Global patterns of body size evolution are driven by precipitation in legless amphibians

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Abstract

Body size shapes ecological interactions across and within species, ultimately influencing the evolution of large-scale biodiversity patterns. Therefore, macroecological studies of body size provide a link between spatial variation in selection regimes and the evolution of animal assemblages through space. Multiple hypotheses have been formulated to explain the evolution of spatial gradients of animal body size, predominantly driven by thermal (Bergmann's rule), humidity ('water conservation hypothesis'), and resource constraints ('resource rule', 'seasonality rule') on physiological homeostasis. However, while integrative tests of all four hypotheses combined are needed, the focus of such empirical efforts needs to move beyond the traditional endotherm-ectotherm dichotomy, to instead interrogate the role that variation in lifestyles within major lineages (e.g., Classes) play in creating neglected scenarios of selection via analyses of largely overlooked environment-body size interactions. Here, we test all four rules above using a global database spanning 99% of modern species of an entire Order of legless, predominantly underground-dwelling amphibians (Gymnophiona, or caecilians). We found a consistent effect of increasing precipitation (and resource abundance) on body size reductions (supporting the water conservation hypothesis), while Bergmann's, the seasonality and resource rules are rejected. We argue that subterranean lifestyles minimize the effects of aboveground selection agents, making humidity a dominant selection pressure – aridity promotes larger body sizes that reduce risk of evaporative dehydration, while smaller sizes occur in wetter environments where dehydration constraints are relaxed. We discuss the links between these principles with the physiological constraints that may have influenced the tropically-restricted global radiation of caecilians.

Keywords: Bergmann's rule, resource rule, seasonality rule, water conservation hypothesis, body size, caecilians, Gymnophiona

Introduction

The evolution of predictable geographic patterns of trait distribution across animal species is one of the most intriguing features of biodiversity (Gaston & Blackburn, 2000). Variation in fecundity, longevity, metabolic rates, and diversification are shaped by spatial gradients in natural selection (Brown *et al.*, 2004; Scharf *et al.*, 2015; Pincheira-Donoso & Hunt, 2017; Schluter & Pennell, 2017). Importantly, the dependence of these traits on environmental factors is intrinsically influenced by body size, which varies through space (Peters, 1983; Smith & Lyons, 2013). Therefore, understanding the role of environment-body size relationships in the evolution of biodiversity patterns is a primary ambition in macroecology (Gaston *et al.*, 2008). For nearly two centuries, a range of 'ecogeographic rules' have aimed to elucidate the drivers behind geographic patterns of body size evolution. The leading rule, Bergmann's rule – increases in body sizes toward colder climates as greater body mass, relative to surface area, reduces heat loss (Bergmann, 1847) – has set the theoretical benchmark for research on large-scale patterns of animal size (James, 1970; Blackburn *et al.*, 1999; Meiri & Dayan, 2003). However, evidence from across the animal kingdom reveals that Bergmann's rule tends to hold in endotherms (Freckleton *et al.*, 2003; Meiri & Dayan, 2003; de Queiroz & Ashton, 2004; Olson *et al.*, 2009; but see Riemer *et al.*, 2018), while its validity is inconsistent in ectotherms (Ashton & Feldman, 2003; Olalla-Tarraga *et al.*, 2006; Olalla-Tarraga & Rodriguez, 2007; Pincheira-Donoso *et al.*, 2007, 2008; Adams & Church, 2008; Pincheira-Donoso & Meiri, 2013; Feldman & Meiri, 2014; Moreno-Azocar *et al.*, 2015; Amado *et al.*, 2019; Slavenko *et al.*, 2019). These discrepancies have discredited temperature as a primary driver of body size clines (Pincheira-Donoso, 2010; Meiri, 2011; Olalla-Tarraga, 2011). Essentially, while larger body size optimises preservation of endothermic metabolic heat, the dependence of ectotherms on external sources of heat requires them to gain body heat in the first place (Ashton & Feldman, 2003; Olalla-Tarraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008).

