilarity Modelling (GDM). This method is widely used to identify the contributions of different factors to explaining beta diversity patterns (e.g. Blois et al., 2013; Capinha et al., 2015; Fitzpatrick et al., 2013). We focused only on turnover (reflecting replacement), to the exclusion of nestedness (reflecting species loss), in light of multiple studies showing that turnover dominates amphibian beta diversity in regions below the 37th parallel north, which encompasses all of Africa (Azevedo et al., 2021; Baselga et al., 2012; Jiménez-Robles et al., 2017); however, we acknowledge that a comprehensive understanding of beta diversity requires evaluating both turnover and nestedness (Baselga, 2010) and suggest this as an objective for future study on the endemic amphibians of the GC region.

We calculated species turnover among grid cells with >5 species, thereby minimizing possible effects of nestedness that might arise when species in locations with very low species richness are subsets of species in areas with relatively high species richness (Ulrich & Gotelli, 2007; Wright & Reeves, 1992). We built GDM models using all possible combinations of bioclimatic variables (after removing those deemed to be colinear, as described above). We then consecutively excluded from the full model the bioclimatic variable with the smallest contribution. In each iteration, we calculated the relative variable importance (percentage of explained deviance between a model with and without a variable) and significance (p -value <.05) through matrix permutations for each variable ($n = 1000$). According to Wagner and Fortin (2015), model selection using AIC is not applicable to analyses of regression matrices such as GDM. Thus, we used a comparable approach that involves selection of the model with the highest explained deviance (Azevedo et al., 2021). This approach retained only important bioclimatic variables after more than 160 successive permutations (following the 0.16 optimization level suggested by Heinze et al., 2018). All analyses were done in R using the package *betapart* (Baselga, 2010; Baselga et al., 2018).

We used I-splines to identify the most important bioclimatic variables that could account for the nonlinear monotonic

relationships between variables and species turnover (i.e. partial ecological distance). We produced the models using the R-package *gdm* (Ferrier et al., 2007). We then used GDMs to predict species turnover across the entire study area (background of bioclimatic variables). The results were clustered with the unweighted pair group method using arithmetic averages (UPGMA) to define bioregions with similar species composition. UPGMA is a frequently used agglomerative hierarchical clustering approach with good performance in clustering dissimilarity for bioregionalization studies (Kreft & Jetz, 2010).

Table S5 shows the ODMAP (Overview, Data, Model, Assessment, and Prediction) standardized protocol (Zurell et al., 2020) used in this study. All R code used in the analyses is included in Appendix S2.

3 | RESULTS

3.1 | Range size

Species distribution modelling had sufficient predictive power for occurrences, as evidenced by the AUC. Only two species had $AUC < 0.75$ and were mapped using the MCP approach. Of the 117 species with >10 unique records, 50 had good modelling performance ($AUC > 0.75$) and were used for removing unsuitable habitats within the MCP polygons. For all 164 species with ≥ 3 unique records, we obtained a mean range size (\pm s.d.) of $192,312 \pm 253,870$ km² (median = 84,089 km²; Table S6). The mean range size for species with 3–10 records was

$51,508 \pm 145,239$ km² (median = 4091 km²; Table S6), while that for species with >10 records was $248,875 \pm 266,343$ km² (median = 159,309 km²; Table S6).

3.2 | Patterns of species richness and endemism

Endemic amphibian richness (mean = 44; range 5–131 species; Figure 4a; Table S7) was strongly concentrated in the lower GC region that includes the Democratic Republic of Congo (e.g. some forests in Lulimba town within South Kivu Province, Kalemie town, on the western shore of Lake Tanganyika, and other forests located along Lakes Tanganyika and Mweru, extending to the Mbuji-Mayi in Kasai-Oriental Province), Nigeria-Cameroon mountains (e.g. Mountains Obudu, Oku, Bamenda, Bamboutos, Manengouba, Cameroun, Tchabal-Mbabo, Tchabal Gangdaba), Republic of Congo, Equatorial Guinea, and Gabon. Other areas of high endemic species richness were in the Upper Guinean-Congolian forest along the coasts of Togo, Ghana (e.g. Cape Coast in Central Region, Axim and Sekondi in Western Region etc.), Cote d'Ivoire (e.g. Grand-Bassam and Sud-Comoé in southeastern Cote d'Ivoire), Guinea, Sierra Leone, and Liberia (Figure 4a). In sum, the lower GC forest, particularly forests of Cameroon (mean = 131 species), Gabon (mean = 71 species), Nigeria (mean = 64 species), Equatorial Guinea (mean = 59 species), Republic of Congo (mean = 58 species), Democratic Republic of Congo (mean = 52 species) and Cote D'Ivoire (mean = 50 species), stood out as centres of endemic amphibian species richness in the GC region (Figure 4a; Table S7).

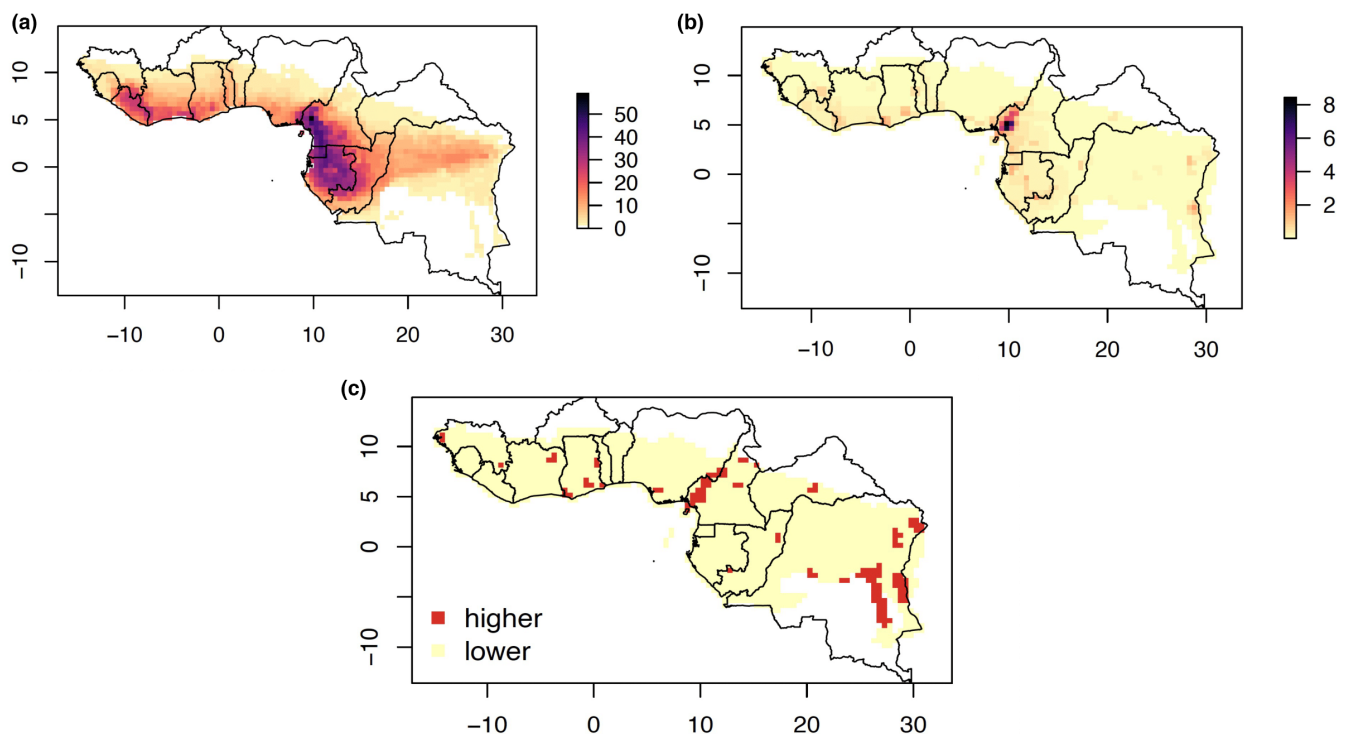


FIGURE 4 Geographic patterns of (a) species richness, (b) weighted endemism and (c) significant weighted endemism of endemic amphibians of the African Guineo-Congolian forest.

