

# Predator traits determine food-web architecture across ecosystems

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88 **Abstract**

89 Predator-prey interactions in natural ecosystems generate complex food webs that  
90 have a simple universal body-size architecture where predators are systematically larger  
91 than their prey. Food-web theory shows that the highest predator-prey body-mass ratios  
92 found in natural food webs may be especially important as they create weak interactions with  
93 slow dynamics that stabilize communities against perturbations and maintain ecosystem  
94 functioning. Identifying these vital interactions in real communities typically requires arduous  
95 identification of interactions in complex food webs. Here, we overcome this obstacle by  
96 developing predator-trait models to predict average body-mass ratios based on a database  
97 comprising 290 food webs from freshwater, marine and terrestrial ecosystems across all  
98 continents. We analyzed how species traits constrain body-size architecture by changing the  
99 slope of the predator-prey body-mass scaling. Across ecosystems, we found high body-  
100 mass ratios for predator groups with specific trait combinations including (1) small  
101 vertebrates and (2) large swimming or flying predators. Including the metabolic and  
102 movement types of predators increased the accuracy of predicting which species are  
103 engaged in high body-mass ratio interactions. We demonstrate that species traits explain  
104 striking patterns in the body-size architecture of natural food webs that underpin the stability  
105 and functioning of ecosystems, paving the way for community-level management of the most  
106 complex natural ecosystems.

107

## 108 Introduction

109 Prey rarely if ever give up their lives willingly to their predators. Predators overcome  
110 their prey's resistance by being, on average, larger than their prey, yielding a systematic  
111 pattern in communities where the non-cannibalistic average ratio of predator-to-prey body  
112 mass (hereafter: body-mass ratio) is higher than unity<sup>1,2</sup>. The notable exceptions to this  
113 include when animals cooperate to overcome larger prey (e.g. pack hunters) and where  
114 consumers are parasites or parasitoids. The variation in body-mass ratios within food webs  
115 typically spans several orders of magnitude and includes some predators that are smaller  
116 than their prey<sup>3</sup>, but is dominated by situations of the larger feeding on the smaller. The  
117 varying body-mass ratios limit which trophic interactions are realized in a community<sup>4-6</sup>, and  
118 the strength of these interactions<sup>7-9</sup>. Predators typically exert the strongest feeding pressure  
119 on prey that are one to two orders of magnitude smaller<sup>1</sup>, while weaker interaction strengths  
120 are realized with prey that are smaller or larger than this size<sup>10,11</sup>. Specifically, interactions of  
121 predators with small prey are characterized by high body-mass ratios that yield weak  
122 interactions with slow dynamics, which play a central role in maintaining food-web stability<sup>12-</sup>  
123 <sup>16</sup> and ecosystem functioning<sup>10,17,18</sup>. Moreover, they also buffer natural communities against  
124 perturbations from global warming<sup>19</sup>, eutrophication<sup>20</sup> and secondary extinction waves<sup>21</sup>.  
125 Therefore, identifying these unique interactions is paramount to determining the stability of  
126 natural food webs to perturbations and functioning, but applications of this concept to natural  
127 communities have been hampered by the difficulty of describing the myriads of interactions  
128 present in natural food webs. Using traits of predator species as proxies of body-mass ratios  
129 and the resulting interaction strengths that they govern could provide the means to  
130 understand which species are drivers of community stability and functioning without having  
131 to perform the often logistically and economically impossible task of quantifying entire  
132 interaction networks. This approach could ultimately help predict how extinctions, invasions  
133 and other anthropogenic environmental changes affect community stability and functioning  
134 through shifts in community trait structure.

135 Despite the importance of understanding how species traits affect body-mass ratios,  
136 there is much uncertainty about these relationships. A pioneering study<sup>22</sup> showed that  
137 vertebrate predators exhibit systematically higher body-mass ratios than invertebrates and  
138 this has been supported by subsequent analyses also documenting higher body-mass ratios  
139 in aquatic versus terrestrial communities<sup>1</sup>. These studies also found that predator-prey body-  
140 mass scaling is superlinear with slopes higher than unity, meaning that body-mass ratios  
141 increase with body mass (see Supplementary Figure 1, red line). However, other studies

