

# Body stoichiometry of heterotrophs: assessing drivers of interspecific variations in elemental composition.

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# Body stoichiometry of heterotrophs: assessing drivers of interspecific variations in elemental composition.

**Running title:** Body stoichiometry of heterotrophs.

## ABSTRACT

- **Aim:** To document how body stoichiometry of heterotrophs varies globally and to assess phylogenetic, trophic, habitat and body mass drivers of this interspecific variation in elemental composition, focusing on carbon (C), nitrogen (N) and phosphorus (P).
- **Location:** Worldwide.
- **Time period:** 1930 – 2018.
- **Major taxa studied:** Amphibians, fishes (Euteleostomorpha and Otomorpha), invertebrates, mammals, microbes and sauropsids (birds and reptiles).
- **Methods:** We compiled from the scientific literature a global database of body elemental composition of heterotrophs in marine, freshwater and terrestrial realms. We used model selection and ANCOVA analyses to investigate the proportion of variance in elemental composition explained by taxonomic groups, diet, habitat and body mass. We assessed the phylogenetic signal in body stoichiometry using Blomberg's K and Pagel's  $\lambda$  statistics. We assessed the phylogenetic structure of interspecific variation in body stoichiometry using mixed models with nested taxonomic levels as random factors. We finally assessed the co-variation in elemental composition using linear models.
- **Results:** Our database currently gathers 17848 independent observations on 1491 species. Body elemental composition was found to be widely variable among species with the four assessed drivers significantly contributing to this variation. Taxonomic group is the strongest contributor to interspecific variance for the stoichiometric traits studied, followed by habitat, diet and body mass. More precisely, stoichiometric traits are generally variable at the three taxonomic levels studied

(class, order and family), resulting in a significant but relatively modest phylogenetic signal. Finally, we found significant co-variation among the three body elemental contents, resulting in taxonomic group-specific C:N:P spectrums.

- **Main conclusions:** Our global synthesis of body stoichiometry of heterotrophs reveals a strong interspecific variability that is only modestly explained by the species attributes investigated: body mass, habitat and diet. It further reveals that this taxonomically structured residual variation in body stoichiometry seems to be constrained along taxonomic group-specific elemental spectrums.

**KEYWORDS:** body elemental composition, ecological stoichiometry, growth rate hypothesis, nutrient content, phylogenetic conservatism, stoichiometric homeostasis.

## 58 INTRODUCTION

59 Ecological stoichiometry theory revolves around the main idea that the growth and reproduction of an  
60 organism depends on its ability to acquire nutrients in appropriate proportions from its environment  
61 (Sterner & Elser, 2002). Following this theory, the body elemental composition of an organism is thus a  
62 critical parameter of its ecology. Autotrophic life forms generally harbor a substantial plasticity in  
63 terms of elemental composition that greatly varies in response to nutrient and light modification of  
64 their environment (Aerts & Chapin, 1999; Duarte, 1992). In contrast, heterotrophic organisms  
65 generally present much less plastic variation in their elemental composition (Lemmen et al., 2019), a  
66 phenomenon called stoichiometric homeostasis. Although the idea of a strict homeostasis of  
67 heterotrophs has been recurrently falsified (Persson et al., 2010), it constitutes a convenient  
68 approximation, at least for metazoans. This approximation is further used in many stoichiometric  
69 models of community and ecosystem dynamics (Andersen et al., 2004).

70

71 Understanding how body nutrient contents vary among organisms and assessing putative drivers of  
72 such variations constitute a cornerstone of ecological stoichiometry. Various hypothesized drivers of  
73 stoichiometric variations among organisms have been put forward. The growth rate hypothesis (Elser  
74 et al., 2003; Elser, Dobberfuhl, MacKay, & Schampel, 1996) states that fast growing organisms should  
75 have lower N:P ratios than slow growing ones. Besides, organisms with large metabolic rates may  
76 consume larger amounts of C and thus may have lower C:N and C:P ratios. Since larger organisms tend  
77 to have lower metabolic rates per unit mass (Brown, Gillooly, Allen, Savage, & West, 2004) and lower  
78 growth rates, body mass should be positively related to C:N, C:P and N:P. Diet of organisms may also  
79 influence their stoichiometric needs. Since predators have access to preys with larger N and P  
80 contents, they may have been selected (or less counter-selected) to have larger N and P contents  
81 (Sterner & Elser, 2002). Finally, some phylogenetically-conserved traits may profoundly influence  
82 stoichiometric constraints of organisms. For instance, the presence of a skeleton should increase P  
83 content (Simkiss & Wilbur, 1989), while homeothermic organisms are likely to have larger C needs  
84 than poikilothermic individuals (Sterner & Elser, 2002).