As a result, macroecological theories of animal size have explored alternative sources of selection as drivers of body size evolution. The roles that resource abundance and humidity play in metabolic and physiological homeostasis as functions of body size (Rosenzweig, 1968; Yom-Tov & Nix, 1986; Brown & Sibly, 2006; McNab, 2010), have led to the formulation of a range of competing hypotheses: (*i*) the 'resource rule', suggests that increasing resource abundance (primary productivity) relaxes the constraints on upper limits of body size, permitting the evolution of larger species (Rosenzweig, 1968; Geist, 1987; Yom-Tov & Geffen, 2006; McNab, 2010), while not selecting against small body sizes. The mechanisms are potentially multiple. For example, more productive areas may facilitate energy investment into body growth without a trade-off with reproduction (Roff, 2002; McNab, 2010). Also, in poorly productive regions (e.g., deserts), fitness can benefit from reductions in resource requirements via smaller body size (McNab, 2010); (*ii*) The ‘water conservation hypothesis’ (WCH), predicts stronger selection for larger size towards arid environments, given that rates of desiccation decrease with increasing body mass (Nevo, 1973; Olalla-Tarraga *et al.*, 2009; Gouveia & Correia, 2016). This may be especially prevalent in organisms prone to dehydration, such as amphibians. Importantly, the WCH’s predictions conflict with the resource rule. First, the WCH predicts larger size in arid regions, while the resource rule predicts larger size in productive (usually wet) areas. Also, such predictions are sensitive to thermoregulation (ectothermy vs endothermy), body structures (e.g., skin permeability), and lifestyle (e.g., habitat) among lineages, because factors such as energetic requirements and osmoregulation are expected to influence the adaptive trajectories of body size. For example, while heat production implies high metabolic expenditure of energy for endotherms, the dependence of ectotherms on environmental heat neutralises such pressures (Brown *et al.*, 2004; Angilletta, 2009); finally (*iii*) the ‘seasonality (or ‘fasting-endurance’) rule’, predicts that increasing seasonality selects for increased body size to enhance tolerance to unstable environments (Lindsey, 1966; Boyce, 1979; Calder, 1984). Given the contrasting mechanisms that these hypotheses offer to explain the same phenomenon, evidence supporting them has been conflicting across lineages (Meiri *et al.*, 2005; Yom-Tov & Geffen, 2006; Olalla-Tarraga & Rodriguez, 2007; Olalla-Tarraga *et al.*, 2009; Oufiero *et al.*, 2011; Pincheira-Donoso & Meiri, 2013; Gouveia & Correia, 2016; Kelly *et al.*, 2018; Amado *et al.*, 2019). Furthermore, our understanding of body size macroecology has fundamentally been advanced based on above-ground organisms, while analyses on fossorial lineages remain anecdotal (e.g., Meiri & Dayan, 2003; Measey & Van Dongen, 2006; Feldman & Meiri, 2014).

We employ the most comprehensive global dataset of caecilian amphibians (Order Gymnophiona) to date, to test the core predictions of the above four rules. Caecilians are tropically widespread amphibians that combine peculiar features expected to alter the way selection from environmental factors operates on homeostasis relative to most tetrapods (Vitt & Caldwell, 2014). They have elongated, legless bodies that predominantly occupy underground microhabitats (“fossoriality”; Pough *et al.*, 2015) that offer relatively stable thermal environments isolated from multiple pressures that operate above-ground (Buffenstein & Jarvis, 2002; Wells, 2007; Healy *et al.*, 2014). Their skins are also highly permeable, which intensifies selection from climatic factors (Steele & Louw, 1988; Wells, 2007). Our study thus provides the most comprehensive analysis of the classic and emerging hypotheses underlying body size evolution rules.

Material and Methods

Species data

We gathered an exhaustive global-scale dataset on caecilians spanning body size data for >99% (207 out of 208; Suppl. Table 1) of the world's known species. We followed the taxonomy in Frost (2018). To investigate the above set of hypotheses, we used the largest recorded total body length (from snout to tail tip) as the proxy for body size, as this is the most commonly reported measure of size for caecilians (Wells, 2007; Pough *et al.*, 2015). Data were collected from the primary literature (which includes all species described recently) and from monographic books (Suppl. Material 2). In addition, we created an environmental dataset (see below), extracted from distribution maps, for 93% of the species – 40 of which were originally created as part of this study (Fig. 1; Suppl. Table 1). This dataset is part of XXX (details blinded following requirements from the Editorial Office – to be disclosed upon acceptance).

