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# Environmental correlates of body size distribution in Cyprinidae (Actinopterygians) depend on phylogenetic scale

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Abstract – The pattern of increasing species body size with increasing latitude has been noticed in different groups of animals. Here, we used seven key environmental factors and independent contrasts to assess body size latitudinal clines in Cyprinidae at two phylogenetic levels (inter- and intragenera), which were defined using a genus-level supertree. Model selection procedures revealed that environmental factors shaping body size variation in Cyprinidae differed according to the phylogenetic scale considered. At the higher phylogenetic level, we found that both temperature (negative effect) and habitat availability (positive effect of drainage basin surface area) constituted mechanistic explanations of large-scale body size distribution. No temperature-related body size cline was observed at the intragenus level. Instead, competitive interaction (negative effect of species richness), habitat availability (positive effect of drainage basin surface area), migration ability and available energy (positive effects of glacial coverage and actual evapotranspiration) constitute alternative explanations at this lower phylogenetic scale. We conclude that (i) at the intergenus level, cyprinids do show a tendency to be smaller at high temperatures and larger at low temperatures, (ii) this tendency no longer exists at the intragenus level, (iii) latitude per se is a weak predictor of body size clines whatever the taxonomic level analysed, (iv) generalising geographical body size patterns may be rendered difficult by the superimposition of a series of mechanisms across different taxonomic scales, and (v) habitat size, here acting positively at both taxonomic scales, may play a major role in shaping riverine species body size clines.

Key words: supertree; environmental factors; freshwater; independent contrasts; macroecology

## Introduction

The study of predictable patterns of morphological variation across environmental space is central to evolutionary ecology (Griffiths 2013). One of the patterns noticed in different groups of animals – including both endotherms and ectotherms – is that of increasing species body size with increasing latitude (see for a review Blackburn et al. 1999; Pincheira-Donoso 2010; Meiri 2011; Olalla-Tárraga 2011). The decrease in size of endotherm or ectotherm species may be driven by temperature (e.g. for ectotherms, the temperature hypothesis; Kozłowski et al. 2004) or by other factors (e.g. energy availability, interspecific competition, migration ability, among others) than temperature itself (Teplitsky & Millien 2014). Until now, the underlying mechanisms behind the latitudinal distribution of body size are still highly debated (Shelomi 2012; Teplitsky & Millien 2014), and few large scale, explicit tests of the mechanical hypotheses at the origin of this observed phenomenon have been carried out.

Freshwater teleosteans have long been considered one of the rare groups of ectotherms that shows a

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clear pattern of size increase ‘from the equator towards the pole’ (Knouft 2004; Blanchet et al. 2010). However, the taxonomic scale at which this pattern applies is controversial (Blanck & Lamouroux 2007). The Cyprinidae constitute the largest freshwater teleostean family, with almost 300 genera and 2600 species occupying Eurasia, Africa and North America; they span a wide spectrum of environmental conditions and range sizes (Nelson 2006). Because of their dramatic variation in body size – a 250-fold amplitude between *Danionella* (1 cm) and *Catlocarpio* (2.5 m) – and their wide distribution, they represent ideal candidates to test environment–body size relationships. Here, we use a genus-level supertree of Cyprinidae (Gaubert et al. 2009) to test which key environmental factors may have significantly shaped the distribution of body size within this large family of ectotherms (see Lindsey 1966), and at which taxonomic levels those environmental factors act. As trait variation across species results from both environmental and historical forces (Taylor & Gotelli 1994), it appears relevant to use a phylogenetic framework to control for the effects of phylogenetic constraints or conservatism on geographical body size patterns (Diniz-Filho & Bini 2008; Escarguel et al. 2008; Algar et al. 2009). Furthermore, fixing a taxonomic scale defined by a phylogenetic tree allows testing at which taxonomic scales the environment – body size interactions are actually acting (Cruz et al. 2005).