142 have proposed that the scaling relationship is either sublinear (decreasing body-mass ratios  
 143 with body mass; Supplementary Figure 1, yellow line)<sup>2,22,23</sup> or superlinear<sup>1,2,23,24</sup>, depending  
 144 on the ecosystem type<sup>2,23</sup>, predator metabolic group<sup>23–25</sup> or resource supply<sup>26</sup>. Additionally,  
 145 besides body mass and metabolic type, little is known about how body-mass ratios vary with  
 146 other species traits and across different ecosystem types. Predator and prey movement  
 147 types and feeding behavior are likely to influence scaling relationships by limiting maximum  
 148 achievable attack speeds<sup>24,27</sup>. Interaction dimensionality, which describes whether predators  
 149 forage in three dimensions (e.g. the water column of lakes and oceans) or on two-  
 150 dimensional surfaces (e.g. epigeic terrestrial or benthic aquatic predators), also influences  
 151 predator-prey attack rates<sup>24,28</sup>. As these variables affect the likelihood and strength of  
 152 predator attack rates and scale with individual body mass, we expected that they should also  
 153 modify the scaling relationship between predator and prey body masses.

154

155 *Insert Fig. 1 here*

156

157 Here, we provide a comprehensive assessment of how species traits modulate  
 158 predator-prey body-mass scaling relationships and body-mass ratios in natural, complex  
 159 food webs across an unprecedented range of ecosystems. To do so, we collated the most  
 160 extensive global food-web database (GlobAI daTabasE of traits and food Web Architecture,  
 161 GATEWAY version 1.0) to date, comprising 290 food webs (with 222,151 feeding links  
 162 between 5736 species; see Supplementary Table 1) distributed across the globe (Fig. 1),  
 163 and including information on four different species traits and five ecosystem types (see  
 164 Supplementary Table 2). First, we analyzed the scaling of predator and prey body masses  
 165 over 17 orders of magnitude (fresh masses ranging from the  $2 \cdot 10^{-9}$  g protozoan *Bodo*  
 166 *saltans*, to the  $275 \cdot 10^6$  g sperm whale *Physeter microcephalus*). Some prior studies  
 167 advocated the use of major axis regressions to account for the bidirectional causality  
 168 between predator and prey body mass<sup>1</sup>, whereas others used mixed-effects models to  
 169 include random effects of the study<sup>2</sup>. As these two types of analyses are mutually exclusive  
 170 in traditional statistics, we used Bayesian modelling to implement a combination of major  
 171 axis regressions with mixed effects. Second, we tested for the importance of co-factors in  
 172 this scaling relationship (ecosystem type, predator and prey metabolic types, interaction  
 173 dimensionality, predator and prey movement types). These analyses address relationships  
 174 between species traits and food-web architecture across ecosystems. Third, we developed  
 175 predictions of average body-mass ratios of predators by their traits, which identifies  
 176 ecological attributes that broadly predict ecological perturbation stability and functioning in  
 177 natural communities without requiring detailed knowledge of complex food-web structure.

## 178 Results

179 In our first analysis, we addressed the scaling of predator and prey body masses.  
180 Ordinary least squares (OLS) regressions relating these two variables generate different  
181 slopes depending on which variable is chosen as the independent variable (Fig. 2, magenta  
182 and blue lines). This discrepancy arises because there is no unidirectional causal  
183 relationship between the two variables and because both have measurement errors of the  
184 same magnitude, which renders major axis regression the appropriate tool for analyzing  
185 these data<sup>31</sup>. Thus, we used Bayesian modelling to fit a major axis regression, which makes  
186 no assumptions about a causal relationship between the variables. The major axis  
187 regression showed that the overall allometric scaling relationship between predator and prey  
188 body mass was superlinear, exhibiting a slope higher than unity (Fig. 2, black solid line,  
189 Bayesian major axis regression, slope = 1.315, 95% CI: 1.307-1.323). This suggests that the  
190 body-mass ratios between predators and their prey increase with the masses of prey and  
191 predators (i.e. the distance between the regression line and the dashed diagonal indicating  
192 equally sized predator-prey pairs). On average, interactions between relatively large  
193 predator and prey species are characterized by higher body-mass ratios than interactions  
194 between smaller species. The Bayesian approach also allowed us to fit mixed-effects  
195 models to the data, particularly the random effects on the intercept of the different studies  
196 (database variable: link.citation; see Supplementary Table GATEWAY metadata). This  
197 yielded a very similar scaling relationship as the non-mixed major axis regression (Fig. 2,  
198 green line). Based on the similarity of the results and statistical arguments (see Methods),  
199 we have based the following analyses on Bayesian major axis regressions, while results of  
200 the analyses with Bayesian mixed-effects major axis regressions are shown in the  
201 supplement.