Environmental predictors

To investigate the role of environmental factors as drivers of geographic variation in body size across caecilians, we created a dataset covering a range of candidate predictors representing geographic location, climate and primary productivity. To extract these data, we first obtained maps of extant known geographic distribution for all species available at the IUCN archive (www.iucnredlist.org). We created maps for 40 species for which this information was unavailable, by collecting the geographic position system (GPS) coordinates provided in the papers in which they were described. In some cases, these records are only available for the specimens officially assigned to the type series, while additional existing records are only shown in maps. In those cases, we obtained the exact GPS position of each additional point in the published maps using Google Earth Pro. This protocol resulted in a dataset covering 191 caecilian species (92% of their global diversity). The remaining species were not mapped because their distributions remain unknown, unclear or inadequately described. To create a species-level dataset of environmental and geographic predictors, we assigned to each species a single value per predictor, calculated as the average of all values obtained by dividing the geographic range polygon of each variable for each species into 2.5 arc-minute grid cells (~5x5 kilometres) using ArcGIS 10.0.

Firstly, we used latitude (in degrees from the Equator) given its classical status as geographic predictor. Latitude data were extracted as the midpoint from each individual species map. Second, a set of climatic predictors were obtained from the WorldClim 2 (www.worldclim.org) archive (Hijmans *et al.*, 2005; Fick & Hijmans, 2017), and are expressed at a spatial resolution of 2.5 arc-minutes (~5 km at the equator). These data are the result of collections of monthly measurements of multiple bioclimatic variables conducted between 1950-2000 by a large number of scattered weather stations around the world, and interpolated for areas of poorer coverage (Hijmans *et al.*, 2005). The climatic variables consist of mean annual temperature (averaged across the 12 months of the year, in degrees Celsius), temperature seasonality (calculated as the SD of the annual mean temperature x100, in degrees Celsius), mean annual precipitation (the amount of rainfall measured in millimetres a year), and precipitation seasonality (coefficient of variation of monthly precipitation across the year). Finally, we used net primary productivity (NPP, the net amount of solar energy converted to plant organic matter through photosynthesis – measured in units of elemental carbon per year, on a spatial resolution of 0.25°, gC/m^2/yr, log transformed) as a proxy for resource availability (Imhoff *et al.*, 2004). These data were then assigned to each caecilian species in our dataset, and all extractions of variables and their visualization on climatic maps (Figure 1; Supplementary Material 3) were performed using ArcGIS software version 10.0 (www.esri.com).

Quantitative analyses and phylogenetic control

We performed phylogenetic regressions to investigate the role of environmental factors in shaping spatial gradients of caecilian body size. We first tested for latitudinal gradients in body size by regressing log-transformed total body length against (absolute) latitude. Although latitude is a classic 'catch-all' predictor in macroecology, it represents a proxy for a set of environmental conditions that vary through space. Therefore, we further performed phylogenetic univariate and multiple regressions of log(body size) per species against environmental temperature (mean and seasonal range), annual precipitation (mean and seasonal range), and NPP. This series of regression analyses were subsequently repeated for the American (predominantly South American) assemblage of caecilians, as it concentrates 48% of the world's species (the rest being spread throughout the global tropics; Fig. 1). Similarly, the analyses were further repeated for all caecilians excluding the family Typhlonectidae (a clade of large, aquatic species; Wells, 2007; Pough *et al.*, 2015), to directly address our core questions on fossorial species only, and then for the Typhlonectidae only. In all analyses, predictors were log-transformed and then scaled to have zero mean and unit variance. While log-transformation provided the best model checks of homogeneity of variance and normality of residuals, scaling prevented any instability of regression models caused by the inclusion of explanatory variables measured on different scales and with values far from the intercept. We performed the univariate regressions to demonstrate what conclusions might be drawn from naïve analyses of single environmental factors, and to confirm the robustness of the multiple regression results. We then considered the significance of the explanatory variables in a full multiple regression of their main effects (i.e. excluding interactions among explanatory variables), as a direct comparison of the relevance of temperature (classical heat-conservation mechanism for Bergmann's rule), the NPP (as a proxy for the resource rule) and the effects of rainfall on body size (as predicted by the WCH and the seasonality rule). For all analyses we used Akaike's Information

Criterion (AIC) to compete the information content of rival models. For univariate regressions, each explanatory variable was considered important if its regression lay >2 AIC units below the null model.

To further assess the multiple regressions, we performed multi-model inference analyses. We used AIC and Akaike model weights to reduce the whole set of models employing a dredging approach that retains a confidence subset of models that lay within 6 AIC units of the most informative model. This method removes models that have spurious parameter estimates due to poor model fit above the chosen AIC threshold (Richards, 2005; Harrison *et al.*, 2018). The importance of each explanatory variable was judged according to AIC-weighted mean effect sizes averaged across the subset of regression models, and are presented as AIC-weighted slope estimates +/- 95% confidence intervals to estimate the significance of the effect of each predictor on body size (Table 1). This procedure is robust given that information is contained in well-fitting but non-optimal models for parameter estimates (with confidence intervals), which would, in contrast, be lost with a single best-fit model (i.e., a step-wise approach) (Burnham *et al.*, 2011). These analyses were performed using the package 'MuMIn' (Barton, 2017) implemented in R (R Development Core Team, 2017).