85

86 Many works have investigated stoichiometric patterns in specific taxonomic groups (see our  
87 compilation in Table S1). To sum up these pieces of work, (i) most studies have focused on carbon (C),  
88 nitrogen (N) and phosphorus (P) contents of organisms, or on their associated ratios C:N, C:P and N:P;  
89 (ii) the putative drivers of elemental composition mainly focused on phylogeny/taxonomy, diet, body  
90 mass, ontogeny and habitat; (iii) empirical patterns and their magnitude are variable between the  
91 different taxonomic groups studied. More specifically, evolutionary history is a significant predictor of  
92 stoichiometric traits in various groups when analyzed with analyses of variances based on taxonomic  
93 groups, especially at large taxonomic levels (phyla, classes, orders): in terrestrial insects (Fagan et al.,  
94 2002; Martinson et al., 2008; Wiesenborn, 2013; Woods, Fagan, Elser, & Harrison, 2004), fishes  
95 (Hendrixson, Sterner, & Kay, 2007; McIntyre & Flecker, 2010; Vanni, Flecker, Hood, & Headworth,  
96 2002), aquatic invertebrates (Evans-White, Stelzer, & Lamberti, 2005; González et al., 2018), lizards  
97 (González, Fariña, Kay, Pinto, & Marquet, 2011) and fungi (Zhang & Elser, 2017). In contrast, most of  
98 these studies found little or no phylogenetic signal in body stoichiometry, probably because of too low  
99 sample sizes (Blomberg, Garland, & Ives, 2003). Diet is also a recurrent predictor of body  
100 stoichiometry across taxonomic groups. Roughly, predators tend to have larger N and/or P contents  
101 than herbivores and/or detritivores in terrestrial insects (Fagan et al., 2002; González et al., 2011;  
102 Wiesenborn, 2013), fishes (McIntyre & Flecker, 2010) and aquatic invertebrates (Evans-White et al.,  
103 2005). In contrast with these general findings, Vanni et al. (2002) evidenced in their study similar P  
104 contents between predator and herbivorous fishes, and González et al. (2008) evidenced lower P  
105 contents in predators compared to detritivores in aquatic invertebrates. Finally, Martinson et al.  
106 (2008) evidenced similar N contents between herbivores and detritivores in terrestrial arthropods.  
107 Body mass is a less straightforward predictor of body stoichiometry. When studied at the intraspecific  
108 level, correlations between body mass and elemental contents are strongly species-specific in sign,  
109 significance and magnitude (Arbačiauskas, Lesutienė, & Gasiūnaitė, 2013; Hendrixson et al., 2007; but  
110 see González et al., 2018; Woods, 2004). When studied at the interspecific level, correlations between  
111 body mass and elemental contents are also variable across taxonomic groups with positive, negative,  
112 hump-shape or non-significant relationships. Moreover, allometric relationships tend to vanish when  
113 controlling for phylogenetic effects (e.g., González et al., 2018; González et al., 2011; Hendrixson et al.,  
114 2007). A fewer number of works have studied the effect of ontogeny on body stoichiometry. Fagan et  
115 al. (2002) did not find any ontogenetic signal in insects, while González et al. (2011) found larger C:N  
116 ratios in larvae than adult arthropods. Many studies failed to detect a significant effect of habitat on

body stoichiometry or detected either a significant but low habitat effect or a species-specific habitat effect (Arbačiauskas et al., 2013 for crustaceans; Evans-White et al., 2005 for aquatic invertebrates; González et al., 2011 for arthropods and lizards; Milanovich, Maerz, & Rosemond, 2015 for salamanders). Some works however did succeed in evidencing habitat effects in fishes (Hendrixson et al., 2007), aquatic invertebrates (González et al., 2018) and fungi (Zhang & Elser, 2017).

122

As illustrated above, syntheses on the ecological stoichiometry of heterotrophs are until now taxonomically segmented with heterogeneous data analysis approaches and variable sets of stoichiometric drivers studied. They end up with contrasted or sometimes contradictory results that hamper a general understanding of the ecological stoichiometry of heterotrophs. The aim of the present study is thus to compile a unified database of heterotroph body elemental contents (C, N and P) and associated ratios (C:N, C:P and N:P), in order to conduct a general analysis across taxonomic groups. We will use this database to assess i) the variability of body elemental contents and their co-variations documented worldwide across heterotrophs; and ii) the importance of four putative drivers for these variations: evolutionary history, diet, body mass and habitat.

132

## 133 **METHODS**

### 134 **Data compilation**

We assembled three already compiled extensive datasets synthesizing information about aquatic animals (Vanni et al., 2017), fungi (Zhang & Elser, 2017) and insects (Fagan et al., 2002). We completed this dataset using published literature up to the end of August 2019. We conducted this literature search on ISI Web of Knowledge and Google Scholar. Search terms included 'nutrient content', 'body compo\*', 'nutrient compo\*', 'chemical compo\*', 'protein content', 'carbon content', 'nitrogen content', 'phosphorus content' and 'ecological stoichiometr\*' together with 'ontogen\*', 'allometr\*', 'body size', 'trophic', 'trophy', 'diet\*'. Preliminary attempts based on more specific keywords did not enable us to collect much data. We therefore relied on such broad keywords search with the limitation that we could not systematically consult all the articles found. We therefore do not pretend to have been exhaustive. In this literature search, we paid particular attention to collect data on taxa that were less

145 informed by previous syntheses, especially mammals and sauropsids. To do this, we reiterated the  
146 search including group names and synonyms in the query. A list of the data sources is found in  
147 Appendix 1.

148

149 We included in our database all data with at least one observation of body carbon, nitrogen or  
150 phosphorus content or one of their ratio, except that we removed the values of C content for the fungi  
151 group when C content was virtually set to an average value (Zhang & Elser, 2017). We used the  
152 program 'Plot Digitizer' v2.6.8 to extract data from graphs. When only body protein content was given  
153 in a publication, we divided this number by 6.25 to estimate nitrogen content (Persson et al., 2010).  
154 We broadly taxonomically grouped organisms as amphibians, fishes (separating two distinct groups:  
155 Euteleosteiomorph and Otomorpha), invertebrates, mammals, microbes or sauropsids (birds and  
156 reptiles). We recorded the main diet of the organism as being either herbivore, carnivore, detritivore  
157 or omnivore. We recorded the main habitat of the organism as being either terrestrial, freshwater or  
158 marine. We finally used the log-transformed dry mass of an organism in subsequent statistical  
159 analyses. When necessary, we converted fresh (wet) mass to dry mass considering dry mass to be  
160 28.82% of wet mass for mammals, 34.98% for birds, 26.80% for reptiles, 23.50% for fishes and 20.46%  
161 for amphibians. We obtained these ratios from the weighted average by number of observations for  
162 mammals (Arnould, Boyd, & Speakman, 1996; Gerhart, White, Cameron, & Russell, 1996; Kremen et  
163 al., 2013; Reilly & Fedak, 1990; Schlesinger & Potter, 1974; Spray & Widdowson, 1950; Studier, Sevic,  
164 & Wilson, 1994), birds (Grimshaw, Ovington, Betts, & Gibb, 1958; Kremen et al., 2013; Sturges,  
165 Holmes, & Likens, 1974), reptiles (Barron, 1997; Dierenfeld, Alcorn, & Jacobsen, 2002), fishes (Lantry &  
166 O'Gorman, 2007) and amphibians (Dierenfeld et al., 2002; MacCracken & Stebbings, 2012; Takahara,  
167 Miyasaka, Genkai-Kato, & Kohmatsu, 2008). When diet, body mass or habitat of the organism were  
168 not mentioned in the publication, we gathered them from other publications and specified the  
169 corresponding references in the database. Typing errors for species names were checked by using the  
170 Open Tree Taxonomy's taxon resolution name service together with the 'rotl' R package (Michonneau,  
171 Brown, Winter, & Fitzjohn, 2016), from which we also imputed the taxonomy levels for most of the  
172 species. We also assembled a dated phylogenetic tree for a subset (n = 344) of the species present in  
173 the dataset with the 'datelife' R package (Sánchez-Reyes & O'Meara, 2019).