202

203 *Insert Fig. 2 here*

204

205 In our second analysis, we used major axis regressions to fit six models of predator-  
206 prey body mass scaling that each contained one co-variable (ecosystem type, predator or  
207 prey metabolic type, predator or prey movement type, interaction dimensionality; see  
208 Supplementary Table 2 for variable description). Model comparisons demonstrated that  
209 adding any of these co-variables improves the fit substantially over the simple scaling model  
210 (Table 1, lower WAIC scores indicate higher model adequacy). According to these WAIC  
211 ranks, the best-performing models included predator metabolic type (rank 1) or predator  
212 movement type (rank 2) as co-variables, whereas models including the same trait variables

213 of the prey led to lower ranks (Table 1, ranks 4 and 6). Hence, WAIC values suggested that  
 214 predator traits were more important for determining body-mass scaling than prey traits.

215

216 *Insert Table 1 here*

217

218 While the overall relationship was superlinear (Fig. 3, black solid lines), the  
 219 relationships for ectotherm and endotherm vertebrate predators exhibited strong sublinear  
 220 scaling, implying that the body-mass ratios of vertebrate predators decrease with their body  
 221 mass (Fig. 3a). As vertebrate prey often have vertebrate predators, a similar pattern might  
 222 be expected for the scaling relationship within the prey metabolic groups. Surprisingly, we  
 223 found superlinear scaling for all vertebrate prey groups (Fig. 3b). Together, these results  
 224 suggest that the sublinear scaling characterizes vertebrate predators irrespective of whether  
 225 their prey are vertebrate or invertebrate species.

226 The second most important co-variable in our analyses was predator movement type.  
 227 Interestingly, we found that swimming, flying and sessile predators exhibit superlinear  
 228 scaling relationships that are similar to the overall model, whereas walking predators exhibit  
 229 sublinear scaling (Fig. 3c). Although many walking predators feed on walking prey, our  
 230 analyses of the prey movement type show superlinear scaling across groups (Fig. 3d).  
 231 Similar to the metabolic groups, this implies that changes in predator-prey body-mass ratios  
 232 are mainly driven by predator movement type, irrespective of prey movement type. Together,  
 233 our analyses of species' traits suggest that the traits of predators have stronger implications  
 234 for scaling relationships and body-mass ratios than the traits of their prey.

235

236 *Insert Fig. 3 here*

237

238 Comparing the two environmental characteristics showed that ecosystem type (WAIC  
 239 rank 3) improved the model substantially more than interaction dimensionality (2D vs. 3D;  
 240 rank 5, Table 1). Among ecosystem types, marine, stream and terrestrial aboveground  
 241 ecosystems follow superlinear scaling similarly to the overall relationship (although streams  
 242 followed steeper scaling relationships), whereas lake and terrestrial belowground  
 243 ecosystems exhibit sublinear scaling, parallel to each other (Fig. 4a). Both 2D and 3D  
 244 interaction dimensionality demonstrate superlinear scaling with a slope similar to the overall  
 245 pattern. However, 3D interactions tend to involve predator-prey pairs with greater body-mass  
 246 ratios compared to 2D interactions (Fig. 4b). Although many marine or lake interactions  
 247 occur in the pelagic 3D part of the ecosystem, ecosystem type does not completely overlap  
 248 with interaction dimensionality as these aquatic ecosystems also include benthic 2D  
 249 interactions.