The weighted endemism metric identified the Nigeria-Cameroon mountains (southern Nigeria through southwestern Cameroon), which comprise the Cameroonian Highland forest ecoregion, as an area of high endemism (Figure 4b).

Spatial patterns of species richness and weighted endemism contrasted with those based on the results of the randomization test for significant endemism (Figure 4c). This finding was expected, as the randomization test incorporates endemic species richness in calculating weighted endemism. The randomization test for significant endemism returned four major areas of significant weighted endemism that were higher than random. While three areas of significant weighted endemism were found in the lower GC region (Nigeria-Cameroon mountains, Democratic Republic of Congo and Cote d'Ivoire), we identified only one such area in the upper GC forest in Ghana (Figure 4c).

The result of the sensitivity analyses in relation to the mapping strategy and exclusion of species with <3 unique records (Figure S3) showed that exclusion had no effect on the results of the species richness and endemism. This demonstrated the stability of the results, suggesting that our approach was robust.

3.3 | Patterns of species turnover

The GDM analyses captured 29.10% of deviation (model deviance = 1056.20; p -value < .001) and identified endemic areas according to the heterogeneous turnover patterns of amphibians in the GC forests. Geographic distance was by far the strongest predictor of turnover (55.90%), and three bioclimatic variables – precipitation of the warmest quarter (5.50%), mean temperature of the wettest quarter (4.30%), and mean diurnal temperature range (3.50%) – also contributed. The GDM-fitted I-splines further supported the conclusion that geographic distance between grid cells was a dominant predictor of turnover (Figure 5). The nonlinear shapes of the GDM curves showed an increasing rate of community compositional change with increasing geographic distance between grid cells.

The clustering analysis of the turnover component of compositional dissimilarity using UPGMA identified five bioregions for GC endemic amphibians, which coincided partly with the different ecoregions (Figure 6) as follows: (1) forested areas in Cote d'Ivoire, Senegal, western/southern Burkina Faso, Ghana and southern parts of Togo and Benin; (2) areas in northern and eastern parts of Burkina Faso, Benin (excluding southern region), Togo (excluding southern region), Nigeria (excluding southern region), northern Cameroon, and northern Central African Republic; (3) forested areas in southern Nigeria, Cameroon, Equatorial Guinea, western Central African Republic, Gabon, Republic of Congo, and western/northern parts of Democratic Republic of Congo; (4) forested areas in southern and eastern parts of Central African Republic and some northern parts of Democratic Republic of Congo; and (5) forested areas in southern and eastern parts of Democratic Republic of Congo.

4 | DISCUSSION

As expected, we found that species richness and endemism in amphibians of the GC region are geographically unevenly distributed. Nevertheless, the centres of endemic species richness identified in our study largely overlapped with areas of high endemism. We found the Nigeria-Cameroon mountains to be the areas of highest species richness and endemism for GC amphibians. The importance of the Nigeria-Cameroon mountains, previously identified as a centre of amphibian biodiversity (Penner et al., 2011), was confirmed. Our results are consistent with previous studies that have identified montane regions as areas of high vertebrate species richness and endemism (e.g. Kafash et al., 2020; Rahbek et al., 2019; Shipley & McGuire, 2023). The Nigeria-Cameroon mountains consist of dense humid rain forests and deep gorges flanked by towering mountains (e.g. Obudu Plateau, Mounts Cameroon, Oku, Bamenda, Bamboutos, Manengouba, Tchabal-Mbabo, Tchabal Gangdaba, etc.), which results in diverse climate and vegetation types and a variety of habitats for amphibian species (Penner et al., 2011). Montane regions are regarded as both museums and cradles of biodiversity, where old taxa have survived because of relatively stable climates or the mitigation of climate change impacts by altitudinal range shifts (Barthlott et al., 2005; Kreft & Jetz, 2007; Mutke & Barthlott, 2005) and where new taxa are rapidly emerging because of new ecological opportunities caused by recent uplifts in the mountain. Combined with limited gene flow and dispersal barriers, these factors have resulted in radiations of many clades, resulting in large numbers of range-restricted species on mountains (Fjeldså & Lovett, 1997; Gentry, 1982; Hughes & Eastwood, 2006).

Another prominent centre of species richness and endemism for amphibians is forested areas in Democratic Republic of Congo, Cote d'Ivoire, and Ghana. These forests have previously been shown to be centres of species richness for diverse taxa, including plants and animals (Burgess et al., 2002; de la Estrella et al., 2012; Küper et al., 2004; Linder, 2001; Linder et al., 2005, 2012; Penner et al., 2011; Sosef et al., 2017). Our results are consistent with the hypothesis that climatic history during the Pleistocene accounts for some variation in species richness and endemism patterns across the GC region (Jansson, 2003; Maley, 1996). Previous studies (e.g. Murali et al., 2021; Penner et al., 2011) have reported that areas with high biodiversity in GC often coincide with areas where Pleistocene refugia may have existed. Areas of high endemism identified in our study (forested and montane ecosystems in southwestern Cameroon, southern parts of Nigeria, Cote d'Ivoire, and Ghana) have previously been postulated as refugia for narrow-ranged and endemic amphibian species in the GC region (Maley, 1996; Penner et al., 2011).

The IUCN Red List showed that about 36% of endemic GC amphibian species in our study are threatened with extinction. The high values of endemic species richness coupled with increasing threats from human activity emphasize the outstanding importance of the GC region for global amphibian conservation. Although the GC region was previously covered by forests, only a fraction of these