Our results will be discussed in view of a series of mechanistic hypotheses that may explain geographical body size patterns in freshwater teleosteans: (i) a larger size at maturation is achieved at lower temperature (temperature hypothesis; Kozłowski et al. 2004), (ii) large-bodied species are favoured in seasonal environments of higher latitudes because they metabolise fat stores at lower weight-specific rates than smaller species (environmental predictability hypothesis; Rodríguez et al. 2008) or during periods of resource abundance larger animals can maximise their growth and increase body size to survive periods of resource shortages (the seasonality hypothesis; Boyce 1979), (iii) small taxa are predominant at low latitudes because of their inability to disperse into high latitudes, notably after the last Pleistocene glaciations (migration ability hypothesis; Blackburn et al. 1999), (iv) energy availability acts positively on body size as large body size must be maintained by an important food supply (primary productivity hypothesis; Rosenzweig 1968; Olalla-Tárraga et al. 2006), (v) increased interspecific competition for resources can favour the coexistence of smaller species (competitive interaction hypothesis; Ashton et al. 2000), (vi) larger habitats (i.e. for riverine fishes, the size of the drainage basin; Oberdorff et al. 1995) are needed to maintain populations of larger sized species (habitat availability hypothesis; Hawkins & Diniz-Filho 2006).

## Material and methods

Our selection of taxa relied on a genus-level supertree of Cyprinidae (Gaubert et al. 2009), to date the most exhaustive phylogeny available for the family. The supertree has terminal leaves equivalent to genus-level taxa. When genera were not monophyletic, they were split into several species-level taxa, so the supertree has more ‘genus-level’ taxa (leaves) than the number of genera traditionally considered for Cyprinidae. We also adjusted recent taxonomic changes (e.g. synonymy) using Fishbase (Froese & Pauly 2012).

We assembled a data set of one dependent variable (body size) and seven environmental (predictor) factors for 364 genus-level terminal taxa for which the data were complete in 530 river drainage basins (Table S1). Maximum standard length (mSL) was chosen as a proxy of body size to remove the effect of caudal fin’s length variability accompanying total length (Webb 1982). Data were extracted from Fishbase (Froese & Pauly 2012; last date of access: 10 February 2012). Missing data were completed either using available morphometric ratios (converting total length or fork length into standard length) in Fishbase or measurements from the literature (1041 species; Table S2). We used the mean of mSL when a terminal taxon (genus) was represented by several species. We consider the use of mean mSL as a biologically sound proxy as there was a significant, positive correlation between the means and mSL of randomly sampled species within each genus (log-transformed values: $R^2 = 0.82$; data not shown).

The distribution of taxa and environmental factors was extracted from a worldwide database of freshwater fish occurrences per drainage basin (Brosse et al. 2013). Only native species were included in the analysis. We used a series of seven predictors linked to the mechanistic hypotheses put forward to explain geographical body size patterns (Blanchet et al. 2010): (i) drainage basin surface area (to test the habitat availability hypothesis), (ii) drainage basin mean annual temperature (to test the temperature hypothesis, assuming that mean air temperature is a good surrogate for mean water temperature; Oberdorff et al. 1995), (iii) mean absolute value of the lowest latitudinal ranges for each species within a genus, (iv) drainage basin mean annual actual evapotranspiration (a measure of water–energy balance closely associated with productivity (Hawkins et al. 2003), to test the primary productivity hypothesis), (v) coefficients of variation of actual evapotranspiration (to test the environmental predictability hypothesis and the closely related seasonality hypothesis), (vi) glacier coverage during the last glacial maximum (LGM) (i.e. the percentage of drainage basin area that was under ice during the LGM, to test the migration ability hypothesis) and (vii) native species richness (to test the competitive interaction hypothesis) (see Tisseuil et al. 2013 for data sources and definition). We calculated mean values for each variable when terminal taxa were represented by several species. When necessary, variables were ln- or arcsin-transformed to improve normality.

We combined an inter- and intrageneric analysis to assess whether different environmental factors could act on body size distribution within Cyprinidae depending on taxonomic scales. For the intergeneric analysis, we used the method of independent contrasts with the genus-level supertree of Cyprinidae of Gaubert et al. (2009) as a backbone to remove the effect of phylogenetic constraints across lineages, assuming Brownian motion of character evolution (Felsenstein 1985) and heritability of ecological characteristics (Webb et al. 2002). Given that our supertree had no estimates of branch length, we used two different methods of relative branch length attribution to assess whether those could have an influence on the calculation of independent contrasts: (i) all branch lengths were set to one, assuming a random speciation model (Garland et al. 1992; Ackerly 2000), and (ii) height was assigned to each node of the supertree as one less than the number of leaves below or at that node; path-segment lengths were then calculated between each node, as the difference between the height of the upper and lower nodes (Grafen 1989). The latter branch length 'correction' has been shown to improve the performance of independent contrasts when character evolution deviates from Brownian motion and when errors occur in branch length estimates (Díaz-Uriarte & Garland 1996, 1998). Internal node pairwise comparisons were removed from the analyses. Independent contrasts were calculated with the PDAP module 1.07 (Midford et al. 2005) implemented in Mesquite 2.74 (Maddison & Maddison 2007).