250

251 *Insert Fig. 4 here*

252

253         Finally, we addressed how well we can predict which predators in a food web have the  
 254 highest average body-mass ratios compared with their prey in the absence of information on  
 255 food-web structure and traits of the prey species. The statistical models thus included the  
 256 predator traits (body mass, metabolic and movement type) and ecosystem type as  
 257 independent variables (“predator-trait model”, see Methods for details and Supplementary  
 258 Table 4 for parameters). The overall predator-trait model fitted the data well (Fig. 5a). We  
 259 found that predictive accuracy varied across ecosystem types and with the fraction of target  
 260 predators (Fig. 5b). We anticipated that typically a low fraction of predators will be chosen for  
 261 applied population management and used a fraction of target predators of 25% as an  
 262 arbitrary example to illustrate our results (Fig. 5b, grey area; note that qualitatively similar  
 263 results could be obtained for any fraction of 30% or lower). At this fraction of target  
 264 predators, the accuracy of the predator-trait model predictions is almost always higher than  
 265 the prediction accuracy when the same fraction of predators is chosen at random (Fig. 5b,  
 266 diagonal line). An exception to this pattern were the terrestrial belowground systems (Fig.  
 267 5b), potentially as a consequence of the substantially higher degree of omnivory in soil  
 268 communities<sup>29</sup> or the widespread use of poison by soil predators<sup>32</sup>. In contrast, the predator-  
 269 trait model had high accuracy in streams (89%), marine (61%), terrestrial aboveground  
 270 (64%) and lake ecosystems (61%), exceeding the 25% accuracy of random predictions (Fig.  
 271 5b, diagonal line in the grey area). This implies that for these ecosystems the predator-trait  
 272 model improves the predictions by a factor between 2.44 (marine and lake ecosystems) and  
 273 3.56 (streams), which is close to the maximum improvement factor of 4 (occurring with 100%  
 274 prediction accuracy relative to the 25% random prediction accuracy at a fraction of target  
 275 predators of 25%, grey shaded area in Fig. 5b).

276

277 *Insert Fig. 5 here*

278

## 279 Discussion

280         Using a global database of 290 food webs we show that (1) the overall allometric  
 281 scaling relationship between predator and prey body mass is superlinear, implying that the  
 282 largest species have the highest body-mass ratios and that (2) predator traits (metabolic and  
 283 movement type) are more important than prey traits in determining these scaling

284 relationships. Subsequently, we developed a predator-trait model that successfully predicted  
 285 the predators with the highest average body-mass ratio. Food-web theory has shown that  
 286 these high body-mass ratios yield weak interactions with slow dynamics that are critically  
 287 important for buffering communities against external perturbations and maintaining  
 288 ecosystem functioning<sup>10,12–15,17,18</sup>. Historically, these theoretical results have had little real-  
 289 world application, as they require the logistically challenging task of assessing all or at least  
 290 a large fraction of the food-web links. By focusing on predator traits and ecosystem type  
 291 while discarding prey traits and the specific links of the food-webs, our predator-trait model  
 292 provides a generalizable and feasible solution that can bridge the gap between food-web  
 293 theory and applied ecosystem conservation. For instance, our results suggest that  
 294 population protection of small vertebrates (e.g. mustelids) and large swimming (e.g. sharks)  
 295 or flying predators (e.g. birds of prey) might be most effective at buffering natural  
 296 communities against external perturbations such as extinctions, invasions, pollution,  
 297 eutrophication and warming. This trait-based approach enables the management of  
 298 perturbation vulnerability in natural communities without detailed knowledge of the food-web  
 299 structure.

300         Within the debate over the allometric scaling relationships of predator and prey body-  
 301 masses in natural food webs, the superlinear relationship presented here is consistent with  
 302 some prior studies<sup>1,2,23</sup>, while deviating from others that demonstrate sublinear scaling<sup>2,22,23</sup>.  
 303 Our comparison of regression methods suggests that this discrepancy could be partially  
 304 attributed to the alternative use of major axis regressions<sup>1</sup> (consistently yielding superlinear  
 305 scaling) or ordinary least square (OLS) regressions<sup>2,22,23</sup> (suggesting superlinear or sublinear  
 306 scaling depending on which is the independent variable). Our comparison of the two OLS  
 307 regressions with either predator or prey mass as the independent variable reveals  
 308 substantial uncertainty as they make opposite predictions on how body-mass ratios scale  
 309 with predator and prey mass, and there is no *a priori* argument over which OLS regression  
 310 should be preferred. Hence, major axis regressions are the most appropriate statistical  
 311 method because: (1) there is no *a priori* expectation for a causal relationship between  
 312 predator and prey mass, and (2) both body masses are quantified with the same  
 313 measurement error<sup>31</sup>. Our results show that major axis regression is not only statistically  
 314 more appropriate but also that the choice of statistical approach has important biological  
 315 implications for interpretation of the allometric scaling relationship. This approach, combined  
 316 with our newly compiled food-web database, has enabled refining our understanding of how  
 317 the scaling relationship between predator and prey body mass varies across ecosystems  
 318 and between predator-prey combinations of different movement type and metabolic group.