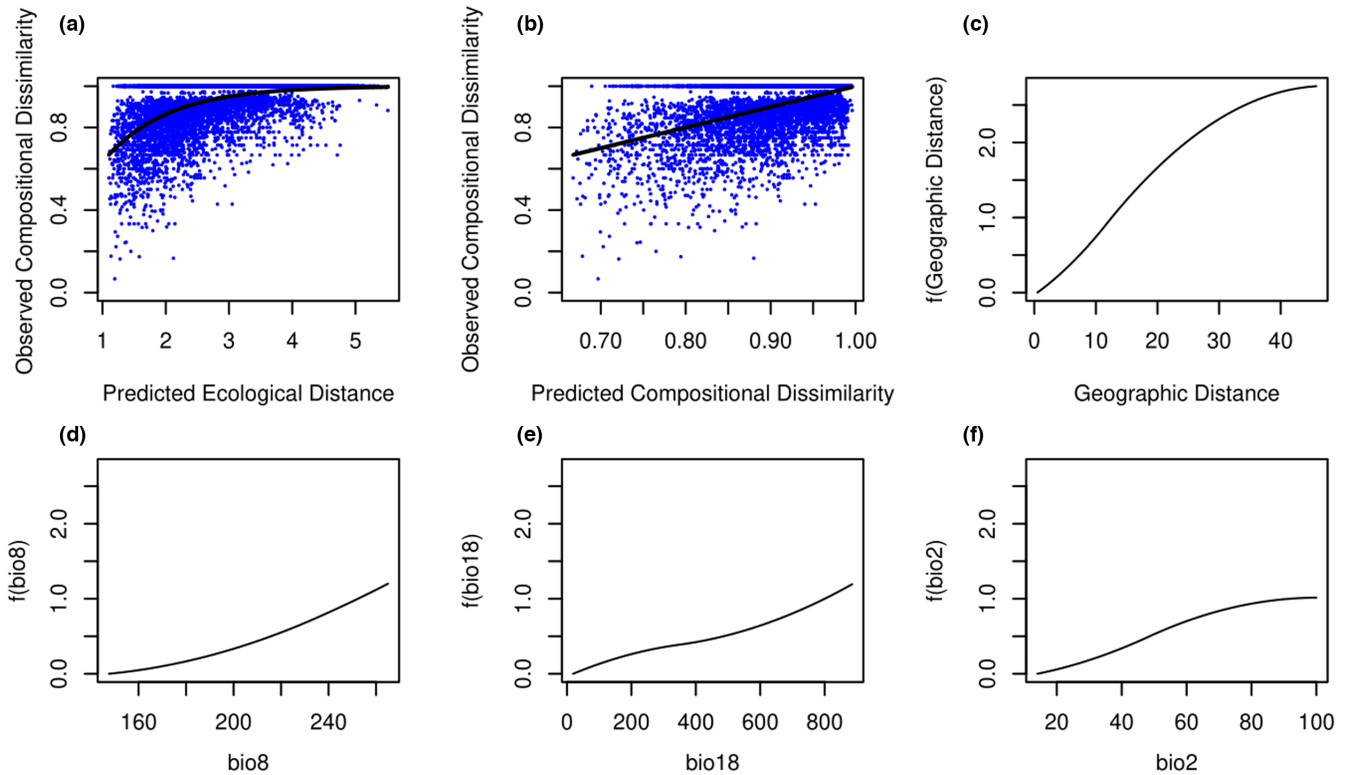


FIGURE 5 Generalized dissimilarity model (GDM) I-spline showing (a) the relationship between observed compositional dissimilarity and the linear predictor of the regression equation from GDM (predicted ecological distance between site pairs); (b) relationship between observed and predicted compositional dissimilarity; and (c–f) partial functions for variables significantly associated with endemic amphibian species turnover. The maximum height reached by each curve indicates the total amount of compositional turnover associated with that variable (relative contribution of the variable to the species turnover), assuming all other variables are constant. The slope of each function indicates the rate of the compositional species turnover observed along the gradient. Abbreviations: BIO8=mean temperature of the wettest quarter; BIO18=precipitation of warmest quarter and BIO2=Mean Diurnal temperature Range.

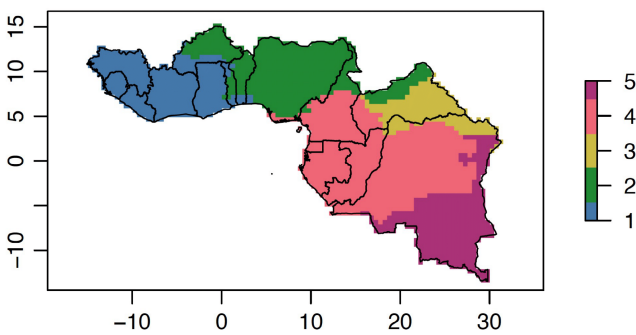


FIGURE 6 Bioregions of species richness of endemic amphibians in the GC forest based on the UPGMA hierarchical clustering. The five clusters (demarcated with colours) show the relative abundances of similar species within each bioregion.

forests remains undisturbed (CILSS, 2016). With increasing human settlement and cultivation across the GC region, the vegetation has been grossly modified by deforestation, fire, grazing, agricultural practices, soil disturbance, and altered drainage arising from the use of chemical fertilizers and pesticides in farmland (Carr et al., 2015; CILSS, 2016). To date, the main driver of habitat loss in this region is the transformation of natural habitats into agricultural land (Carr et al., 2015; Chazdon, 2003; GBF, 2023; Geist & Lambin, 2002;

MEA, 2005) due to increasing demand for food and money by growing human populations (Burgess et al., 2007). For instance, from 2002 to 2021, agricultural land in the GC region doubled while forest cover was reduced. High forest losses were recorded in Benin, Côte d'Ivoire, Ghana, Guinea, Nigeria, Sierra Leone, and Togo (Global Forest Watch, 2023). A growing body of studies (e.g. Blyth et al., 2002; Burgess et al., 2002, 2007; Chidumayo et al., 2011; Nneji et al., 2019; Plumptre et al., 2004) has reported adverse effects of habitat alteration on the temporal and spatial compositions of vertebrates. These considerations underscore the urgent need for improved conservation plans for endemic amphibians and their associated habitats in the GC region. The results we present here could help guide future regional biodiversity studies and the identification of priority areas for the conservation of endemic amphibians in the GC region.

Using GDM, we identified several factors that could explain amphibian species richness and endemism patterns in the GC region. As predicted, we found that turnover is primarily influenced by the geographic distance between grid cells and secondarily by environmental differences (i.e. climatic variation). This suggests that dispersal limitation (geographic distance) is more important than niche limitation (environmental difference) in regulating amphibian beta diversity. Penner et al. (2011) highlighted

potential geographical barriers in the GC region (mountains, Cameroon volcanic line, rivers) that could limit species dispersal across the entire region. These constraints may increase vulnerability to extinction in the face of rapid climate change (Araújo & Pearson, 2005). The generally low dispersal ability of amphibians (Blaustein et al., 1994; Wells, 2007) relative to most other animal taxa also increases the likelihood of local extinction, particularly among endemics that are sensitive to environmental change (Chen et al., 2011).

Other than geographic distance, precipitation of the warmest quarter, mean temperature of the wettest quarter, and mean diurnal temperature range best predicted species turnover. Several previous studies have found one or more of these bioclimatic variables to be important in explaining the observed distribution and richness patterns of amphibians (Ballesteros-Barrera et al., 2022; Barrett et al., 2014; Guo et al., 2021). Bioclimatic factors such as precipitation and temperature are especially likely to influence ecological processes and biological functioning in amphibians (Olden & Rooney, 2006). Variables related to extreme environmental conditions (precipitation of the warmest quarter and mean temperature of the wettest quarter) emerged as important in explaining the turnover in GC endemic amphibians, similar to previous studies on amphibians (Bolitho & Newell, 2022; Guo et al., 2021). Precipitation of the wettest quarter has also been linked to both tree diversity and water availability (Soares & Brito, 2007). Tree diversity and cover may sustain amphibian diversity in various direct and indirect ways, while water availability plays a pivotal role in the breeding and life cycle of amphibians. The role of two temperature variables in determining turnover accords with studies that have linked temperature to immune function in amphibians (Miller et al., 2018). The coupling of water and temperature variables as predictors of turnover suggests that environmental change may have dramatic impacts on endemic amphibians of the GC region, especially if geographical patterns of precipitation and temperature shift independently.

We acknowledge several important caveats. One, already mentioned, is that we focused exclusively on the turnover component of beta diversity; consideration of nestedness in future studies may provide further insight. Another is that most of the data used in the study were sourced from biological collections. On the one hand, this underscores the value of specimen data from museums and other repositories for baseline ecological studies (Beck et al., 2012; Powney & Isaac, 2015); at the same time, however, our dataset has limitations that are inherent to information assembled from collections, such as patchy sampling effort and lack of taxonomic revisions. Museum data are also subject to potential biases, such as erroneous identification and over- or underrepresentation of certain areas, habitat types, and species (Elith & Leathwick, 2009; Oliveira et al., 2016). While we took several steps to ensure high data quality and mitigate biases associated with the occurrence records, the patterns revealed in our study may, to some extent, reflect differences among sampled locations rather than between those locations and the overall GC region.