All regression models included phylogenetic control. We employed Jetz & Pyron's (2018) phylogeny, from which we extracted all 183 caecilians species (88% of the Order's diversity) for which geographic, and hence environmental, data are available (Supplementary Table 1). We tested the significance of the value of Pagel's lambda, which measures the influence of shared evolutionary history on the divergence of regression residuals among species (Pagel, 1999). Phylogenetic regressions were performed using the 'ape' (Paradis *et al.*, 2004) and 'nlme' (Pinheiro *et al.*, 2018) packages in R.

Results

Body size varies considerably across caecilians, ranging from 112mm in the smallest species (*Grandisonia brevis* and *Microcaecilia iwokramae*), to over 1,600mm in the largest (*Caecilia guntheri*; Figs. 1, 2; Supplementary Table S1). The frequency distribution of raw body size across species is significantly right-skewed (Shapiro-Wilk's test, $W = 0.77$, $df = 206$, $P<0.001$; Fig. 2), which remains significantly right-skewed in the log-transformed data ($W = 0.97$, $df = 206$, $P<0.001$; Fig. 2).

Latitudinal gradients of body size

Our analyses failed to identify a signal for latitude in shaping the distribution of caecilian body sizes either globally or in the new world (Table 1; Fig. 3). The same analyses repeated for America, and for fossorial and aquatic caecilians separately, showed qualitatively identical results (Table 1). All findings remained consistent with and without phylogenetic control.

Environmental predictors of body size

Our phylogenetic regression analyses incorporating environmental variables revealed consistently high degrees of phylogenetic signal in model residuals, with Pagel's lambda of 0.57 for the multiple regression with all predictors (ΔAIC=96.2 comparing model with optimised lambda to a model with lambda fixed to zero). Regarding tests of the four core rules, our analyses based on the global dataset revealed that body sizes across species decrease with increasing annual precipitation, supporting the WCH (Table 1; Fig. 3). Likewise, analyses performed for fossorial and aquatic families separately revealed significant increases in body size at drier regions among underground-dweller species, in both the multiple and the univariate models (while the analyses restricted to aquatic caecilians failed to identify any significant predictors of body size variation). In contrast, measures of temperature, productivity and seasonality (either in temperature or in rainfall) showed no effect on body size variation (Table 1; Fig. 3), rejecting the three competing hypotheses. The univariate global model showed a nearly significant role for NPP as a driver of body size variation, but the relationship is negative, in opposition to the resource rule (Table 1; Fig. 3). These findings remained consistent across multi- and univariate regression analyses, which retained decreases in annual precipitation as the only significant predictor of larger body sizes through space (Table 1; Fig. 3). The models restricted to American caecilians failed to show effects for any of the predictors (the univariate model revealed a marginally non-significant effect of NPP on body size gradients. However, consistent with the global univariate model, the relationship is negative, thus conflicting with the core prediction of the resource rule). None of the models identified either measures of temperature as predictors of body size variation, rejecting Bergmann's rule and the heat-conservation mechanism (Table 1).

Discussion

Our study provides global-scale evidence supporting the WCH in an entire Order of predominantly fossorial tetrapods, while it reinforces the limited generality of Bergmann's rule and its alternatives (Blackburn *et al.*, 1999; Olalla-Tarraga *et al.*, 2009; Pincheira-Donoso, 2010), especially among ectotherms. In contrast with predictions from classic macroecological rules (Bergmann, 1847; James, 1970; Blackburn *et al.*, 1999; McNab, 2010), our analyses failed to identify a role for temperature, resource abundance, seasonality or latitude as drivers of caecilian body size gradients. Instead, we show that decreases in precipitation significantly constrain the minimum ‘viable’ body size for fossorial (but not for aquatic) species, favouring larger sizes as aridity increases. Thus, in contrast with the positive relationship between precipitation (as a prevailing driver of resource abundance) and body size predicted by the resource rule (Yom-Tov & Geffen, 2006; McNab, 2010), the relationship we observed is the opposite, with wetter environments correlating positively with NPP but favouring smaller body sizes (and the only analysis that identified NPP as a marginally non-significant predictor is negatively correlated with body size, opposing the resource rule; Table 1). Macroecological studies on amphibians have revealed highly conflicting evidence for a role of temperature as an agent of spatial gradients in body size (Feder *et al.*, 1982; Ashton, 2002; Olalla-Tarraga & Rodriguez, 2007; Adams & Church, 2008; Cvetkovic *et al.*, 2009), and the only known study on caecilians, on one species, showed a link with elevation (Measey & Van Dongen, 2006). In contrast, the role of water-deprivation as a source of selection for larger body size as an adaptation to reduce rates of evapotranspiration has increasingly gained support (Olalla-Tarraga *et al.*, 2009; Gouveia & Correia, 2016; Amado *et al.*, 2019). Our evidence, stemming from a complete coverage of caecilians, strongly supports the hypothesis that increases in body size are promoted by aridity – in particular among non-aquatic species, which reinforces the functional role of water conservation. Consequently, we suggest an explanation that relies on the hydroregulatory advantages of larger body size in water-deprived environments, and the life history advantages emerging in environments in which selection from humidity is relaxed.