174

## 175 **Elemental content variability**

176 We assessed the range of elemental contents for each taxonomic group. We also assessed the  
 177 presence of “stoichiometric spectrums”, that is of significant co-variations between body C, N and P  
 178 contents among heterotrophs. We visually assessed these spectrums using three-dimensional plots.  
 179 We then statistically tested the significance of these spectrums using multiple regressions explaining C  
 180 content as a function of N and P contents both on the full dataset and on each taxonomic group  
 181 separately. We also assessed the three pairwise Pearson’s correlations between C, N and P contents  
 182 both on the full dataset and on each taxonomic group separately.

183

## 184 **Stoichiometric drivers**

185 We first assessed the significance of four stoichiometric drivers (taxonomic group, diet, body mass and  
 186 habitat) on elemental contents (C, N and P) and elemental ratios (C:N, C:P, N:P) with additive linear  
 187 models without interactions between drivers. We built 15 models corresponding to all the possible  
 188 combinations of these four drivers and performed a model selection based on the Akaike information  
 189 criterion (AIC). We retained the ‘best’ model (i.e., the model that best fitted the data) with the lowest  
 190 AIC plus the other models with a difference in AIC below 10 ( $\Delta AIC < 10$ , Burnham & Anderson, 2002).  
 191 We also computed the corresponding model weights (W). We then assessed the magnitude of these  
 192 drivers using partial eta-squared (partial  $\eta^2$ ) on the full model (with the four drivers). Partial  $\eta^2$   
 193 compute the ratio between the variance explained by a stoichiometric driver and the sum of this  
 194 variance plus the variance of the residuals. It therefore measures the proportion of the remaining  
 195 variance explained by a driver once the effects of the other drivers are factored out.

196

197 For visualization purposes, we also used the ‘sequential ANCOVA’ procedure described in Fagan et al.  
 198 (2002). This consists, for each driver in turn, in fitting an additive linear model with the three other  
 199 drivers, and in assessing the effect of the focal driver on the residuals of this model. By doing this, we  
 200 are conservative on the effect of each driver. For categorial variables, comparison among groups was  
 201 done with non-parametric Kruskal-Wallis rank sum test with post-hoc Dunn’s test of multiple



comparisons with Bonferroni corrections. Before analyses, body mass was log-transformed. The body mass of microbes was not informed in the studied data sets, so this group was not included in these analyses.

## Evolutionary history

We computed the phylogenetic signal of stoichiometric traits (C, N, P, C:N, C:P, N:P) with two statistics: Blomberg's K (Blomberg et al., 2003) and Pagel's  $\lambda$  (Pagel, 1999). The significance of phylogenetic signal was also assessed with both the randomization test of Blomberg et al. (2003) and the likelihood ratio test associated with Pagel's  $\lambda$ . For such phylogenetic analyses, we used species-averaged values of stoichiometric traits. We also fitted linear mixed models for each stoichiometric trait separately, using diet, habitat and body mass as fixed factors and taxonomic classes, orders and families as nested random factors using the 'nlme' R package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). The variance in stoichiometric traits explained by the fixed factors was evaluated with the marginal  $R^2$  and the variance explained both by the fixed and random factors by the conditional  $R^2$  using the 'MuMIn' R package (Barton, 2019). In addition, we assessed the variance components associated with each taxonomic level by using the 'ape' R package (Paradis & Schliep, 2018).

All statistical analyses were performed with R v3.6.1 (R development core team 2017). We used the package 'AICcmodavg' for model selection (Mazerolle, 2019) and 'yarr' (Phillips, 2017) and 'plot3D' (Soetaert, 2019) for data visualization. ANCOVAs (type III) were performed using the 'car' package (Fow & Weisberg, 2019) together with the 'FSA' (Ogle, Wheeler, & Dinno, 2020) and 'rcompanion' (Mangiafico, 2020) R packages for Dunn's tests and compact letter display for lists of comparisons. We managed phylogenetic data with 'ape' package (Paradis & Schliep, 2018) and phylogenetic signal was calculated with the 'phytools' package (Revell, 2012).

## RESULTS

### Data compilation

Our database gathers 56 sources of information (original publications or previous syntheses). It compiles information of 373 studies and contains 17,848 independent stoichiometric observations on 1,491 species. It successfully compiles information for the seven main taxonomic groups considered (amphibians, fishes-Euteleosteiomorpha, fishes-Otomorpha, invertebrates, mammals, microbes and sauropsids), although with variable sample sizes (Fig. S2a). A diverse array of diets (Fig. S2b) and habitats (Fig. S2c) are sampled in most taxonomic groups. The range of body mass within each group is substantial (Fig. S2d). This compilation therefore enables us to conduct the statistical analyses envisioned, although we must recognize the fact that our sample of heterotrophs is substantially unbalanced among taxonomic groups, diets, habitats and body masses, and is factorially incomplete as inherent to such literature syntheses.

## **Elemental content variability**

Across the full dataset, elemental contents present limited variabilities, with C content (first and third quartiles at 41 and 48.1 respectively) varying less than N content (8.2;11) and P content (0.7;2.1). Still, some organisms present important deviations from these median ranges with C content varying from 4.1 to 65.3, N content from 0.2 to 19 and P content from 0.04 to 11.4. Within each taxonomic group studied, empirical variability in elemental contents is of similar magnitude, with largely overlapping distributions between the various groups (Fig. 1). Some differences between taxonomic groups are however noticeable: amphibians have above-average N contents (Fig. 1b), mammals have above-average C and N contents (Fig. 1a,b), microbes have below-average N and P contents (Fig. 1b,c), sauropsids have below-average C contents (Fig. 1a) and invertebrates have below-average P contents (Fig. 1c). Some invertebrate species present low to very low C and N contents, these species correspond to some marine gelatinous organisms. Also, there is less overlap in P contents between the different taxonomic groups (Fig. 1c). As a consequence of low body N and P content, microbes have larger C:N and C:P ratios than other organisms (Fig. 1d,e). Also, invertebrates have above-average N:P ratio (Fig. 1f) and sauropsids below-average C:P and N:P ratios (Fig. 1e,f).

