

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

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4 **Running head:** Macroecology of body size in caecilians

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Abstract

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

51

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

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55 Introduction

56 The evolution of predictable geographic patterns of trait distribution across animal species is one of the most
57 intriguing features of biodiversity (Gaston & Blackburn, 2000). Variation in fecundity, longevity, metabolic
58 rates, and diversification are shaped by spatial gradients in natural selection (Brown *et al.*, 2004; Scharf *et*
59 *al.*, 2015; Pincheira-Donoso & Hunt, 2017; Schluter & Pennell, 2017). Importantly, the dependence of these
60 traits on environmental factors is intrinsically influenced by body size, which varies through space (Peters,
61 1983; Smith & Lyons, 2013). Therefore, understanding the role of environment-body size relationships in the
62 evolution of biodiversity patterns is a primary ambition in macroecology (Gaston *et al.*, 2008). For nearly two
63 centuries, a range of 'ecogeographic rules' have aimed to elucidate the drivers behind geographic patterns of
64 body size evolution. The leading rule, Bergmann's rule – increases in body sizes toward colder climates as
65 greater body mass, relative to surface area, reduces heat loss (Bergmann, 1847) – has set the theoretical
66 benchmark for research on large-scale patterns of animal size (James, 1970; Blackburn *et al.*, 1999; Meiri &
67 Dayan, 2003). However, evidence from across the animal kingdom reveals that Bergmann's rule tends to
68 hold in endotherms (Freckleton *et al.*, 2003; Meiri & Dayan, 2003; de Queiroz & Ashton, 2004; Olson *et al.*,
69 2009; but see Riemer *et al.*, 2018), while its validity is inconsistent in ectotherms (Ashton & Feldman, 2003;
70 Olalla-Tarraga *et al.*, 2006; Olalla-Tarraga & Rodriguez, 2007; Pincheira-Donoso *et al.*, 2007, 2008; Adams
71 & Church, 2008; Pincheira-Donoso & Meiri, 2013; Feldman & Meiri, 2014; Moreno-Azocar *et al.*, 2015;
72 Amado *et al.*, 2019; Slavenko *et al.*, 2019). These discrepancies have discredited temperature as a primary
73 driver of body size clines (Pincheira-Donoso, 2010; Meiri, 2011; Olalla-Tarraga, 2011). Essentially, while
74 larger body size optimises preservation of endothermic metabolic heat, the dependence of ectotherms on
75 external sources of heat requires them to gain body heat in the first place (Ashton & Feldman, 2003; Olalla-
76 Tarraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008).

77 As a result, macroecological theories of animal size have explored alternative sources of selection
78 as drivers of body size evolution. The roles that resource abundance and humidity play in metabolic and
79 physiological homeostasis as functions of body size (Rosenzweig, 1968; Yom-Tov & Nix, 1986; Brown &
80 Sibly, 2006; McNab, 2010), have led to the formulation of a range of competing hypotheses: (i) the 'resource
81 rule', suggests that increasing resource abundance (primary productivity) relaxes the constraints on upper
82 limits of body size, permitting the evolution of larger species (Rosenzweig, 1968; Geist, 1987; Yom-Tov &
83 Geffen, 2006; McNab, 2010), while not selecting against small body sizes. The mechanisms are potentially
84 multiple. For example, more productive areas may facilitate energy investment into body growth without a
85 trade-off with reproduction (Roff, 2002; McNab, 2010). Also, in poorly productive regions (e.g., deserts),
86 fitness can benefit from reductions in resource requirements via smaller body size (McNab, 2010); (ii) The