Natural selection from precipitation and the macroecology of body size

Although our results identified precipitation as the only significant driver of geographic gradients of body size in caecilians, the observed negative relationship between precipitation (or NPP) and body size is incompatible with the prediction of the resource rule. Essentially, although selection from resource availability affects body size across animals in general (in different directions depending on whether abundance is low or high), such effects are expected to differ between endotherms and ectotherms given their differences in metabolic demands (Angilletta, 2009). Indeed, the production of constant, high body heat in endotherms is ‘exceedingly’ costly (Angilletta, 2009), being thus implicated in the evolution of most life history adaptations (Stearns, 1992; Brown & Sibly, 2006; Angilletta, 2009). In contrast, such resource-intensive thermoregulation is not an issue in ectotherms (Meiri *et al.*, 2013). Hence, we suggest that the global macroecology of caecilian body sizes is caused by a relaxation of selection from water-deprivation on body size as species occupy wetter environments, consistent with the WCH. Towards the dry extreme of the wetness spectrum, the evolution of larger body size reduces relative rates of water loss. We suggest that for fossorial amphibians, such as most caecilians, the levels of soil moisture are a primary source of selection on body size mediated by the need to maintain stable levels of body water. Caecilians have especially high rates of evaporative water loss through the body surface (Wells, 2007) compared to other vertebrates, including amphibians, which is thought to constrain them to their fossorial lifestyles (Steele & Louw, 1988; Wells, 2007). Even the ‘dermal scales’ that cover the skin of caecilians do not seem to reduce rates of water loss (Wells, 2007), having instead a role in underground locomotion (Duellman & Trueb, 1994; Wells, 2007). Therefore, as wetness declines, the lower bound of body size is progressively constrained towards larger body mass for hydric homeostasis, leading to the prediction that towards drier environments the minimum level of body size across species increases. The same principle could potentially affect selection on offspring size.

On the other hand, towards the wet end of the spectrum, where hydroregulatory constraints that force caecilians to remain above a ‘minimum viable’ body size are gradually relaxed as humidity increases, selection is predicted to maximise life history pace via body size reductions. In line with this view, mass-specific rates of life history productivity (e.g., faster production of offspring biomass) and metabolism have been shown to consistently increase as body size decreases (Peters, 1983; Brown & Sibly, 2006; Sibly & Brown, 2007; Meiri *et al.*, 2012). Given that fitness can be defined as birth rates minus death rates (Brown & Sibly, 2006), this scaling principle is expected to express particularly when lifestyle minimises mortality rates (e.g., via reduced predation). Fossorial lifestyles, in particular, buffer the intensity of selection from climatic and ecological pressures (Buffenstein & Jarvis, 2002; Sibly & Brown, 2007; Healy *et al.*, 2014). Therefore, the fitness gains resulting from increases of productivity are expected to drive adaptive evolution of smaller body sizes in caecilians as hydroregulatory constraints are relaxed towards wetter environments.