5 | CONCLUSION AND RECOMMENDATIONS

We evaluated spatial patterns of richness and determinants of turnover in endemic amphibians of the GC biodiversity hotspot. Patterns of species richness and endemism are not uniform across this region – the Nigeria-Cameroon mountains and forested regions of the Democratic Republic of Congo, Cote d'Ivoire and Ghana host a higher richness of endemic amphibians than other areas. We encourage more studies on other taxonomic groups to test the generality of this unbalanced spatial pattern of endemic species richness in the GC region. Also, we recommend a more detailed study investigating the effects of disturbance-related environmental variables on amphibians as well as other taxonomic groups endemic to the region. Effective conservation plans in key areas of richness for endemic amphibians are needed to ensure the long-term persistence and survival of this highly threatened fauna. Our study advances the understanding of GC endemic amphibians by identifying geographic distance and a subset of bioclimatic variables (precipitation of the warmest quarter, mean temperature of the wettest quarter and mean diurnal temperature range) as major determinants of species turnover. However, studies involving a broader range of taxa are needed to evaluate other contemporary environmental and historical factors affecting the biodiversity of the GC region as a whole. Regional- and continental-scale conservation plans often identify priority areas critical to the persistence of their conservation targets. However, fine-scale research and planning will help to refine the understanding of where actions could be taken for greatest effect within these priority areas and to inform what those actions should be.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13717>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the main text and supplementary material of this article. Scripts and datasets used are available on Dryad (Nneji et al. (2019), patterns of species richness and turnover in endemic amphibians of the Guineo-Congolian rain forest. Dryad, Dataset, <https://doi.org/10.5061/dryad.8931zcrv9>).

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REFERENCES

- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541–545. <https://doi.org/10.1111/ecog.01132>
- Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, 27, 249–268. [https://doi.org/10.1016/S0306-4565\(01\)00094-8](https://doi.org/10.1016/S0306-4565(01)00094-8)
- Anthony, N. M., Atteke, C., Bruford, M. W., Dallmeier, F., Freedman, A., Hardy, O., Ibrahim, B., Jeffery, K. J., Johnson, M., Lahm, S. A., Lepengue, N., Lowenstein, J. H., Maisels, F., Mboumba, J.-F., Mickala, P., Morgan, K., Ntie, S., Smith, T. B., Sullivan, J. P., ... Gonder, M. K. (2015). Evolution and conservation of central African biodiversity: Priorities for future research and education in The Congo Basin and gulf of Guinea. *Biotropica*, 47(1), 6–17. <https://doi.org/10.1111/btp.12188>
- Araújo, M. B., & Pearson, R. G. (2005). Equilibrium of species' distributions with climate. *Ecography*, 28, 693–695. <https://doi.org/10.1111/j.2005.0906-7590.04253.x>
- Aukema, J. E., Pricope, G., & Husak, G. (2017). Biodiversity areas under threat: Overlap of climate change and population pressures on the world's biodiversity priorities. *PLoS One*, 12, 1–21. <https://doi.org/10.1371/journal.pone.0170615>
- Azevedo, J. A., Nogueira, de, C., Antonelli, A., & Faurby, S. (2021). Contrasting patterns of phylogenetic turnover in amphibians and reptiles are driven by environment and geography in Neotropical savannas. *Journal of Biogeography*, 48, 2008–2021. <https://doi.org/10.1111/jbi.14131>
- Ballesteros-Barrera, C., Tapia-Pérez, O., Zárate-Hernández, R., Leyte-Manrique, A., Martínez-Bernal, A., Vargas-Miranda, B., Martínez-Coronel, M., & Ortiz-Burgos, S. (2022). The potential effect of climate change on the distribution of endemic anurans from Mexico's tropical dry Forest. *Diversity*, 14, 650. <https://doi.org/10.3390/d14080650>
- Barrett, K., Nibbelink, N. P., & Maerz, J. C. (2014). Identifying priority species and conservation opportunities under future climate scenarios: Amphibians in a biodiversity hotspot. *Journal of Fish and Wildlife Management*, 5(2), 282–297. <https://doi.org/10.3996/022014-JFWM-015>
- Barthlott, W., Mutke, J., Rafiqpoor, M. D., Kier, G., & Kreft, H. (2005). Global centres of vascular plant diversity. *Nova Acta Leopoldina*, 92(342), 61–83.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., Gómez-Rodríguez, C., & Lobo, J. M. (2012). Historical legacies in world amphibian diversity revealed by the turnover and Nestedness components of Beta diversity. *PLoS One*, 7(2), e32341. <https://doi.org/10.1371/journal.pone.0032341>
- Baselga, A., Orme, C. D. L., Villéger, S., De Bortoli, J., & Leprieux, F. (2018). R Package 'betapart'. Partitioning Beta Diversity into Turnover and Nestedness Components, Version 1.5.0.
- Beck, J., Ballesteros-Mejia, L., Buchmann, C. M., Dengler, Ü., Fritz, S. A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M., & Dormann, C. F. (2012). What's on the horizon for macroecology? *Ecography*, 35, 673–683. <https://doi.org/10.1111/j.1600-0587.2012.07364.x>
- Bekoff, M., & Mech, L. D. (1984). Simulation analyses of space use: Home range estimates, variability, and sample size. *Behavior Research Methods, Instruments, and Computers*, 16, 32–37.
- Bell, R. C., Parra, J. L., Badjedjea, G., Barej, M. F., Blackburn, D. C., Burger, M., Channing, A., Dehling, J. M., Greenbaum, E., Gvozdík, V., Kielgast, J., Kusamba, C., Lötters, S., McLaughlin, P. J., Nagy, Z. T., Rödel, M.-O., Portik, D. M., Stuart, B. L., VanDerWal, J., ... Zamudio, K. R. (2017). Idiosyncratic responses to climate-driven forest fragmentation and marine incursions in reed frogs from Central Africa and the Gulf of Guinea Islands. *Molecular Ecology*, 26, 5223–5244. <https://doi.org/10.1111/mec.14260>
- Bharti, D. K., Edgcombe, G. D., Karanth, K. P., & Joshi, J. (2021). Spatial patterns of phylogenetic diversity and endemism in the Western Ghats, India: A case study using ancient predatory arthropods. *Ecology and Evolution*, 11, 16499–16513. <https://doi.org/10.1002/ece3.8119>
- Blaustein, A. R., Wake, D. B., & Sousa, W. P. (1994). Amphibian declines: Judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, 8(1), 60–71.
- Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Ferrier, S., Veloz, S. D., He, F., Liu, Z., Manion, G., & Otto-Bliesner, B. (2013). Modeling the climatic drivers of spatial patterns in vegetation composition since the last glacial maximum. *Ecography*, 36, 460–473. <https://doi.org/10.1111/j.1600-0587.2012.07852.x>
- Blomquist, S. M., & Hunter, M. L., Jr. (2009). A multi-scale assessment of habitat selection and movement patterns by northern leopard frogs (*Lithobates [Rana] pipiens*) in a managed forest. *Herpetological Conservation Biology*, 4, 142–160.
- Blyth, S., Groombridge, B., Lysenko, I., Miles, L., & Newton, A. (2002). *Mountain watch: Environmental change and sustainable development in mountains*. UNEP-WCMC.
- Boenke, M. (2011). *Terrestrial habitat and ecology of Fowler's toads (Anaxyrus fowleri)*. M.Sc. thesis. Department of Biology, McGill University.
- Bolitho, L., & Newell, D. (2022). Extensive range contraction predicted under climate warming for two endangered mountaintop frogs from the rainforests of subtropical Australia. *Scientific Reports*, 12, 20215. <https://doi.org/10.1038/s41598-022-24551-5>
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002). Habitat loss and extinction in the