319         Despite the overall superlinear relationship between predator and prey body mass, our  
 320 analyses identified several species' traits and ecosystem characteristics that are associated

321 with a sublinear scaling relationship. Most notably, both ectotherm and endotherm vertebrate  
322 predators demonstrate strong sublinear scaling, making predator metabolic type the most  
323 important factor among those we considered for predicting predator-prey body-mass scaling  
324 relationships. Consistent with previous research<sup>1,22,23</sup>, we found that large vertebrate  
325 predators tend, on average, to feed on prey that are more equally sized (e.g. orcas feeding  
326 on minke whales), whereas small vertebrate predators consume relatively smaller prey (e.g.  
327 arctic foxes preying on lemmings). This result suggests that large and small vertebrate  
328 predators may be constrained by different factors, such as the limitations of maximum attack  
329 speed which are only experienced by the largest species<sup>27</sup>. Interestingly, some (often large)  
330 vertebrate predators hunt in groups to attack larger prey to improve their attacking success  
331 and overcome the body mass and speed constraints. Indeed, the next most important factor  
332 in our analysis was predator movement type, which separates species categories of different  
333 speeds (e.g. flying predators are faster than walking predators). In our analysis, walking  
334 predators demonstrate sublinear scaling in contrast to all other movement types. The highest  
335 body-mass ratios were observed for the largest swimming and flying predators. Further  
336 investigations of the physiological constraints related to predator movement type, metabolic  
337 type and relative predator-prey body masses on predator feeding rates would help illuminate  
338 the processes behind these observed patterns.

339       Generally, our model selection results suggest that predator metabolic and movement  
340 traits had much stronger effects on the scaling relationship than the equivalent prey traits.  
341 This is partially supported by the greater similarity between the major axis regression  
342 (accounting for bi-directional causalities) and the OLS regression with prey body mass as  
343 the dependent variable. We therefore conclude that top-down prey selection by predators  
344 has a stronger effect on prey mass than does the bottom-up influence of prey mass on  
345 predator masses. It is likely that both top-down and bottom-up influences are important, but  
346 our results indicate the dominance of the former, which stimulated the development of the  
347 predator-trait models of our third analyses predicting which predators have the highest  
348 average body-mass ratios across food webs.

349       Our results also identify ecosystem type as an important co-factor of the predator-prey  
350 body-mass scaling relationship, which is generally consistent with prior studies<sup>23,24,33</sup>. We  
351 expected this effect to be partially explained by the habitat dimensionality of the interaction  
352 (2D or 3D), which has important consequences for the strength of predator attack rates<sup>24,28</sup>.  
353 Although we found an effect of interaction dimensionality with overall higher body-mass  
354 ratios in 3D than in 2D habitats, surprisingly it did not explain the different scaling  
355 relationships between different ecosystem types. This may be explained by the fact that the  
356 ecosystem type varies across food webs, whereas variance in interaction dimensionality  
357 plays an important role across the different predator-prey pairs with food webs. The superior

358 explanatory power of the model including ecosystem type compared to that including  
 359 interaction habitat dimensionality suggests that there are ecosystem characteristics not  
 360 related to dimensionality, such as laminar viscosity, that may have a stronger effect on  
 361 predator-prey interactions. We found relatively high body-mass ratios and a very steep body-  
 362 mass scaling relationship in stream ecosystems. The streams exhibit some differences to  
 363 the other ecosystem types of our database: (1) the higher physical drag force of the water,  
 364 (2) the higher dependence on allochthonous resources, (3) the dendritic environmental  
 365 structure, and (4) the relatively narrower range of body masses included in our data. While  
 366 each of these points could be responsible for the difference in scaling relationships, the last  
 367 point calls for additional data on stream interactions between larger species such as fish to  
 368 see if the steep increase in the scaling relationship holds. While terrestrial aboveground and  
 369 marine interactions exhibited superlinear scaling relationships as the overall relationship,  
 370 those of lake and terrestrial belowground systems were sublinear. Furthermore, the lack of  
 371 vertebrate predators with high body masses and high body-mass ratios may at least partially  
 372 explain this for soil communities, but this surprising result requires more mechanistic  
 373 investigation of the so far untested similarity between lake and belowground interactions.