We find a substantial amount of pairwise co-variation between elemental contents: when all taxonomic groups are analyzed together, there is a positive Pearson's correlation coefficient of 0.43 between C and N contents, of 0.20 between N and P contents and a slight negative correlation of -0.05 between C and P contents. We find an even stronger positive correlation of 0.48 between C:N and C:P ratios. When we jointly analyze the three elemental contents, we find that N and P contents together explain 29% of the variance in C contents, that C and P together explain 31% of the variance in N contents, while P content is less well explained by C and N at 5%. These general relationships hide more complex patterns when data are analyzed at the taxonomic group level (Fig. 2, Table S3). Indeed three-way relationships are strongly variable among taxonomic groups (Fig. 2).

## **Stoichiometric drivers**

Overall, the four stoichiometric drivers studied had significant effects on body stoichiometry. The full model including the four drivers assessed was always selected for the six stoichiometric traits (Table 1, Table S4). For four traits, C, N, C:P and N:P, it was the best model and was totaling almost all the Akaike weights. For P, it was the best model totaling 98 per cent of Akaike weights. And for C:N, it was the second best model, totaling 14 per cent of Akaike weights. For this last trait, a model without the habitat effect had a larger weight.

Taxonomic group was the most influent driver among the four studied for all stoichiometric traits except carbon content (Fig. 3). This effect was especially large for P, C:P and N:P with partial eta-squared values above 0.1 (Fig. 3). Habitat was the strongest driver for C and the second most influent driver for four other stoichiometric traits (except C:N), while diet and body mass had only minor effects with partial eta-squared below 0.05 for all traits studied (Fig. 3). We also found that the effects of habitat, diet and body mass were group-specific, both in terms of magnitude and significance (Tables S5-10).

Our analysis based on sequential ANCOVAs confirmed these results (Fig. 4, Figs. S11-15). When looking at the results for P content (Fig. 4), we detected significant differences of sizable magnitude

between the different taxonomic groups, while differences between diets, habitats and body mass were small once the effects of other drivers had been accounted for (Fig. 4). We obtained similar results for the other stoichiometric traits (Figs. S11-15).

## Evolutionary history

We found a significant ( $p < 0.05$ ) phylogenetic signal with both methods and for the six stoichiometric traits (Table S16). Computed values of  $K$  were below 1 for the six stoichiometric traits, indicating that phylogenetically related species have less similar trait values than expected under a Brownian motion model of evolution (Fig. 5). Computed values of  $\lambda$  were close to 1, indicating that traits are as similar among species as awaited under a Brownian motion model of evolution (Fig. 5). Consequently, the two studied statistics provide somehow contradictory results, with  $K$  and  $\lambda$  suggesting a shallow and strong phylogenetic signal respectively.

Our complementary analysis based on mixed models sheds light on this apparent contradiction by revealing the phylogenetic hierarchical structure of the variation of stoichiometric traits. Indeed, we found for the six stoichiometric traits large effects of taxonomic classifications at the three taxonomic levels considered (families, orders and classes, Table 2). For C, N and P contents, phylogenetic variation was strongly structured among classes, while variations among orders and families had lower and similar magnitudes (Table 2). For the C:N, C:P and N:P ratios, the largest variations were among families, followed by among-classes variations and among-orders variations (Table 2). Moreover, the predictive power of the linear mixed models of the six stoichiometric traits were largely greater when taxonomy was accounted for, as shown by the low marginal- and high conditional  $R^2$  values (Table 2).

## DISCUSSION

*Analyzing interspecific variations among heterotrophs*

309 To date, our compilation of body elemental contents of heterotrophs constitutes the most  
 310 comprehensive resource to study the ecological stoichiometry of natural organisms with 17,848  
 311 independent observations on 1,491 species. Analyzing this database revealed widely variable carbon,  
 312 nitrogen and phosphorus contents, as well as associated ratios (Fig. 1). We also evidenced sizeable  
 313 levels of two and three-way co-variations of these elemental contents, but we found that these co-  
 314 variations greatly vary between the different taxonomic groups considered (Fig. 2). The four assessed  
 315 drivers significantly contribute to the observed interspecific variation in body elemental composition  
 316 (Table 1), with taxonomic group being the strongest contributor, followed by habitat, diet and body  
 317 mass (Fig. 3). Finally, we detected a significant variation of the six stoichiometric traits at the three  
 318 nested taxonomic levels studied (classes, orders and families, Table 3). This leads to a significant but  
 319 relatively modest phylogenetic signal (Fig. 5).

320

321 Consistently with available knowledge, vertebrates harbor larger levels of phosphorus content than  
 322 invertebrates and microbes, since the skeleton contains a large amount of P (Hendrixson et al., 2007).  
 323 Microbes present lower values of nitrogen content. Since our database contains many terrestrial fungi  
 324 from the synthesis of Zhang & Elser (2017), this fact may principally highlight the necessary adaptation  
 325 of such organisms to the frequent conditions of nitrogen limitation in the soil. This may also indicate  
 326 the potential failure of the strict homeostasis assumption for these organisms (Danger et al. 2016).  
 327 Mammals tend to have larger carbon and nitrogen contents. Large values of carbon content in  
 328 mammals are probably due to their necessary lipid reserves to sustain their endothermy (Klaassen &  
 329 Nolet, 2008). Finally, some invertebrate taxa present very low levels of carbon and nitrogen. These  
 330 organisms belong to marine gelatinous taxa such as jellyfishes (Ikeda, 1974). Indeed, in these  
 331 organisms, chloride, sodium and other minerals make up the bulk of organism dry mass (Khong et al.,  
 332 2016). Besides, we observed a large between group variability in stoichiometric co-variations (Fig. 2).  
 333 For instance, we found a strong positive co-variation between C and N content in invertebrates (Fig.  
 334 2a-b), while in fishes and sauropsids, the strongest covariation is negative between C and P contents  
 335 (Fig. 2a,c). These sharp differences in stoichiometric co-variations among the taxonomic group  
 336 considered suggest that these groups may face different physiological and life-history constraints.  
 337 Indeed, insect exoskeletons are rich in chitin that contains both C and N, while vertebrate skeletons  
 338 contain calcium phosphate and thus P.