Multiple linear models were applied to determine the best set of variables (transformed into independent contrasts) in explaining the body size variation pattern based on streamline information-theoretic model selection. We used the automated model selection function 'dredge' from library 'MuMIn' (Bartoń 2011) in R statistical package (R Development Core Team 2010) to run models for all possible combinations of the explanatory variables and then selected the best-fitted models based on the Akaike Information Criterion (AIC), using $\Delta$AIC <2 as a cut-off criterion to delineate a 'top model set' (Grueber et al. 2011). Relative importance of the predictor variables was calculated using function 'model.avg' as a sum of the Akaike weights over all of the selected models in which the parameter of interest appears. Mean absolute latitude values were included in the model selection procedure to test if other latitudinal-related variables not analysed here significantly improved the model fit. We checked for multicolinearity among factors using the variance inflation factor (VIF) procedure ('vif' function from library 'car' in R statistical package; R Development Core Team 2010). The VIF provides an index that measures how much the variance of an estimated regression coefficient is increased because of colinearity, with values above 5 showing high multicolinearity. Our analyses revealed no strong colinearity among predictors (maximum VIF = 4.42). Multiple linear regressions were performed using a zero intercept model (i.e. removing the constant) to meet the 'assumption of independence' required by independent contrasts (Felsenstein 1985).

For the intrageneric analysis, trends in body size within genus-level lineages were analysed to assess if different mechanistic hypotheses were supported when changing of phylogenetic scale. For this purpose, we extracted from our database 124 genus-level taxa regrouping from 2 to 69 species each. As the supertree of Cyprinidae (Gaubert et al. 2009) uses genus-level taxa as leaves and given the few number of exhaustive phylogenies within the cyprinid genera considered, we did not use phylogenetic information within genera. Instead, we fitted linear mixed-effects (LME) models allowing to decompose variance across species by coding the random-effects error structure as a hierarchical taxonomic – genus in our case – effect (Link & Barker 2006). As for the across-lineage analysis, we applied multiple linear models and an automated model selection based on AIC to determine the best set of predictive factors. We also included mean absolute latitude as a predictor variable in the model selection procedure. We detected no strong colinearity among predictors (maximum VIF = 4.59). The R-squared coefficient based on likelihood ratio (of the model and the intercept model) was used as a measure of goodness-of-fit of the selected mixed models. LME models were conducted in R statistical package (R Development Core Team 2010) with the 'lme' function from library 'nlme' (Pinheiro et al. 2011).

To assess the effect of taking into consideration the phylogenetic history in body size distribution among genus-level taxa of cyprinids, we also ran an intergeneric analysis without a phylogenetic backbone. In that case, methodology and model selection followed the procedure detailed above for the intrageneric analysis.

## Results

For the intergeneric analysis, inferences from independent contrast estimates based on the two methods of branch length ‘correction’ (equal and path-segment) were similar. The best set of models explaining intergeneric geographical clines in body size identified temperature (negative effect) as having the strongest influence, with the highest values of ‘relative variable importance’ and statistically significant effects (Tables 1 and 2; Fig. 1). At this taxonomic level, drainage basin surface area (positive effect) also presented high values of ‘relative variable importance’ and marginally significant effects on body size variation patterns (Tables 1 and 2; Fig. 1). According to the models, latitude per se had no significant effect. Without phylogenetic control for character evolution among genus-level taxa (i.e. not using the supertree as a backbone), the linear models displayed very poor predictive power and identified AET (negative effect), glacial coverage (positive effect) and temperature (negative effect) as having the strongest influences on body size, although AET was most often nonsignificant and the latter two variables were never significant (see Table S3).