- hotspots of biodiversity. *Conservation Biology*, 16, 909–923. <https://doi.org/10.1046/j.1523-1739.2002.00530.x>
- Buckley, L. B., & Jetz, W. (2008). Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 17836–17841. <https://doi.org/10.1073/pnas.0803524105>
- Burgess, N. D., Balmford, A., Cordeiro, N. J., Fjeldså, J., Kuper, W., Rahbek, C., Sanderson, E. W., Scharlemann, J. P. W., Sommer, J. H., & Williams, P. H. (2007). Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation*, 134, 164–177. <https://doi.org/10.1016/j.biocon.2006.08.024>
- Burgess, N. D., D'Amico Hales, J., Underwood, E., & Dinerstein, E. (2004). *Terrestrial ecoregions of Africa and Madagascar – A conservation assessment*. Island Press.
- Burgess, N. D., Rahbek, C., Larsen, F. W., Williams, P., & Balmford, A. (2002). How much of the vertebrate diversity of sub-Saharan Africa is catered for by recent conservation proposals? *Biological Conservation*, 107, 327–339. [https://doi.org/10.1016/S0006-3207\(02\)00071-X](https://doi.org/10.1016/S0006-3207(02)00071-X)
- Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348, 1248–1251. <https://doi.org/10.1126/science.aaa8913>
- Carr, J., Adeleke, A., Angu, A. K., Belle, E., Burgess, N., Carrizo, S., Choimes, A., Coulthard, N., Darwall, W., Foden, W., Garreau, J., Gatarabirwa, W., Hicks, C., Kapijimpanga, D. R., King, E., Koenig, K., Martinez, S., Meng, H., Kofi, N. S., ... Walters, G. (2015). *Ecosystem profile Guinean forests of West Africa biodiversity hotspot*. Critical Ecosystem Partnership Fund.
- Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6, 51–71. <https://doi.org/10.1078/1433-8319-00042>
- Chen, S., Jiang, G., Zhang, J., Li, Y., & Qian, H. (2011). Species turnover of amphibians and reptiles in eastern China: Disentangling the relative effects of geographic distance and environmental difference. *Ecological Research*, 26, 949–956. <https://doi.org/10.1007/s11284-011-0850-3>
- Chidumayo, E., Okali, D., Kowero, G., & Larwanou, M. (Eds.). (2011). *Climate change and African forest and wildlife resources*. African Forest Forum.
- CILSS. (2016). *Landscapes of West Africa – A window on a changing world*. U.S. Geological Survey EROS, 47914 252nd St, Garretson, SD 57030, USA.
- Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., Pollock, C., Richman, N. I., Soulsby, A.-M., & Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography*, 23, 40–45. <https://doi.org/10.1111/geb.12096>
- Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núñez, P. V., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H., Losos, E., & Hubbell, S. P. (2002). Beta-diversity in tropical forest trees. *Science*, 295, 666–669. <https://doi.org/10.1126/science.1066854>
- Crisp, M. D., Laffan, S., Linder, H. P., & Monro, A. (2001). Endemism in the Australian flora. *Journal of Biogeography*, 28, 183–198. <https://doi.org/10.1046/j.1365-2699.2001.00524.x>
- Cruz, C. G., López, M. L., Villaseñor, J. L., & Ortiz, E. (2014). Potential species distribution modeling and the use of principal component analysis as predictor variables. *Revista Mexicana de Biodiversidad*, 85, 189–199. <https://doi.org/10.7550/rmb.36723>
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Daru, B. H., Elliott, T. L., Park, D. S., & Davies, T. J. (2017). Understanding the processes underpinning patterns of phylogenetic regionalization. *Trends in Ecology & Evolution*, 32, 845–860. <https://doi.org/10.1016/j.tree.2017.08.013>
- Daskin, J. H., & Pringle, R. M. (2018). Warfare and wildlife declines in Africa's protected areas. *Nature*, 553, 328–332. <https://doi.org/10.1038/nature25194>
- de Klerk, H. M., Crowe, T. M., Fjeldsá, J., & Burgess, N. D. (2002). Patterns of species richness and narrow endemism of terrestrial bird species in the Afrotropical region. *Journal of Zoology (London)*, 256, 327–342.
- De la Estrella, M., Mateo, R. G., Wieringa, J. J., Mackinder, B., & Muñoz, J. (2012). Legume diversity patterns in west Central Africa: Influence of species biology on distribution models. *PLoS One*, 7, e41526. <https://doi.org/10.1371/journal.pone.0041526>
- Deb, C., Jamir, N., & Kikon, Z. (2017). Distribution prediction model of a rare orchid species (*Vanda bicolor* Griff.) using small sample size. *American Journal of Plant Sciences*, 8, 1388–1398. <https://doi.org/10.4236/ajps.2017.86094>
- Dennis, R. L. H., Shreeve, T. G., & Williams, W. R. (1998). Faunal structures among European butterflies: Evolutionary implications of bias for geography, endemism and taxonomic affiliation. *Ecography*, 21, 181–203. <https://doi.org/10.1111/j.1600-0587.1998.tb00672.x>
- Dervo, B. K., Bærum, K. M., Skurdal, J., & Museth, J. (2016). Effects of temperature and precipitation on breeding migrations of amphibian species in southeastern Norway. *Scientifica*, 2016, 1–8. <https://doi.org/10.1155/2016/3174316>
- Duellman, W. E., & Trueb, L. (1994). *Biology of amphibians*. Johns Hopkins University Press.
- Duivenvoorden, J., Svenning, J.-C., & Wright, S. (2002). Beta diversity in tropical forests. *Science*, 295, 636–637. <https://doi.org/10.1126/science.295.5555.636>
- Elith, J. (2002). Quantitative methods for modeling species habitat: Comparative performance and an application to Australian plants. In S. Ferson & M. Burgman (Eds.), *Quantitative methods for conservation biology* (pp. 39–58). Springer.
- Elith, J., & Leathwick, J. (2009). Conservation prioritisation using species distribution modelling. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritization: Quantitative methods and computational tools*. Oxford University Press.
- Ernst, C., Verheggen, A., Mayaux, P., Hansen, M., & Defourny, P. (2012). Central African forest cover and forest cover change mapping. In C. de Wasseige (Ed.), *The forests of The Congo basin – State of the forest 2010* (p. 276). Publications Office of the European Union.
- Farooq, H., Azevedo, J. A. R. A., Soares, A., Antonelli, A., & Faurby, S. (2021). Mapping Africa's biodiversity: More of the same is just not good enough. *Systematic Biology*, 70(3), 623–633. <https://doi.org/10.1093/sysbio/syaa090>
- Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity & Distributions*, 13, 252–264. <https://doi.org/10.1111/j.1472-4642.2007.00341.x>
- Ficetola, G. F., & Maiorano, L. (2016). Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance. *Oecologia*, 181, 683–693. <https://doi.org/10.1007/s00442-016-3610-9>
- Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology and Evolution*, 1, 0089. <https://doi.org/10.1038/s41559-016-0089>
- Fitzpatrick, M. C., Sanders, N. J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A. D., & Dunn, R. R. (2013). Environmental and historical imprints on beta diversity: Insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768), 20131201. <https://doi.org/10.1098/rspb.2013.1201>
- Fjeldså, J., & Lovett, J. C. (1997). Geographical patterns of old and young species in African forest biota: The significance of specific montane