339

# 340 *Predicting stoichiometric traits in heterotrophs*

341 Our compiled database can be used to predict the main stoichiometric traits, i.e., body C, N and P  
342 contents and C:N, C:P and N:P ratios in heterotrophic organisms, accounting for their phylogenetic  
343 position, habitat, diet and body mass. Our analyses revealed that these four putative drivers  
344 significantly influence the stoichiometric traits studied (Fig.3). However, the magnitude of habitat, diet  
345 and body mass are small compared to the observed variations between taxonomic groups and to the  
346 remaining residual variations (Fig.4, Fig. S11-15). This modest magnitude of effects of the drivers  
347 studied may be partly explained by their relatively crude resolution in our database. Indeed, diet types  
348 may be more finely assessed thanks to discrete trophic levels, functional trophic guilds or isotopic  
349 niches (Majdi et al., 2018; McIntyre & Flecker, 2010). In the same vein, habitat definition may be more  
350 finely detailed so as to account for finer-scale habitat variation or environmental variables may be  
351 used instead (Zhang & Elser, 2017). Thus, we consider our analysis of stoichiometric drivers to be  
352 conservative, since it may underestimate the real effects of habitat and diet on interspecific variation  
353 in body elemental composition of heterotrophs. Complementing our current database with more  
354 accurate habitat and diet descriptions would thus constitute an interesting path for future progresses.

355

356 The larger effect of taxonomy on body stoichiometry (Fig. 3-4) with a significant phylogenetic signal for  
357 the six traits studied is also promising (Fig. 5). However, the large variability near the tips of the  
358 phylogeny (within families, Table 2) should make the imputation of stoichiometric traits from  
359 phylogenetic relatives a challenging task. We must recognize however that our phylogenetic analyses  
360 were based on relatively crude phylogenetic trees due to the taxonomic breadth of our database, so  
361 that more phylogenetically local analyses might provide clearer signals. Another related line of  
362 progress would consist in considering interactions between drivers in prediction models. The complete  
363 database was not amenable to such analyses, since it was not factorially complete. But analyses  
364 focused on particular phylogenetic groups would enable such more detailed treatments. Finally, on  
365 top of their effect on interspecific variation, habitat, diet and body mass are further likely to impact  
366 intraspecific variation in body elemental composition, as it has been recurrently evidenced in previous  
367 studies on specific taxonomic groups (Table S1, Lemmen et al., 2019). Our global database currently

368 contains too few intraspecific repetitions to handle a meaningful global analysis on intraspecific  
369 variation in heterotrophs. This is clearly a line of progress that should be explored in the future.

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## 519 **DATA ACCESSIBILITY STATEMENT**

520 -The compiled database will be deposited on Zenodo upon acceptance of publication.

521 -The R script used for the statistical analyses will be deposited on Github upon acceptance of  
522 publication.

523

524

## 525 TABLES

526 **Table 1** Stoichiometric drivers assessed by model selection.

Stoichiometric trait	Model	K	n	AIC	ΔAIC	Cum W
C	C ~ Group + Diet + Size + Habitat	13	4353	30415.24	0	0.98
	C ~ Group + Diet + Habitat	12		30423.42	8.21	1
N	N ~ Group + Diet + Size + Habitat	13	4748	20249.25	0	1
P	P ~ Group + Diet + Size + Habitat	13	4209	10606.47	0	0.98
	P ~ Group + Size + Habitat	10		10614.98	8.51	1
C:N	C:N ~ Group + Diet + Size	11	4384	15618.57	0	0.86
	C:N ~ Group + Diet + Size + Habitat	13		15622.14	3.56	1
C:P	C:P ~ Group + Diet + Size + Habitat	12	3821	45794.64	0	1
N:P	N:P ~ Group + Diet + Size + Habitat	13	3949	28144.76	0	1

527 K: number of estimated parameters, n: number of observations, AIC: Akaike Information Criterion,  
528 ΔAIC: difference in AIC with the best model, Cum W: Cumulative AIC weight. Only models with a ΔAIC  
529 below 10 are reported. For a full account of model selection results, see Table S4.

530

531 **Table 2** Magnitude of taxonomic effects on stoichiometric traits.

Model	n	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>	Random effects			
				Class	Order	Family	Residu
C ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3746	0.008	0.948	0.866	0.013	0.070	0.05
N ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3999	0.014	0.909	0.668	0.120	0.119	0.09
P ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3462	0.081	0.723	0.421	0.101	0.176	0.30
CN ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3772	0.077	0.740	0.251	0.106	0.362	0.28
CP ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3242	0.007	0.796	0.266	0.168	0.360	0.20
NP ~ Diet + Habitat + Mass + Taxonomy (C/O/F)	3291	0.009	0.792	0.288	0.140	0.363	0.20