87 'water conservation hypothesis' (WCH), predicts stronger selection for larger size towards arid environments,
88 given that rates of desiccation decrease with increasing body mass (Nevo, 1973; Olalla-Tarraga *et al.*, 2009;
89 Gouveia & Correia, 2016). This may be especially prevalent in organisms prone to dehydration, such as
90 amphibians. Importantly, the WCH's predictions conflict with the resource rule. First, the WCH predicts larger
91 size in arid regions, while the resource rule predicts larger size in productive (usually wet) areas. Also, such
92 predictions are sensitive to thermoregulation (ectothermy vs endothermy), body structures (e.g., skin
93 permeability), and lifestyle (e.g., habitat) among lineages, because factors such as energetic requirements
94 and osmoregulation are expected to influence the adaptive trajectories of body size. For example, while heat
95 production implies high metabolic expenditure of energy for endotherms, the dependence of ectotherms on
96 environmental heat neutralises such pressures (Brown *et al.*, 2004; Angilletta, 2009); finally (*iii*) the
97 'seasonality (or 'fasting-endurance') rule', predicts that increasing seasonality selects for increased body size
98 to enhance tolerance to unstable environments (Lindsey, 1966; Boyce, 1979; Calder, 1984). Given the
99 contrasting mechanisms that these hypotheses offer to explain the same phenomenon, evidence supporting
100 them has been conflicting across lineages (Meiri *et al.*, 2005; Yom-Tov & Geffen, 2006; Olalla-Tarraga &
101 Rodriguez, 2007; Olalla-Tarraga *et al.*, 2009; Oufiero *et al.*, 2011; Pincheira-Donoso & Meiri, 2013; Gouveia
102 & Correia, 2016; Kelly *et al.*, 2018; Amado *et al.*, 2019). Furthermore, our understanding of body size
103 macroecology has fundamentally been advanced based on above-ground organisms, while analyses on
104 fossorial lineages remain anecdotal (e.g., Meiri & Dayan, 2003; Measey & Van Dongen, 2006; Feldman &
105 Meiri, 2014).

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

115

116 **Material and Methods**

117 ***Species data***

118 We gathered an exhaustive global-scale dataset on caecilians spanning body size data for >99% (207 out of
119 208; Suppl. Table 1) of the world's known species. We followed the taxonomy in Frost (2018). To investigate
120 the above set of hypotheses, we used the largest recorded total body length (from snout to tail tip) as the
121 proxy for body size, as this is the most commonly reported measure of size for caecilians (Wells, 2007;
122 Pough *et al.*, 2015). Data were collected from the primary literature (which includes all species described
123 recently) and from monographic books (Suppl. Material 2). In addition, we created an environmental dataset
124 (see below), extracted from distribution maps, for 93% of the species – 40 of which were originally created
125 as part of this study (Fig. 1; Suppl. Table 1). This dataset is part of XXX (details blinded following
126 requirements from the Editorial Office – to be disclosed upon acceptance).

127

128 ***Environmental predictors***

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

143 Firstly, we used latitude (in degrees from the Equator) given its classical status as geographic
144 predictor. Latitude data were extracted as the midpoint from each individual species map. Second, a set of
145 climatic predictors were obtained from the WorldClim 2 (www.worldclim.org) archive (Hijmans *et al.*, 2005;
146 Fick & Hijmans, 2017), and are expressed at a spatial resolution of 2.5 arc-minutes (~5 km at the equator).
147 These data are the result of collections of monthly measurements of multiple bioclimatic variables conducted
148 between 1950-2000 by a large number of scattered weather stations around the world, and interpolated for
149 areas of poorer coverage (Hijmans *et al.*, 2005). The climatic variables consist of mean annual temperature

150 (averaged across the 12 months of the year, in degrees Celsius), temperature seasonality (calculated as the
151 SD of the annual mean temperature x100, in degrees Celsius), mean annual precipitation (the amount of
152 rainfall measured in millimetres a year), and precipitation seasonality (coefficient of variation of monthly
153 precipitation across the year). Finally, we used net primary productivity (NPP, the net amount of solar energy
154 converted to plant organic matter through photosynthesis – measured in units of elemental carbon per year,
155 on a spatial resolution of 0.25°, gC/m²/yr, log transformed) as a proxy for resource availability (Imhoff *et al.*,
156 2004). These data were then assigned to each caecilian species in our dataset, and all extractions of
157 variables and their visualization on climatic maps (Figure 1) were performed using ArcGIS software version
158 10.0 (www.esri.com).