- areas as evolutionary centres. *Biodiversity and Conservation*, 6, 325–346. <https://doi.org/10.1023/A:1018356506390>
- Förderer, M., Rödder, D., & Langer, M. R. (2018). Patterns of species richness and the center of diversity in modern indo-Pacific larger foraminifera. *Scientific Reports*, 8, 8189. <https://doi.org/10.1038/s41598-018-26598-9>
- Gámez, N., Nihei, S. S., Scheinvar, E., & Morrone, J. J. (2017). A temporally dynamic approach for cladistic biogeography and the processes underlying the biogeographic patterns of north American deserts. *Journal of Zoological Systematics and Evolutionary Research*, 55, 11–18. <https://doi.org/10.1111/jzs.12142>
- García, A., Ortega-Huerta, M. A., & Martínez-Meyer, E. (2014). Potential distributional changes and conservation priorities of endemic amphibians in western Mexico as a result of climate change. *Environmental Conservation*, 41(1), 1–12. <https://doi.org/10.1017/S0376892913000349>
- Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and process in macroecology*. Blackwell Science.
- Gaston, K. J., Davies, R. G., Orme, C. D. L., Olson, V. A., Thomas, G. H., Ding, T. S., Rasmussen, P. C., Lennon, J. J., Bennett, P. M., Owens, I. P. F., & Blackburn, T. M. (2007). Spatial turnover in the global avifauna. *Proceedings of the Royal Society of London B*, 274, 1567–1574. <https://doi.org/10.1098/rspb.2007.0236>
- Global Forest Watch. (2023). World Resources Institute. <http://www.globalforestwatch.org> Accessed 23 January 2023.
- Geist, H. J., & Lambin, E. F. (2002). Proximate causes and underlying driving forces of tropical deforestation. *Bioscience*, 52, 143–150. [https://doi.org/10.1641/0006-3568\(2002\)052\[0143:PCAUDF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0143:PCAUDF]2.0.CO;2)
- Gentry, A. H. (1982). Neotropical floristic diversity: Phytogeographical connections between central and South America, pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, 69(3), 557–593. <https://doi.org/10.2307/2399084>
- Graham, C. H., & Hijmans, R. J. (2006). A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography*, 15, 578–587. <https://doi.org/10.1111/j.1466-8238.2006.00257.x>
- Guerin, G. R., Ruokolainen, L., & Lowe, A. J. (2015). A georeferenced implementation of weighted endemism. *Methods in Ecology and Evolution*, 6, 845–852. <https://doi.org/10.1111/2041-210X.12361>
- Guo, K., Yuan, S., Wang, H., Zhong, J., Wu, Y., Chen, W., Hu, C., & Chang, Q. (2021). Species distribution models for predicting the habitat suitability of Chinese fire-bellied newt *Cynops orientalis* under climate change. *Ecology and Evolution*, 11, 10147–10154. <https://doi.org/10.1002/ece3.7822>
- Hardy, O. J., Born, C., Budde, K., Dainou, K., Dauby, G., Duminil, J., Ewédjé, E. B. K., Gomez, C., Heuert, M., Koffi, G. K., Lowe, A. J., Micheneau, C., Ndiaye-Bourabou, D., Piñeiro, R., & Poncet, V. (2013). Comparative phylogeography of African rain forest trees: A review of genetic signatures of vegetation history in the Guineo-Congolian region. *Comptes Rendus Geoscience*, 345(7–8), 284–296.
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. <https://doi.org/10.1890/03-8006>
- Heinze, G., Wallisch, C., & Dunkler, D. (2018). Variable selection – A review and recommendations for the practicing statistician. *Biometrical Journal*, 60(3), 431–449. <https://doi.org/10.1002/bimj.201700067>
- Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, 29, 773–785. <https://doi.org/10.1111/j.2006.0906-7590.04700.x>
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211. <https://doi.org/10.1086/381004>
- Hillman, S. S., Withers, P. C., Drewes, R. C., & Hillyard, S. D. (2009). *Ecological and environmental physiology of amphibians*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198570325.001.0001>
- Huang, X. L., Lei, F. M., & Qiao, G. X. (2008). Areas of endemism and patterns of diversity for aphids of the Qinghai-Tibetan plateau and the Himalayas. *Journal of Biogeography*, 35, 230–240. <https://doi.org/10.1111/j.1365-2699.2007.01776.x>
- Huang, X. L., Qiao, G. X., & Lei, F. M. (2010). Use of parsimony analysis to identify areas of endemism of Chinese birds: Implications for conservation and biogeography. *International Journal of Molecular Sciences*, 11, 2097–2108. <https://doi.org/10.3390/ijms11052097>
- Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America*, 103(27), 10334–10339. <https://doi.org/10.1073/pnas.0601928103>
- Huntley, J. W., Keith, K. D., Castellanos, A. A., Musher, L. J., & Voelker, G. (2019). Underestimated and cryptic diversification patterns across afro-tropical lowland forests. *Journal of Biogeography*, 46, 381–391. <https://doi.org/10.1111/jbi.13505>
- Jansson, R. (2003). Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society of London B*, 270, 583–590. <https://doi.org/10.1098/rspb.2002.2283>
- Jiménez-Robles, O., Guayasamin, J. M., Ron, S. R., & De la Riva, I. (2017). Reproductive traits associated with species turnover of amphibians in Amazonia and its Andean slopes. *Ecology and Evolution*, 7, 2489–2500. <https://doi.org/10.1002/ece3.2862>
- Kafash, A., Ashrafi, S., Yousefi, M., Rastegar-Pouyani, E., Rajabzadeh, M., Ahmadzadeh, F., Grünig, M., & Pellissier, L. (2020). Reptile species richness associated to ecological and historical variables in Iran. *Scientific Reports*, 10, 18167. <https://doi.org/10.1038/s41598-020-74867-3>
- Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. <https://doi.org/10.1038/sdata.2017.122>
- Kazmaier, R. T., Helligren, E. E., & Ruthven, D. C. (2002). Home range and dispersal of Texas tortoises, *Gopherus berlandieri*, in a managed thorn-scrub ecosystem. *Chelonian Conservation Biology*, 4, 488–496.
- Kier, G., & Barthlott, W. (2001). Measuring and mapping endemism and species richness: A new methodological approach and its application on the flora of Africa. *Biodiversity and Conservation*, 10, 1513–1529. <https://doi.org/10.1023/A:1011812528849>
- Kier, G., Holger, K., Lee, M. T., Jetz, W., Ibsch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America*, 106(23), 9322–9327. <https://doi.org/10.1073/pnas.0810306106>
- Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 104(14), 5925–5930. <https://doi.org/10.1073/pnas.0608361104>
- Kreft, H., & Jetz, W. (2010). A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, 37, 2029–2053. <https://doi.org/10.1111/j.1365-2699.2010.02375.x>
- Krishnan, S., Crosby, C., Nandigam, V., Phan, M., Cowart, C., Baru, C., & Arrowsmith, R. (2011). OpenTopography: A services oriented architecture for community access to LIDAR topography. In *Proceedings of the 2nd international conference on computing for Geospatial Research & Applications* (pp. 7:1–7:8). ACM.
- Küper, W., Sommer, J. H., Lovett, J. C., Mutke, J., Linder, H. P., Beentje, H. J., Van Rompaey, R. S. A. R., Chatelain, C., Sosef, M., & Barthlott, W. (2004). Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden*, 91(4), 525–535.