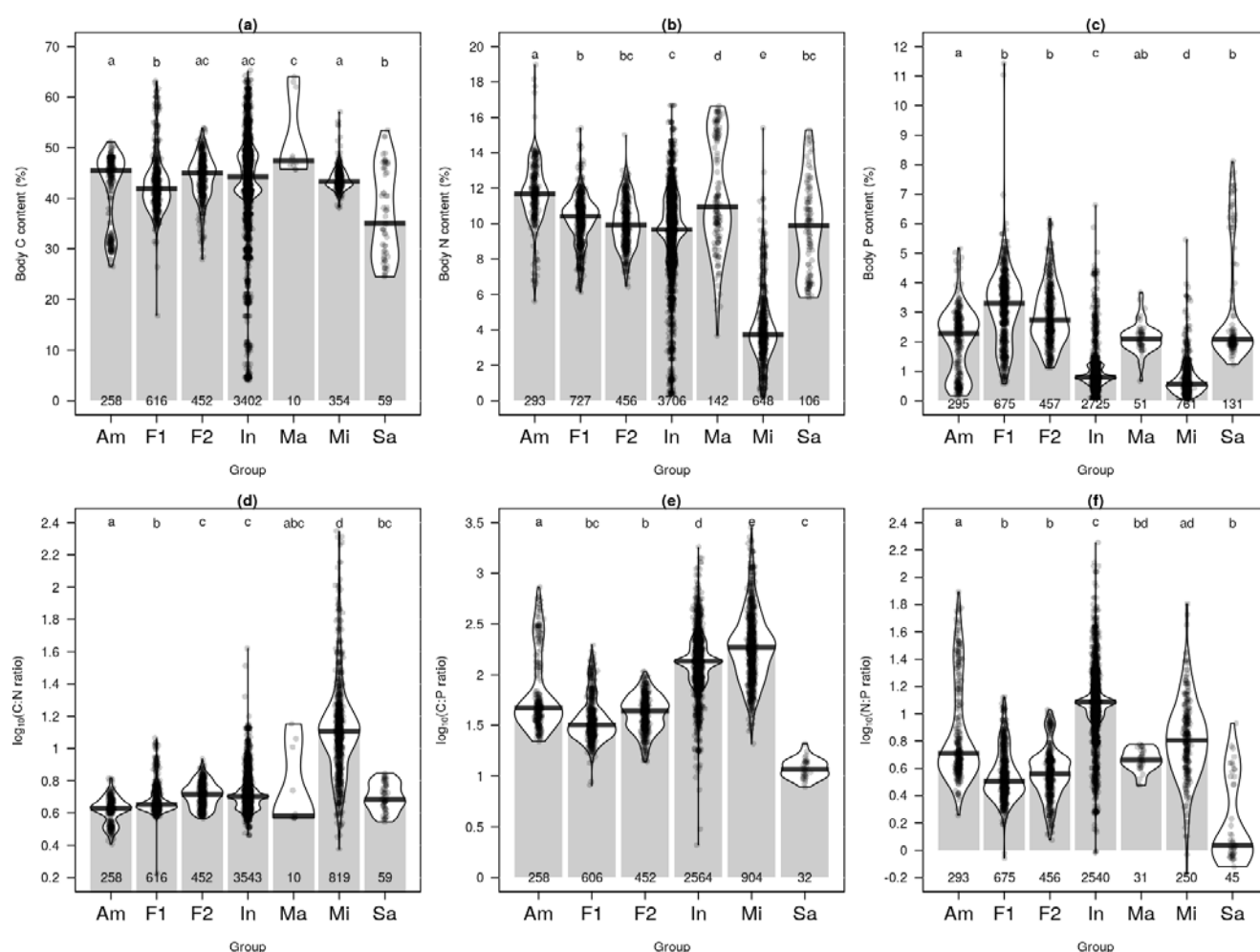
532 n: number of observations.

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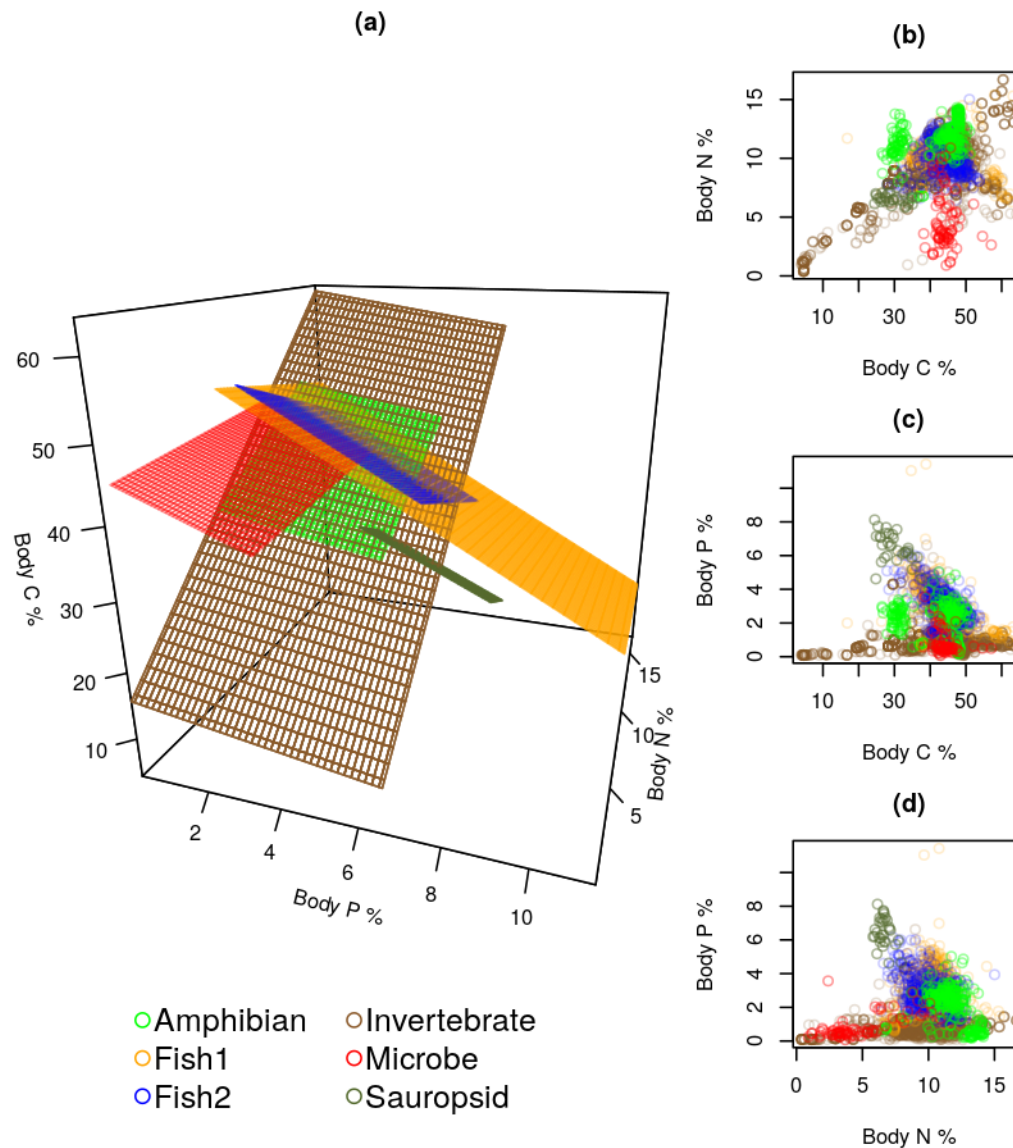
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# 536 FIGURES