159

160 ***Quantitative analyses and phylogenetic control***

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

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

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

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

202

203 **Results**

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

209

210 ***Latitudinal gradients of body size***

211 Our analyses failed to identify a signal for latitude in shaping the distribution of caecilian body sizes either
212 globally or in the new world (Table 1; Fig. 3). The same analyses repeated for America, and for fossorial and

213 aquatic caecilians separately, showed qualitatively identical results (Table 1). All findings remained
214 consistent with and without phylogenetic control.

215

216 ***Environmental predictors of body size***

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

236

237 **Discussion**

238 Our study provides global-scale evidence supporting the WCH in an entire Order of predominantly fossorial
239 tetrapods, while it reinforces the limited generality of Bergmann's rule and its alternatives (Blackburn *et al.*,
240 1999; Olalla-Tarraga *et al.*, 2009; Pincheira-Donoso, 2010), especially among ectotherms. In contrast with
241 predictions from classic macroecological rules (Bergmann, 1847; James, 1970; Blackburn *et al.*, 1999;
242 McNab, 2010), our analyses failed to identify a role for temperature, resource abundance, seasonality or
243 latitude as drivers of caecilian body size gradients. Instead, we show that decreases in precipitation

244 significantly constrain the minimum 'viable' body size for fossorial (but not for aquatic) species, favouring
245 larger sizes as aridity increases. Thus, in contrast with the positive relationship between precipitation (as a
246 prevailing driver of resource abundance) and body size predicted by the resource rule (Yom-Tov & Geffen,
247 2006; McNab, 2010), the relationship we observed is the opposite, with wetter environments correlating
248 positively with NPP but favouring smaller body sizes (and the only analysis that identified NPP as a
249 marginally non-significant predictor is negatively correlated with body size, opposing the resource rule; Table
250 1). [Macroecological studies on amphibians have revealed highly conflicting evidence for a role of](#)
251 [temperature as an agent of spatial gradients in body size \(Feder *et al.*, 1982; Ashton, 2002; Olalla-Tarraga &](#)
252 [Rodriguez, 2007; Adams & Church, 2008; Cvetkovic *et al.*, 2009\), and the only known study on caecilians,](#)
253 [on one species, showed a link with elevation \(Measey & Van Dongen, 2006\). In contrast, the role of water-](#)
254 [deprivation as a source of selection for larger body size as an adaptation to reduce rates of](#)
255 [evapotranspiration has increasingly gained support \(Olalla-Tarraga *et al.*, 2009; Gouveia & Correia, 2016;](#)
256 [Amado *et al.*, 2019\). Our evidence, stemming from a complete coverage of caecilians, strongly supports the](#)
257 [hypothesis that increases in body size are promoted by aridity – in particular among non-aquatic species,](#)
258 [which reinforces the functional role of water conservation. Consequently, we suggest an explanation that](#)
259 [relies on the hydroregulatory advantages of larger body size in water-deprived environments, and the life](#)
260 [history advantages emerging in environments in which selection from humidity is relaxed.](#)

261

262 ***Natural selection from precipitation and the macroecology of body size***

263 Although our results identified precipitation as the only significant driver of geographic gradients of body size
264 in caecilians, the observed negative relationship between precipitation (or NPP) and body size is
265 incompatible with the prediction of the resource rule. Essentially, although selection from resource availability
266 affects body size across animals in general (in different directions depending on whether abundance is low
267 or high), such effects are expected to differ between endotherms and ectotherms given their differences in
268 metabolic demands (Angilletta, 2009). Indeed, the production of constant, high body heat in endotherms is
269 'exceedingly' costly (Angilletta, 2009), being thus implicated in the evolution of most life history adaptations
270 (Stearns, 1992; Brown & Sibly, 2006; Angilletta, 2009). In contrast, such resource-intensive thermoregulation
271 is not an issue in ectotherms (Meiri *et al.*, 2013). Hence, we suggest that the global macroecology of
272 caecilian body sizes is caused by a relaxation of selection from water-deprivation on body size as species
273 occupy wetter environments, consistent with the WCH. Towards the dry extreme of the wetness spectrum,
274 the evolution of larger body size reduces relative rates of water loss. We suggest that for fossorial
275 amphibians, such as most caecilians, the levels of soil moisture are a primary source of selection on body