Body plan and the global radiation of caecilians

The hypothesis that body size adjusts along humidity gradients to maximise hydric homeostasis might shed light on the conditions that have underlain the global radiation of these amphibians. Traditionally, the body mass to surface area ratio has been employed to explain decreasing heat loss rates as body size increases, being therefore favoured towards colder climates (i.e., Bergmann’s rule; James, 1970; Blackburn *et al.*, 1999). However, the thermodynamic efficiency of this relationship strongly depends on the body plan of a lineage. For example, in vertebrates with ‘regular’, legged body plans, the efficiency of increases of body mass in reducing heat loss are straightforward. In contrast, in lineages characterized by disproportionately elongated and narrow body plans (such as caecilians, but also snakes and amphisbaenians), the mass-to-surface hypothesis loses strength as increasing body elongation results in proportional increases in surface area. Therefore, we suggest that an elongated body plan intrinsically facilitates water loss, and hence, the 'naked' amphibian skin of caecilians is expected to only be viable in humid environments. Thus, according to this hypothesis, the radiation of caecilians across increasingly drier environments would demand body mass increases proportional to aridity, which is likely to have been historically prevented by the physical restrictions of their underground lifestyles. Consequently, this is a potential explanation why caecilians are confined to wet environments, compared to the higher levels of environmental tolerance of anurans and salamanders.

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TABLES AND FIGURES

Table 1: Results of multiple and univariate phylogenetic regressions (under the PGLS part of the table), and multi-model inference of caecilian body size against environmental predictors. Phylogenetic regressions all revealed significant phylogenetic signal, with Pagel's lambda ranging between 0.55-0.83 in all models. Significant relationships are in boldface. Geographic (i.e., latitude as predictor) and environmental analyses performed separately.

	PGLS				Univariate Models		Multivariate Models	
Predictors	λ	R^2	*F*(df)	*P*	Slope	95% CI (Lower, Upper)	Slope	95% CI (Lower, Upper)
Global Models								
Latitude	**0.581**	0.002	0.28 (1,181)	0.60	0.037	(-0.054, 0.128)	–	–
Multivariate Model (Environ)[a]	**0.579**	0.05	1.72 (5, 177)	0.13	–	–	–	–
Mean Precipitation	**0.594**	0.03	5.29 (1,181)	**0.02**	**-0.064**	**(-0.120, -0.009)**	**-0.061**	**(-0.122, -0.000)**
Precipitation Seasonality	**0.563**	0.003	0.51 (1,181)	0.48	-0.021	(-0.080, 0.037)	-0.043	(-0.108, 0.022)
Mean Temperature	**0.568**	0.01	1.20 (1,181)	0.27	-0.029	(-0.082, 0.023)	-0.015	(-0.071, 0.041)
Temperature Seasonality	**0.581**	0.01	1.36 (1,181)	0.25	0.034	(-0.024, 0.092)	0.030	(-0.042, 0.102)
Net Primary Productivity	**0.605**	0.02	2.91 (1,181)	0.09	-0.051	(-0.111, 0.008)	-0.038	(-0.105, 0.029)
America Models								
Latitude	**0.593**	0.001	0.07 (1,88)	0.79	0.01	(-0.069, 0.091)	–	–
Multivariate Model (Environ)[a]	**0.615**	0.11	2.09 (5,84)	0.08	–	–	–	–
Mean Precipitation	**0.622**	0.03	2.33 (1,88)	0.13	-0.17	(-0.386, 0.047)	-0.20	(-0.469, 0.059)
Precipitation Seasonality	**0.576**	0.03	2.53 (1, 88)	0.12	-0.15	(-0.336, 0.039)	-0.19	(-0.399, 0.012)
Mean Temperature	**0.584**	0.01	0.5 (1,88)	0.48	-0.17	(-0.648, 0.313)	-0.05	(-0.577, 0.478)
Temperature Seasonality	**0.600**	0.01	0.81 (1,88)	0.37	0.21	(-0.244, 0.659)	0.12	(-0.376, 0.621)
Net Primary Productivity	**0.590**	0.04	3.95 (1,88)	0.05	-0.48	(-0.959, 0.001)	-0.46	(-0.966, 0.035)
Fossorial Species Models								
Latitude	**0.581**	0.003	0.54 (1,170)	0.47	0.02	(-0.034, 0.075)	–	–
Multivariate Model (Environ)[a]	**0.561**	0.06	2.07 (5,166)	0.07	–	–	–	–
Mean Precipitation	**0.590**	0.04	6.52 (1,170)	**0.01**	**-0.19**	**(-0.329, -0.043)**	**-0.18**	**(-0.328, -0.031)**
Precipitation Seasonality	**0.561**	0.003	0.44 (1,170)	0.51	-0.04	(-0.154, 0.079)	-0.08	(-0.209, 0.059)
Mean Temperature	**0.561**	0.01	1.54 (1,170)	0.22	-0.22	(-0.567, 0.132)	-0.15	(-0.527, 0.226)
Temperature Seasonality	**0.579**	0.01	1.94 (1,170)	0.17	0.15	(-0.060, 0.353)	0.12	(-0.125, 0.372)
Net Primary Productivity	**0.603**	0.02	3.04 (1,170)	0.08	-0.24	(-0.515, 0.029)	-0.20	(-0.501, 0.098)