- Lamoreux, J., Morrison, J., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W., & Shuga, H. H. (2006). Global tests of biodiversity concordance and the importance of endemism. *Nature*, 440, 212–214. <https://doi.org/10.1038/nature04291>
- Leprieux, F., Olden, J. D., Lek, S., & Brosse, S. (2009). Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography*, 36, 1899–1912. <https://doi.org/10.1111/j.1365-2699.2009.02107.x>
- Lewin, A., Feldman, A., Bauer, A. M., Belmaker, J., Broadley, D. G., Chirio, L., Itescu, Y., LeBreton, M., Maza, E., Meirte, D., Nagy, Z. T., Novosolov, M., Roll, U., Tallowin, O., Trape, J.-F., Vidan, E., & Meiri, S. (2016). Patterns of species richness, endemism and environmental gradients of African reptiles. *Journal of Biogeography*, 43, 2380–2390. <https://doi.org/10.1111/jbi.12848>
- Linares-Palomino, R., & Kessler, M. (2009). The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography*, 36(2), 280–290. <https://doi.org/10.1111/j.1365-2699.2008.02028.x>
- Linder, H. P. (2001). On areas of endemism, with an example from the African Restionaceae. *Systematic Biology*, 50, 892–912. <https://doi.org/10.1080/106351501753462867>
- Linder, H. P., de Klerk, H. M., Born, J., Burgess, N. D., Fjeldså, J., & Rahbek, C. (2012). The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, 39, 1189–1372. <https://doi.org/10.1111/j.1365-2699.2012.02728.x>
- Linder, H. P., Lovett, J., Mutke, J. M., Barthlott, W., Juergens, N., Rebelo, T., & Kueper, W. (2005). A numerical Re-evaluation of the sub-Saharan Phytocoria of mainland Africa. *Biologische Skrifter*, 55, 229–252.
- Maldonado, C., Molina, C. I., Zizka, A., Persson, C., Taylor, C. M., Albán, J., Chilquillo, E., Rønsted, N., & Antonelli, A. (2015). Species diversity and distribution in the era of big data. *Global Ecology and Biogeography*, 24, 973–984. <https://doi.org/10.1111/geb.12326>
- Maley, J. (1996). The African rain forest: Main characteristics of changes in vegetation and climate from the upper cretaceous to the quaternary. In I. J. Alexander, M. D. Swaine, & R. Watling (Eds.), *Essays on the ecology of the Guinea-Congo rain forest* (Vol. 104, pp. 31–73). Proceedings of the Royal Society of Edinburgh. Section B.
- Malhi, Y., Adu-Bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). African rainforests: Past, present and future. *Philosophical Transactions of the Royal Society B*, 368, 20120312. <https://doi.org/10.1098/rstb.2012.0312>
- McRae, L., Deinet, S., & Freeman, R. (2017). The diversity-weighted living planet index: Controlling for taxonomic bias in a global biodiversity indicator. *PLoS One*, 12(1), e0169156. <https://doi.org/10.1371/journal.pone.0169156>
- MEA. (2005). *Millennium ecosystem assessment synthesis report* (pp. 1–219). Millennium Ecosystem Assessment.
- Miaud, C., & Sanuy, D. (2005). Terrestrial habitat preferences of the natterjack toad during and after the breeding season in a landscape of intensive agricultural activity. *Amphibia-Reptilia*, 26, 359–366.
- Milanovich, J. R., Peterman, W. E., Nibbelink, N. P., & Maerz, J. C. (2010). Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. *PLoS One*, 5, e12189. <https://doi.org/10.1371/journal.pone.0012189>
- Miller, D. A. W., Campbell Grant, E. H., Muths, E., Amburgey, S. M., Adams, M. J., Maxwell, H., Waddle, M. B., Johnson, P. T. J., Ryan, M. E., Schmidt, B. R., Calhoun, D. L., Davis, C. L., Fisher, R. N., Green, D. M., Hossack, B. R., Rittenhouse, T., Walls, S. C., Bailey, L. L., Cruickshank, S. S., ... Sigafus, B. (2018). Quantifying climate sensitivity and climate-driven change in north American amphibian communities. *Nature Communications*, 9, 3926. <https://doi.org/10.1038/s41467-018-06157-6>
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeck, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., ... Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, 10, 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>
- Mohr, C. O. (1947). Table of equivalent populations of north American small mammals. *American Midland Naturalist*, 37, 223–249.
- Morrone, J. J. (2014). Biogeographical regionalisation of the neotropical region. *Zootaxa*, 3782, 1–110. <https://doi.org/10.11646/zootaxa.3782.1.1>
- Murali, G., Gumbs, R., Meiri, S., & Roll, U. (2021). Global determinants and conservation of evolutionary and geographic rarity in land vertebrates. *Science Advances*, 7(42), 1–14. <https://doi.org/10.1126/sciadv.abe5582>
- Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for ecological niche models. *Methods in Ecology and Evolution*, 5, 1198–1205. <https://doi.org/10.1111/2041-210X.12261>
- Mutke, J., & Barthlott, W. (2005). Patterns of vascular plant diversity at continental to global scales. *Biologische Skrifter*, 55, 521–538.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>
- Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37, 191–203. <https://doi.org/10.1111/j.1600-0578.2013.02205.x>
- Nenzen, H. K., & Araujo, M. B. (2011). Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling*, 222, 3346–3354. <https://doi.org/10.1016/j.ecolmodel.2011.07.011>
- Nneji, L. M., Adeola, A. C., Okeyoyin, A. O., Oladipo, O. C., Saidu, Y., Samuel, D., Usongo, J. Y., Adediji, B. E., Omotoso, O., Adeyi, A. O., Ugwumba, O. A., & Ugwumba, A. A. A. (2019). Diversity and distribution of amphibians and reptiles in Gashaka Gumti National Park, Nigeria. *Herpetology Notes*, 12, 543–599.
- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P., & Schneeweiss, G. M. (2018). Hotspots within a global biodiversity hotspot-areas of endemism are associated with high mountain ranges. *Scientific Reports*, 8, 10345.
- Olden, J. D., & Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, 15, 113–120. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>
- Oliveira, U., Paglia, A. P., Brescovit, A. D., de Carvalho, C. J. B., Silva, D. P., Rezende, D. T., Leite, F. S. F., Batista, J. A. N., Barbosa, J. P. P. P., Stehmann, J. R., Ascher, J. S., de Vasconcelos, M. F., De Marco Jr, P., Löwenberg-Neto, P., Dias, P. G., Ferro, V. G., & Santos, A. J. (2016). The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. *Diversity and Distributions*, 22, 1232–1244. <https://doi.org/10.1111/ddi.12489>
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience*. *Diversity and Distributions*, 51(11), 933–938.
- Orme, C. D., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J., & Owens, I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019. <https://doi.org/10.1038/nature03850>
- Ota, H. (1998). Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu archipelago, Japan, with special