Following similar criteria, the best set of LME models explaining intrageneric geographical clines of body size identified four variables. Species richness (negative effect) and drainage basin area (positive effect) had the strongest influence (i.e. highest standardised coefficients and significance values), followed by the significant (positive) effects of glacial coverage and actual evapotranspiration (Table 3). According to the models, latitude per se had no significant effect.

## Discussion

### Environmental correlates of body size distribution in Cyprinidae

Our results support the view that environmental factors shaping body size variation may differ according to the taxonomic level under consideration (Blackburn et al. 1999; Cruz et al. 2005). At the higher phylogenetic scale (intergenus level) within cyprinids, we observed a highly significant, negative effect of temperature (Tables 1 and 2; Fig. 1) and a slightly significant positive effect of drainage basin area. Although latitudinal body size gradients among cyprinids were found worldwide (Lindsey 1966) and regionally (Knouft 2004), latitude per se had no significant effect on body size variations in our study after temperature was taken into account, suggesting no supplementary effect for this synthetic variable. In terms of plausible mechanistic explanations that may have shaped the observed pattern of body size variation across cyprinids worldwide, temperature and habitat availability hypotheses were thus the best candidates. A co-acting implication of adaptive versus nonadaptive mechanisms has been proposed to explain the temperature hypothesis in ectotherms (Angilletta & Dunham 2003; Angilletta et al. 2004). Water temperature affects gametogenesis development (Ray 1960), notably in cyprinids (Billard & Marcel 1986), and empirical studies have already provided support to faster maturation time and smaller body size associated to temperature increase in teleosteans (Pawson et al. 2000; Daufresne et al. 2009; although we used maximum body size, that is from individuals presumably older than at maturation). In addition, regional scale and *in situ* studies have shown a positive correlation between body size and habitat ‘availability’ (e.g. home range size and habitat depth) in teleosteans, possibly due to dispersal capacity at the regional scale (Tales et al. 2004) and predation pressure at the local scale (Harvey & Stewart 1991). Nevertheless, the mechanisms at the origin of the temperature/habitat availability–body size relationships, and the way those two forces may have interacted during the evolutionary history of Cyprinidae, are yet to be determined.

At a lower phylogenetic scale (intragenus level), body size variation in cyprinids was not correlated to temperature. Instead, we observed a different series of environmental factors acting on body size distribution, possibly in some antagonistic way, including

Table 1. Results of the model selection analysis assessing body size across cyprinid genus-level taxa as a function of seven explanatory variables, using equal branch length for the supertree. Values given for each variable are standardised regression coefficients.

| Selected variables | AET | AETcv | DSA | Glac | Lat | SR | T | df | logLik | AICc | delta | weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DSA + T | | | 0.128* | | | | −0.250*** | 3 | −285.077 | 576.200 | 0.000 | 0.129 | 0.095 |
| AETcv + DSA + T | | −0.058 | 0.125* | | | | −0.289*** | 4 | −284.802 | 577.800 | 1.510 | 0.06 | 0.097 |
| DSA + SR + T | | | 0.149 | | | −0.033 | −0.237*** | 4 | −284.988 | 578.100 | 1.880 | 0.05 | 0.095 |
| DSA + Lat + T | | | 0.126* | | −0.040 | | −0.283** | 4 | −284.999 | 578.200 | 1.910 | 0.05 | 0.095 |
| AET + DSA + T | −0.021 | | 0.122 | | | | −0.244*** | 4 | −285.028 | 578.200 | 1.960 | 0.048 | 0.095 |
| Relative importance | 0.143 | 0.179 | 1.000 | 0.000 | 0.147 | 0.149 | 1.000 | | | | | | |

AET, actual evapotranspiration; AETcv, seasonality in AET; DSA, drainage basin surface area; Glac, glacier coverage; Lat, latitude; SR, species richness; T, temperature.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 2. Results of the model selection analysis assessing body size across cyprinid genus-level taxa as a function of seven explanatory variables, using path-segment length for the supertree. Values given for each variable are standardised regression coefficients.