Aquatic Species Models								
Latitude	**0.709**	0.04	0.41 (1,9)	0.54	-0.03	(-0.151, 0.086)	–	–
Multivariate Model (Environ)[a]	**1.000**	0.82	4.62 (5,5)	0.06	–	–	–	–
Mean Precipitation	**0.488***	0.11	1.11 (1,9)	0.32	0.14	(-0.263, 0.538)	0.12	(-0.329, 0.560)
Precipitation Seasonality	**1.000**	0.31	4.12 (1,9)	0.07	-0.05	(-0.250, 0.151)	-0.05	(-0.250, 0.151)
Mean Temperature	**0.671**	0.01	0.07 (1,9)	0.79	0.10	(-1.125, 1.332)	0.10	(-1.125, 1.332)
Temperature Seasonality	**0.519**	0.25	3.06 (1,9)	0.11	-0.52	(-1.262, 0.213)	-0.42	(-0.911, 0.070)
Net Primary Productivity	**0.889**	0.10	1.01 (1,9)	0.34	-0.34	(-0.796, 0.116)	-0.34	(-0.784, 0.113)

[a] This multivariate model combines all five environmental predictors, and excludes latitude.

FIGURE LEGENDS

Figure 1. Global distribution of caecilians. The maps show (A) the distribution of caecilian species-richness (the colour gradient shows variation in the number of coexisting species in the same area, as per the values shown in the vertical bar), and (B) the geographic distribution of median body sizes per grid cell (colour gradients along the horizontal bar displays variation in caecilian body sizes on the map).