537  
538 **Figure 1** Elemental content variation among taxonomical groups. (a) Body C content. (b) Body N  
539 content. (c) Body P content. (d) Log-transformed C:N ratio. (e) Log-transformed C:P ratio. (f) Log-  
540 transformed N:P ratio. Am: Amphibians, F1: Fishes – clade Euteleostei, F2: Fishes – clade  
541 Otomorpha, In: Invertebrates, Ma: Mammals, Mi: Microbes, Sa: Sauropsids (birds and reptiles). Raw  
542 data (points) and distributions (kernel densities) are depicted with the number of observations (at the  
543 bottom for each panel). Different letters indicate significant differences with post-hoc Dunn's tests of  
544 multiple comparisons with Bonferroni corrections that were performed before log-transformation.

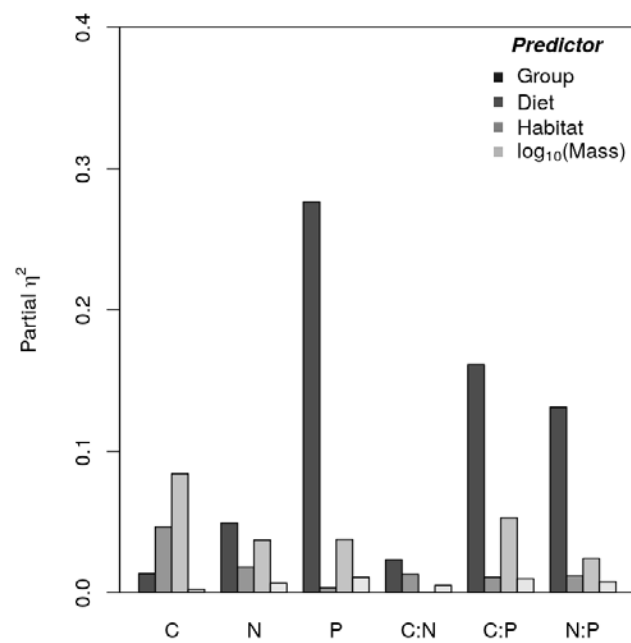


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549 **Figure 2** Co-variations in elemental content composition. (a) Stoichiometric spectrums computed as  
 550 the best-fit planes of the linear regression of C content against N and P contents, for each taxonomical  
 551 group separately.  $R^2 = 0.19$  for amphibians,  $0.38$  for fishes-1 (Euteleosteiomorpha),  $0.39$  for fishes-2  
 552 (Otomorpha),  $0.47$  for invertebrates,  $0.13$  for microbes,  $0.29$  for sauropsids. (b) Two-way relationships  
 553 between C and N contents, raw data. (c) Two-way relationships between C and P contents, raw data.  
 554 (d) Two-way relationships between N and P contents, raw data. There is no mammal data with  
 555 simultaneous measurements of C, N and P contents.

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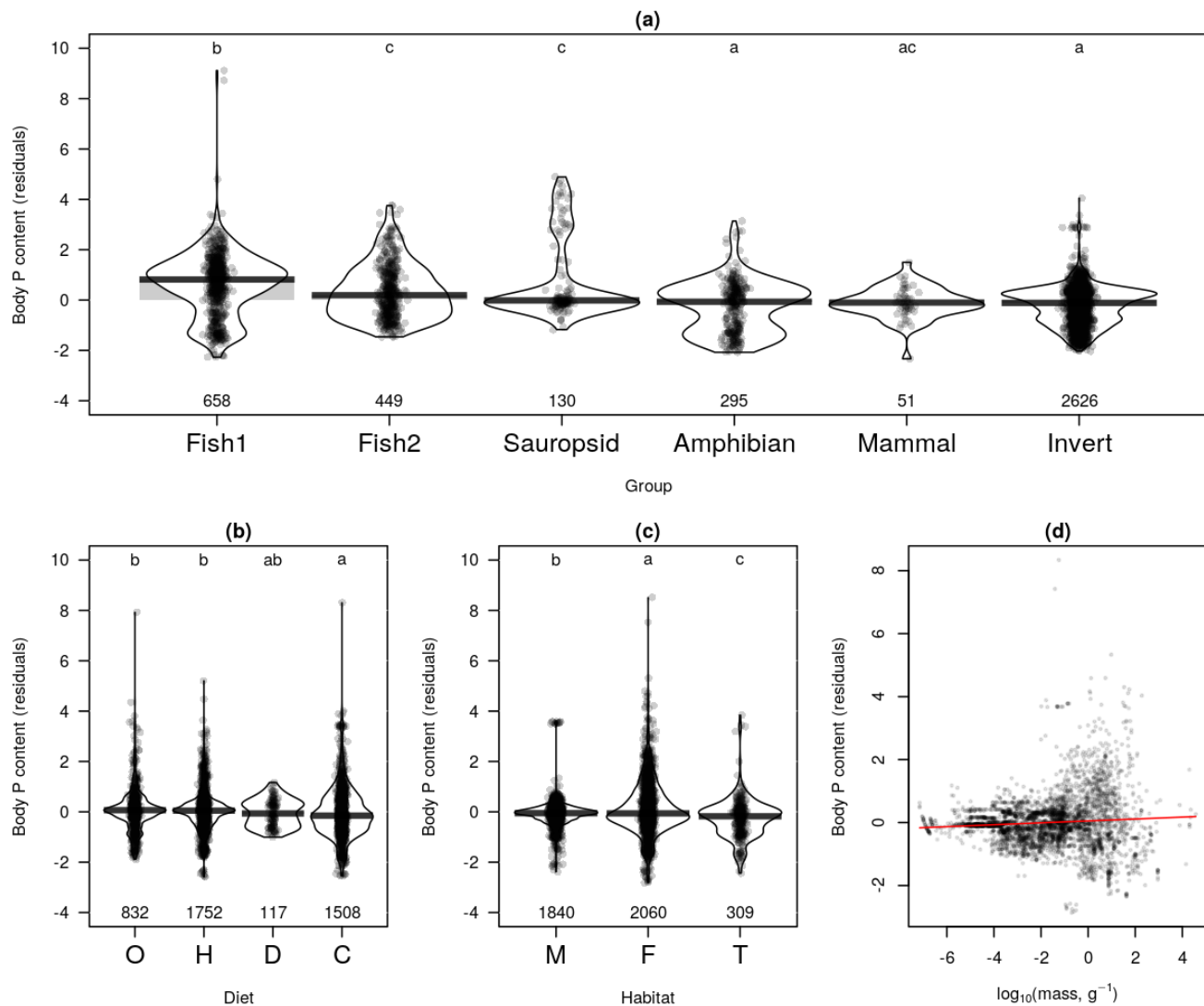
559 **Figure 3** Magnitude of the stoichiometric drivers for the six stoichiometric traits assessed with partial  
 560 eta-squared.