| Selected variables | AET | AETcv | DSA | Glac | Lat | SR | T | df | logLik | AICc | delta | weight | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DSA + Glac + T | | | 0.114 | 0.115 | | | −0.164* | 4 | −282.046 | 572.200 | 0.000 | 0.079 | 0.090 |
| DSA + T | | | 0.137* | | | | −0.224*** | 3 | −283.276 | 572.600 | 0.400 | 0.065 | 0.081 |
| Glac + T | | | | 0.147* | | | −0.170* | 3 | −283.715 | 573.500 | 1.280 | 0.042 | 0.078 |
| AETcv + DSA + Glac + T | | −0.051 | 0.112 | 0.108 | | | −0.202* | 5 | −281.847 | 573.900 | 1.680 | 0.034 | 0.091 |
| AETcv + DSA + T | | −0.070 | 0.133* | | | | −0.272** | 4 | −282.894 | 573.900 | 1.700 | 0.034 | 0.084 |
| DSA + Glac + SR + T | | | 0.134 | 0.113 | | −0.030 | −0.152. | 5 | −281.976 | 574.200 | 1.940 | 0.030 | 0.090 |
| DSA + Glac + Lat + T | | | 0.112 | 0.113 | −0.033 | | −0.192. | 5 | −281.995 | 574.200 | 1.980 | 0.029 | 0.090 |
| Relative importance | 0.000 | 0.217 | 0.867 | 0.685 | 0.094 | 0.096 | 1.000 | | | | | | |

See footnote of Table 1 for abbreviations and significance levels.

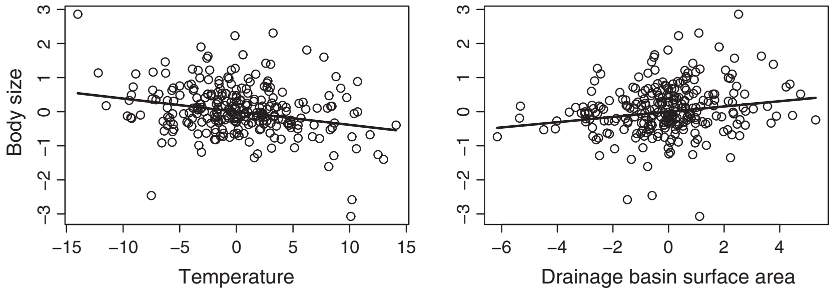

*Fig. 1.* Relationships between the independent contrasts of body size and the two environmental variables showing the highest values of relative importance in the best-fitted models for the intergenus analysis within the Cyprinidae (using path-segment length for the supertree). Simple linear regressions show the general trends of the relationships.

Table 3. Results of the model selection analysis assessing body size within cyprinid genus-level taxa as a function of seven explanatory variables. Values given for each variable are standardised regression coefficients.

| Selected variables | AET | AETcv | DSA | Glac | Lat | SR | T | df | logLik | AICc | delta | weight | $R^2$ (LR-based) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AET + DSA + Glac + SR | 0.122** | | 0.213*** | 0.068* | | −0.327*** | | 7 | −861.621 | 1737.400 | 0.000 | 0.215 | 0.500 |
| AET + AETcv + DSA + Glac + SR | 0.119** | −0.045 | 0.225*** | 0.076** | | −0.350*** | | 8 | −861.185 | 1738.600 | 1.170 | 0.120 | 0.501 |
| AET + DSA + Glac + Lat + SR + T | 0.126** | | 0.207*** | 0.084** | 0.102 | −0.303*** | 0.094 | 9 | −860.245 | 1738.700 | 1.330 | 0.110 | 0.502 |
| AET + DSA + GLAC + SR + T | 0.119** | | 0.222*** | 0.081* | | −0.339*** | 0.039 | 8 | −861.274 | 1738.700 | 1.350 | 0.110 | 0.501 |
| AET + AETCV + DSA + Glac + Lat + SR | 0.124** | −0.081 | 0.213*** | 0.071* | 0.079 | −0.328*** | | 9 | −860.429 | 1739.100 | 1.700 | 0.092 | 0.502 |
| AET + DSA + Glac + Lat + SR | 0.125** | | 0.204*** | 0.064* | 0.031 | −0.311*** | | 8 | −861.458 | 1739.100 | 1.710 | 0.091 | 0.500 |
| Relative importance | 1.000 | 0.287 | 1.000 | 1.000 | 0.398 | 1.000 | 0.298 | | | | | | |

See footnote of Table 1 for abbreviations and significance levels.