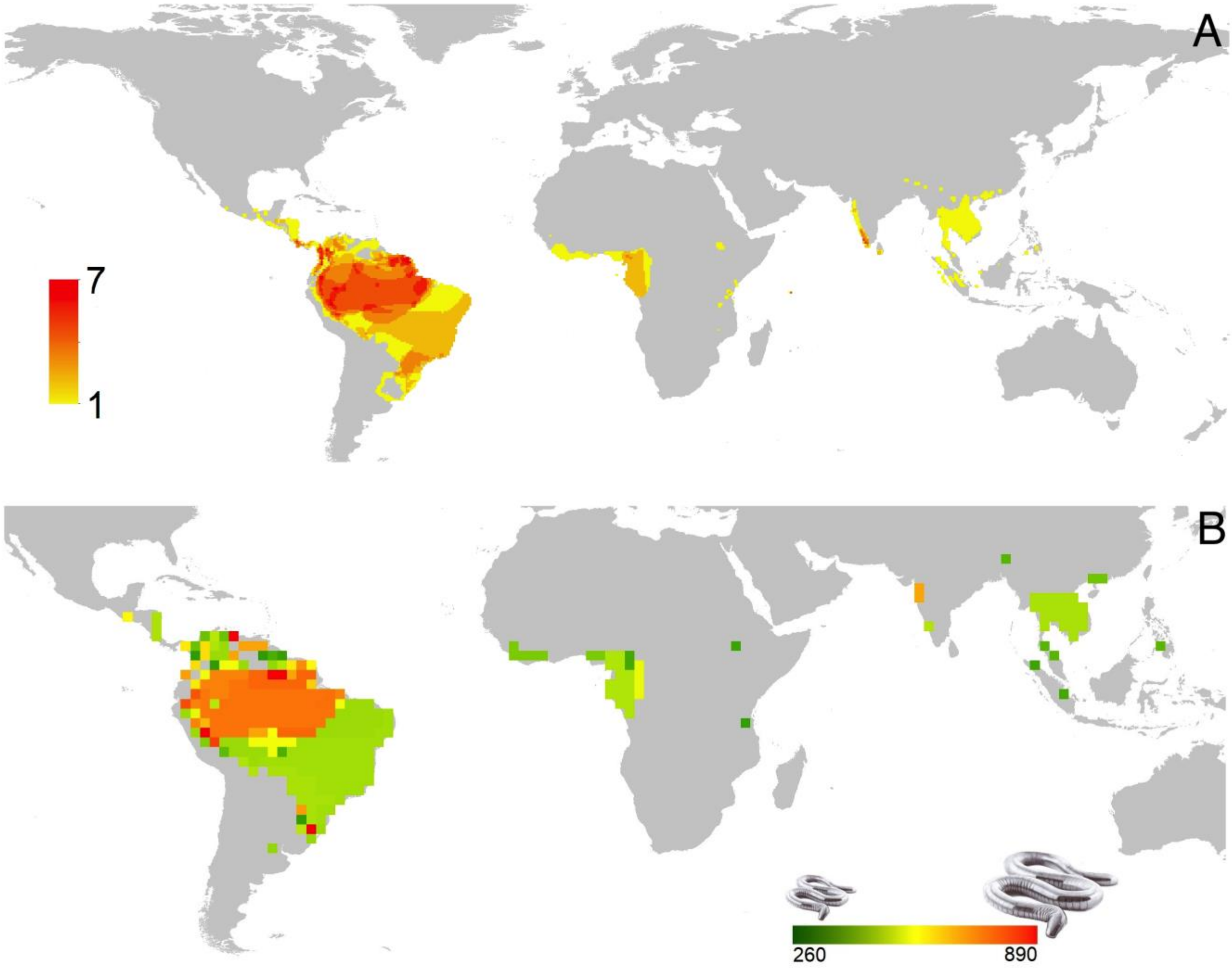

Figure 2. Frequency distribution of caecilian body sizes. Distributions expressed as raw body length (A) and as log-transformed body length (B).

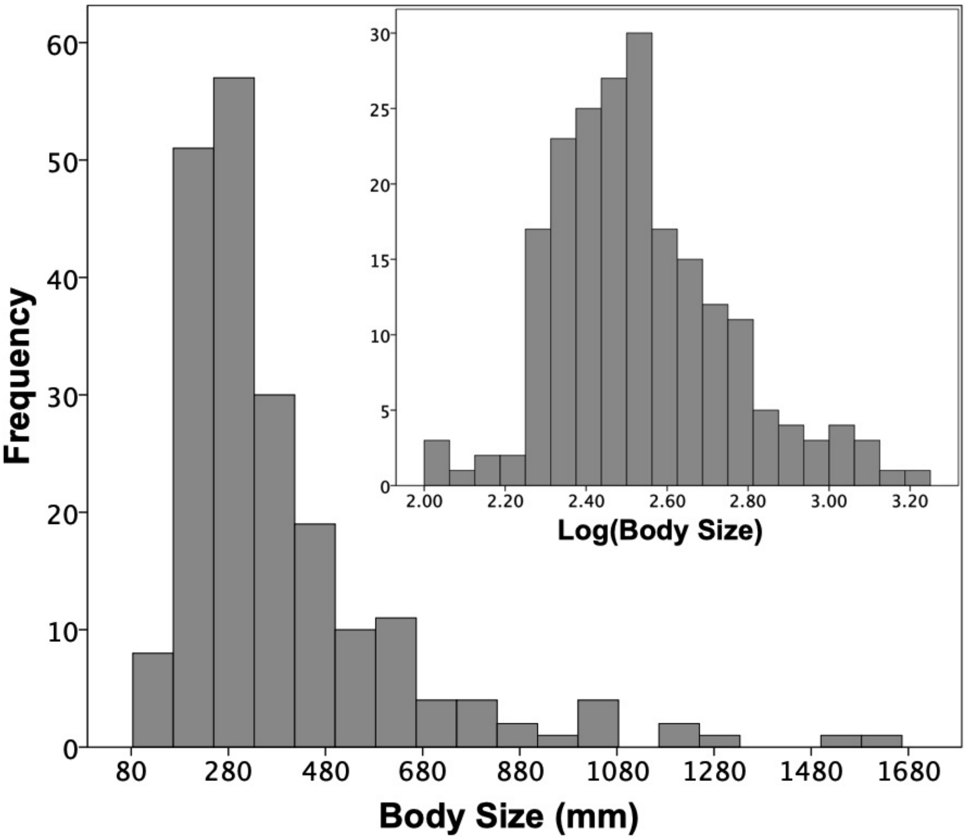

Figure 3. Slopes of phylogenetic regression of log-transformed caecilian body size against log-transformed environmental predictors scaled to zero mean and unit standard deviation in all three analyses, points represent AIC-weighted average slope parameters, and whiskers are 95% confidence intervals. When confidence intervals span zero, the slopes are considered non-significant. Black points and confidence whiskers represent model-averaged slopes from a full multiple regression of body size against environmental parameters. Red points and confidence whiskers represent the slopes of univariate regressions of body size against each environmental predictor.