- reference to their paleogeographical implications. *Researches on Population Ecology*, 40, 189–204. <https://doi.org/10.1007/BF02763404>
- Pearson, D. L., & Cassola, F. (1992). World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): Indicator taxon for biodiversity and conservation studies. *Conservation Biology*, 6, 376–391. <https://doi.org/10.1046/j.1523-1739.1992.06030376.x>
- Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Peterson, A. T. (2006). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34(1), 102–117. <https://doi.org/10.1111/j.1365-2699.2006.01594.x>
- Penner, J., Wegmann, M., Hillers, A., Schmidt, M., & Rödel, M.-O. (2011). A hotspot revisited—a biogeographical analysis of west African amphibians. *Diversity and Distributions*, 17, 1077–1088. <https://doi.org/10.1111/J.1472-4642.2011.00801.X>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Plana, V. (2004). Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. *Philosophical Transactions of the Royal Society B Biological Sciences*, 359, 1585–1594. <https://doi.org/10.1098/rstb.2004.1535>
- Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eliu, G., Segawa, P., Ewango, C., & Kahindo, C. (2004, 2004). Albertine rift. In R. A. Mittermeier, P. Robles Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, & G. A. B. Da Fonseca (Eds.), *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions* (pp. 255–262). CEMEX.
- Portik, D. M., Leaché, A. D., Rivera, D., Barej, M. F., Burger, M., Hirschfeld, M., & Fujita, M. K. (2017). Evaluating mechanisms of diversification in a Guineo-Congolian tropical forest frog using demographic model selection. *Molecular Ecology*, 26, 5245–5263. <https://doi.org/10.1111/mec.14266>
- Powney, G. D., & Isaac, N. J. B. (2015). Beyond maps: A review of the applications of biological records. *Biological Journal of the Linnean Society*, 115, 532–542. <https://doi.org/10.1111/bij.12517>
- Prendergast, J. R., & Eversham, B. C. (1997). Species richness covariance in higher taxa: Empirical tests of the biodiversity indicator concept. *Ecography*, 20, 210–216. <https://doi.org/10.1111/j.1600-0587.1997.tb00363.x>
- Qian, H. (2009). Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution*, 47, 509–514. <https://doi.org/10.1111/j.1759-6831.2009.00043.x>
- Qian, H. (2010). Environment-richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. *Ecological Research*, 25, 629–637.
- Qian, H., Badgley, C., & Fox, D. L. (2009). The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography*, 18, 111–122. <https://doi.org/10.1111/j.1466-8238.2008.00415.x>
- Qian, H., & Ricklefs, R. E. (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, 10(8), 737–744. <https://doi.org/10.1111/j.1461-0248.2007.01066.x>
- Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 8, 15–22. <https://doi.org/10.1111/j.1461-0248.2004.00682.x>
- Qian, H., Wang, X., Wang, S., & Li, Y. (2007). Environmental determinants of amphibian and reptile species richness in China. *Ecography*, 30(4), 471–482. <https://doi.org/10.1111/j.0906-7590.2007.05025.x>
- Rahbek, C., Borregaard, M. K., Antonelli, A., Colwell, R. K., Holt, B. G., Nogués-Bravo, D., Rasmussen, C. M., Richardson, K., Rosing, M. T., Whittaker, R. J., & Fjeldså, J. (2019). Building mountain biodiversity: Geological and evolutionary processes. *Science*, 365, 1114–1119. <https://doi.org/10.1126/science.aax015>
- Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23–27.
- Rodríguez, P., & Arita, H. T. (2004). Beta diversity and latitude in north American mammals: Testing the hypothesis of covariation. *Ecography*, 27, 547–545. <https://doi.org/10.1111/j.0906-7590.2004.03788.x>
- Rohr, J. R., Civitello, D. J., Cohen, J. M., Roznik, E. A., Sinervo, B., & Dell, A. I. (2018). The complex drivers of thermal acclimation and breadth in ectotherms. *Ecology Letters*, 21, 1425–1439. <https://doi.org/10.1111/ele.13107>
- Rosauer, D. F., & Jetz, W. (2015). Phylogenetic endemism in terrestrial mammals. *Global Ecology and Biogeography*, 24, 168–179. <https://doi.org/10.1111/geb.12237>
- Row, J. R., & Blouin-Demers, G. (2006). Kernels are not accurate estimators of home-range size for Herpetofauna. *Copeia*, 4, 797–802.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., & Svenning, J.-C. (2011). The influence of late quaternary climate-change velocity on species endemism. *Science*, 334, 660–664. <https://doi.org/10.1126/science.1210173>
- Schall, J. J., & Pianka, E. R. (1978). Geographical trends in numbers of species. *Science*, 201, 679–686. <https://doi.org/10.1126/science.121.4357.679>
- Shiple, B. R., & McGuire, J. L. (2023). Disentangling the drivers of continental mammalian endemism. *Global Change Biology*, 00, 1–15. <https://doi.org/10.1111/gcb.16628>
- Soares, C., & Brito, J. C. (2007). Environmental correlates for species richness among amphibians and reptiles in a climate transition area. *Biodiversity and Conservation*, 16, 1087–1102. <https://doi.org/10.1007/s10531-006-9070-5>
- Sosef, M. S. M., Dauby, G., Blach-Overgaard, A., van der Burgt, X., Catarino, L., Damen, T., Deblauwe, V., Desein, S., Dransfield, J., & Droissart, V. (2017). Exploring the floristic diversity of tropical Africa. *BMC Biology*, 15, 1–23. <https://doi.org/10.1186/s12915-017-0356-8>
- Steinitz, O., Heller, J., Tsoar, A., Rotem, D., & Kadmon, R. (2006). Environment, dispersal and patterns of species similarity. *Journal of Biogeography*, 33, 1044–1054. <https://doi.org/10.1111/j.1365-2699.2006.01473.x>
- Storch, D., Davies, R. G., Zajiček, S., Orme, C. D. L., Olson, V., Thomas, G. H., Blackburn, T. M., Owens, I. P. F., & Gaston, K. J. (2006). Energy, range dynamics and global species richness patterns: Reconciling mid-domain effects and environmental determinants of avian diversity. *Ecology Letters*, 9, 1308–1320. <https://doi.org/10.1111/j.1461-0248.2006.00984.x>
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306, 1783–1786. <https://doi.org/10.1126/science.1103538>
- Tang, Z., Fang, J., Chi, X., Yang, Y., Ma, W., Mohhamot, A., Guo, Z., Liu, Y., & Gaston, K. J. (2012). Geography, environment, and spatial turnover of species in China's grasslands. *Ecography*, 35, 1103–1109. <https://doi.org/10.1111/j.1600-0587.2012.07713.x>
- Terribile, L. C., Diniz-Filho, J. A. F., Rodríguez, M. Á., & Range, T. F. L. V. B. (2009). Richness patterns, species distributions and the principle of extreme deconstruction. *Global Ecology and Biogeography*, 18, 123–136. <https://doi.org/10.1111/j.1466-8238.2008.00440.x>
- Tuomisto, H., Poulsen, A. D., Ruokolainen, K., Moran, R. C., Quintana, C., Celi, J., & Cañas, G. (2003). Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications*, 13, 352–371. [https://doi.org/10.1890/1051-0761\(2003\)013\[0352:LFPWSH\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0352:LFPWSH]2.0.CO;2)
- Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 241–244. <https://doi.org/10.1126/science.1078037>
- Ulrich, W., & Gotelli, N. J. (2007). Null model analysis of species nestedness patterns. *Ecology*, 88, 1824–1831.

- Urbina-Cardona, J. N., & Loyola, R. D. (2008). Applying niche-based models to predict endangered-Hylid potential distributions: Are Neotropical protected areas effective enough? *Tropical Conservation Science*, 1(4), 417–445. <https://doi.org/10.1177/194008290800100408>
- van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, 39(6), 542–552. <https://doi.org/10.1111/ecog.01509>
- Vié, J. C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2009). *Wildlife in a changing world: An analysis of the 2008 IUCN red list of threatened species*. IUCN.
- Wagner, H. H., & Fortin, M.-J. (2015). Basics of spatial data analysis: Linking landscape and genetic data for landscape genetic studies. In N. Balkenhol, S. A. Cushman, A. T. Storfer, & L. P. Waits (Eds.), *Landscape genetics* (pp. 77–98). Wiley.
- Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, 105(Suppl 1), 11466–11473. <https://doi.org/10.1073/pnas.0801921105>
- Watson, J. W., McAllister, K. R., & Pierce, D. J. (2003). Home ranges, movements and habitat selection of Oregon spotted frogs (*Rana pretiosa*). *Journal of Herpetology*, 37, 292–300.
- Wells, K. D. (2007). *The ecology and behavior of amphibians*. University of Chicago Press.
- White, F. (1979). The Guineo-Congolian region and its relationships to other *Phytochoria*. *Bulletin du Jardin Botanique National de Belgique*, 49, 11–55. <https://doi.org/10.2307/3667815>
- White F. (1983). The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa Unesco/AETFAT/UNSO, Copedith, Paris.
- Whitfield, P. (1984). *Macmillan illustrated animal encyclopedia*. Macmillan Publishing Co., Inc.
- Williams, P. H., De Klerk, H. M., & Crowe, T. M. (1999). Interpreting biogeographical boundaries among Afrotropical birds: Spatial patterns in richness gradients and species replacement, in Afrotropical birds. *Journal of Biogeography*, 26, 459–474. <https://doi.org/10.1046/j.1365-2699.1999.00294.x>
- Wright, D. H., & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia*, 92, 416–4–8–416–4–428.
- Ye, P., Zhang, G., Zhao, X., Chen, H., Si, Q., & Wu, J. (2021). Potential geographical distribution and environmental explanations of rare and endangered plant species through combined modeling: A case study of Northwest Yunnan, China. *Ecology and Evolution*, 11, 13052–13067. <https://doi.org/10.1002/ece3.7999>
- Zizka, A., Azevedo, J., Leme, E., Neves, B., da Costa, A. F., Caceres, D., & Zizka, G. (2020). Biogeography and conservation status of the pineapple family (Bromeliaceae). *Diversity and Distributions*, 26(2), 183–195. <https://doi.org/10.1111/ddi.13004>
- Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Ritter, C. D., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengstron, N., Zizka, V., & Antonelli, A. (2019). Coordinate cleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, 10, 744–751. <https://doi.org/10.1111/2041-210X.13152>
- Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Aroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., ... Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, 43, 1261–1277. <https://doi.org/10.1111/ecog.04960>

BIOSKETCH

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SUPPORTING INFORMATION

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