276 size mediated by the need to maintain stable levels of body water. Caecilians have especially high rates of
277 evaporative water loss through the body surface (Wells, 2007) compared to other vertebrates, including
278 amphibians, which is thought to constrain them to their fossorial lifestyles (Steele & Louw, 1988; Wells,
279 2007). Even the 'dermal scales' that cover the skin of caecilians do not seem to reduce rates of water loss
280 (Wells, 2007), having instead a role in underground locomotion (Duellman & Trueb, 1994; Wells, 2007).
281 Therefore, as wetness declines, the lower bound of body size is progressively constrained towards larger
282 body mass for hydric homeostasis, leading to the prediction that towards drier environments the minimum
283 level of body size across species increases. The same principle could potentially affect selection on offspring
284 size.

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

296

297 ***Body plan and the global radiation of caecilians***

298 The hypothesis that body size adjusts along humidity gradients to maximise hydric homeostasis might shed
299 light on the conditions that have underlain the global radiation of these amphibians. Traditionally, the body
300 mass to surface area ratio has been employed to explain decreasing heat loss rates as body size increases,
301 being therefore favoured towards colder climates (i.e., Bergmann's rule; James, 1970; Blackburn *et al.*,
302 1999). However, the thermodynamic efficiency of this relationship strongly depends on the body plan of a
303 lineage. For example, in vertebrates with 'regular', legged body plans, the efficiency of increases of body
304 mass in reducing heat loss are straightforward. In contrast, in lineages characterized by disproportionately
305 elongated and narrow body plans (such as caecilians, but also snakes and amphisbaenians), the mass-to-
306 surface hypothesis loses strength as increasing body elongation results in proportional increases in surface
307 area. Therefore, we suggest that an elongated body plan intrinsically facilitates water loss, and hence, the

308 'naked' amphibian skin of caecilians is expected to only be viable in humid environments. Thus, according to
 309 this hypothesis, the radiation of caecilians across increasingly drier environments would demand body mass
 310 increases proportional to aridity, which is likely to have been historically prevented by the physical
 311 restrictions of their underground lifestyles. Consequently, this is a potential explanation why caecilians are
 312 confined to wet environments, compared to the higher levels of environmental tolerance of anurans and
 313 salamanders.

314

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476 **TABLES AND FIGURES**

477 **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
 478 environmental predictors. Phylogenetic regressions all revealed significant phylogenetic signal, with Pagel’s lambda ranging between 0.55-0.83 in all models.
 479 Significant relationships are in boldface. Geographic (i.e., latitude as predictor) and environmental analyses performed separately.

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Predictors	PGLS				Univariate Models		Multivariate Models	
	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)

481 ^aThis multivariate model combines all five environmental predictors, and excludes latitude.