species richness (negative effect; strongest influence), drainage basin surface area (positive effect; strongest influence), glacial coverage and actual evapotranspiration (positive effects) (Table 3). Thus, we suggest that body size variation at a finer phylogenetic scale within Cyprinidae may be explained by the combination of four mechanistic hypotheses, namely competitive interaction, habitat availability, migration ability and energy availability. The negative relationship that we found between body size and species richness fits the posited pattern of coexistence of smaller species in the context of increased interspecific competition for resources (Ashton et al. 2000; Blanckenhorn 2000). In addition, in freshwater teleosteans, dispersal is favoured in larger species because of lower migratory cost and occurrence in large river corridors (Bernatchez & Dodson 1987; Knouft 2004; Blanchet et al. 2010; Griffiths 2012). This could explain our findings of body size variation within cyprinid genera conforming to the habitat availability and migration ability mechanistic hypotheses. In line with Rosenzweig's (1968) argumentation that primary productivity could be an important selective pressure on body size as body mass must be maintained by a sufficient food supply, our study also found that body size variation among species of cyprinids was positively correlated to available energy at the intragenus scale. However, while this pattern has been also observed in some ectotherms (e.g. snakes), others show converse-clines (e.g. lizards; Olalla-Tárraga et al. 2006) suggesting that there is no simple answer to the energy availability hypothesis.

Given the superimposition of the mechanistic hypotheses potentially involved (five in total) and of the phylogenetic scales (inter- and intrageneric), our results support the view that deterministic, broadly generalised geographical patterns of body size are difficult to establish (Berke et al. 2012). Eventually, drainage basin area was the only variable to act (positively) on body size variation at both taxonomic scales in cyprinids, further reinforcing the importance of habitat size in riverine ecosystem geographical clines (Biedermann 2003; Griffiths 2013).

### Robustness of the independent contrast analysis and perspectives on the comparative approach in cyprinids

The results of our comparative analysis based on independent contrasts (intergenus level) were consistent across the two methods of branch length attribution applied to the supertree of Cyprinidae. In addition, when discarding the phylogenetic nonindependence of character evolution among genus-level taxa (i.e. not using the supertree), the linear models displayed very poor predictive power (see Table S3). Such lines of evidence suggest – indirectly – that the distribution of body size within cyprinids is not independent of the evolutionary relationships among genera, and as a corollary, that heritability of ecological characteristics occurs within the family (see Taylor & Gotelli 1994). The robustness of our comparative approach was further supported by its nonsensitivity to the branch length attribution methods applied to our supertree, which is in line with the robustness of independent contrasts to branch length calculations (Díaz-Uriarte & Garland 1998).

Although the aim of our study was deterministic (i.e. testing evolutionary correlation between body size and environmental variables), we acknowledge that assessing the relative contribution of the phylogeny on body size distribution and the fit of other evolutionary models than the Brownian motion (e.g. via phylogenetic generalised least squares; Martins & Hansen 1997) may allow to further understand the evolution of body size in cyprinids.

One of the potential caveats of our comparative method may reside in the fact that we used mean maximum standard lengths (mSL) to describe body size distribution among cyprinid genera (see Garamszegi & Møller 2010), although such proxies appeared biologically meaningful (e.g. we observed a positive correlation between means and mSL values among species within genera). In fact, the two-scale phylogenetic assessment of morphological variance distribution among cyprinids conducted here would have been optimal if independent contrasts were calculated by considering at the same time the covariance of evolutionary changes (intergenera) and a fraction of the within-genus covariance (see Felsenstein 2008). Indeed, the potential influence of lower taxonomic rank variation on higher taxonomic rank patterns has recently been put forward (Gaston et al. 2008). The advent of more flexible computing environments (Freckleton 2009) together with the consolidation of our knowledge on the phylogenetic relationships within cyprinid genera should improve our ability to understand body size variation in the Cyprinidae.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Data set (body size and environmental factors) calculated for the 364 genus-level cyprinids under study.

**Table S2.** Maximum standard length (mSL) extracted or calculated for the 1041 species of cyprinids included in the study.

**Table S3.** Results of the model selection analysis assessing body size across cyprinid genus-level taxa as a function of seven explanatory variables, without using a phylogenetic backbone (i.e. supertree).