561

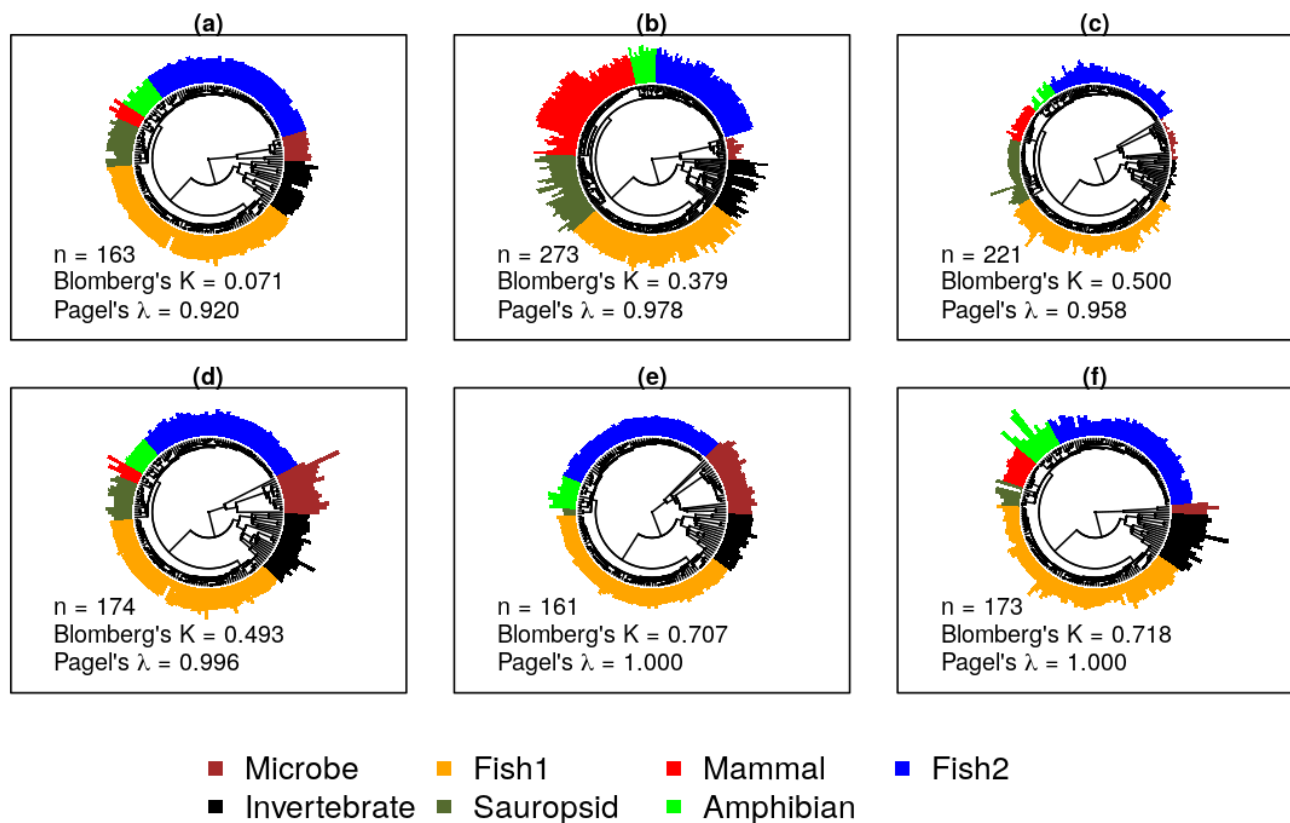
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**Figure 4** Magnitude of the stoichiometric drivers for P content assessed with sequential ANCOVAs. (a) taxonomic groups, (b) diet, (c) habitat and (d) body mass. Raw residuals (points) and distributions (kernel densities) are depicted with the number of observations (at the bottom for panels a-c). Different letters indicate significant differences with post-hoc Dunn's test of multiple comparisons with Bonferroni corrections (panels a-c). The red line panel (d) show the prediction of body P content residuals regressed against log-transformed dry body masses ( $y = 0.03 + 0.05x$ ,  $R^2 = 0.006$ ,  $p < 0.001$ ).



572

573 **Figure 5** Phylogenetic variation of the six stoichiometric traits. (a) Body C content. (b) Body N content.  
574 (c) Body P content. (d) C:N ratio. (e) C:P ratio. (f) N:P ratio. Colored bars represent standardized values  
575 of the traits. Data were log-transformed for stoichiometric ratios. n: number of observations. See Tab.  
576 S16 for more details on phylogenetic signal analyses.

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## 580 APPENDIX 1 – Data sources

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