482 **FIGURE LEGENDS**

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

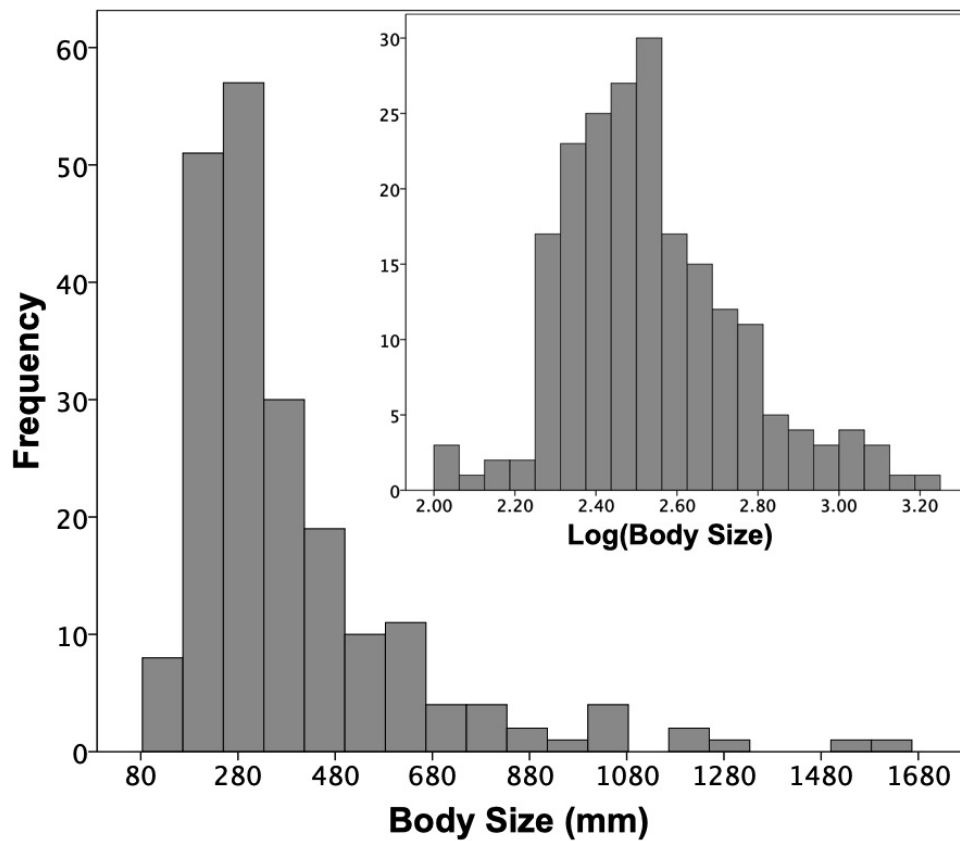
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490 **Figure 2.** Frequency distribution of caecilian body sizes. Distributions expressed as raw body length (A) and
491 as log-transformed body length (B).

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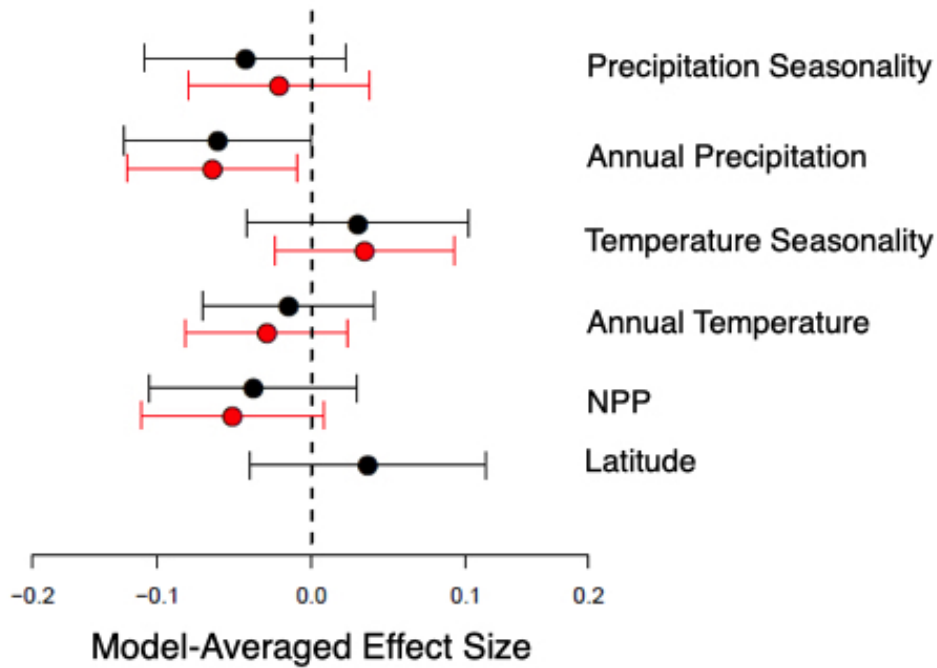
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500 **Figure 3.** Slopes of phylogenetic regression of log-transformed caecilian body size against log-transformed
 501 environmental predictors scaled to zero mean and unit standard deviation in all three analyses, points
 502 represent AIC-weighted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



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