374 Our approach to characterize predator-prey body-mass ratios in natural food webs has  
 375 some limitations. First, in order to encompass a wide range of body masses, taxonomy and  
 376 ecosystem types, we assume that interacting individuals have population-average body  
 377 masses<sup>34</sup>. As in prior studies<sup>1,22,23,33</sup>, we rely on population-averaged body masses, since we  
 378 do rarely have measurements for the actual body masses of the interacting individuals.  
 379 Thus, for many predator species, particularly those with ontogenetic diet shifts, actual body-  
 380 mass ratios are likely to have a lower variation than body-mass ratios calculated from  
 381 population averages. Unfortunately, the lack of individual data for entire food webs across  
 382 ecosystems hampers any alternative approach. As prior comparisons of individual-based  
 383 versus population-based food webs have shown<sup>34,35</sup>, our population-based approach likely  
 384 underestimates the intercepts of the scaling relationships. Second, the study sampling  
 385 design, environmental factors such as temperature and the species' phylogeny may also  
 386 affect the scaling relationship<sup>25,36-38</sup>, and these would ideally be included as co-variables in  
 387 the analyses. As these data were not systematically available for the data sets included, we  
 388 accounted for them by random effects in mixed models<sup>2</sup>, which leaves the need for more  
 389 detailed analyses for future studies. As major axis regressions with random effects are not  
 390 generally available, we addressed this issue by using Bayesian models throughout the  
 391 study, which allowed comparisons with hierarchical models including random effects (i.e.  
 392 mixed-effects models). Although the mixed effects model results do not change our findings  
 393 substantially (see Supplement for a comparison between mixed and non-mixed Bayesian  
 394 models) and, due to potentially confounding clustering effects (see Methods), we have

395 focused our analysis on the model without mixed effects. Third, our analyses were restricted  
396 to predator-prey interactions, whereas interactions of other consumer types such as  
397 parasites, parasitoids or herbivores were excluded. As these interaction types are typically  
398 characterized by different body-mass ratios<sup>1,39,40</sup>, future studies should address their scaling  
399 relationships in our GATEWAY database. Fourth, we employed simple scaling relationships  
400 with up to one single co-variable to gain an in-depth mechanistic understanding, whereas  
401 models with interactions between multiple co-variables were omitted from our analyses of  
402 the predator-prey body-mass scaling. These more complex relationships with higher order  
403 interactive effects, however, could be addressed by black box approaches such as machine  
404 learning algorithms, which could provide accurate predictions of food-web structures<sup>32</sup>. Fifth,  
405 our study illustrates systematic differences in body-mass ratios across ecosystem types and  
406 species' traits, whereas explanations for these differences remain to be revealed by studies  
407 integrating mechanistic models with our data.

408         Our analyses provide insights into how predator and prey body masses scale with  
409 each other in natural food webs. The discovery that predator traits are more important than  
410 prey traits in predicting body-mass scaling and that ecosystem type has a greater effect than  
411 interaction dimensionality offers new possibilities for understanding and predicting  
412 differences in food-web structure, community stability and ecosystem functioning across  
413 community and ecosystem types. Specifically, our results highlight that critically important  
414 high body-mass ratios occur in interactions with predators that are (1) small vertebrates or  
415 (2) large swimming or flying species. With only three species traits (body mass, metabolic  
416 and movement type), our models were able to predict which 25% of the predators possess  
417 the highest average body-mass ratios with surprisingly high accuracy in most ecosystem  
418 types (58-89%). We anticipate that this accuracy will be increased by additional species  
419 traits (e.g. predation strategy, use of poison, sub-habitat association) that compose the  
420 multiple dimensions of natural food webs<sup>6,32</sup>. Our trait-based food-web analyses enable  
421 generalizations of food-web theory from the food webs studied to the vast majority of  
422 communities for which only species and trait information is available. Updated with additional  
423 traits, this approach has great potential for managing ecosystem functioning and stability  
424 against external perturbations such as pollution, eutrophication and warming without full  
425 knowledge of food-web structure. The trait-based body-mass ratio approach therefore  
426 presents an important integration of food-web theory with applied ecosystem management  
427 that provides a theoretical foundation for the community-level conservation of the most  
428 complex natural ecosystems.

429

## Methods

430 We compiled a global database of traits and food-web architecture (GATEWAY version  
431 1.0, see Supplement), where each link is characterized by the taxonomy and trait variables  
432 of both the consumer and the resource (see Supplement metadata for variables). We  
433 included food webs with (1) a sufficient quality in terms of taxonomic resolution, which  
434 prevents nodes aggregating species with very different trophic interactions; (2) a reasonable  
435 completeness integrating all trophic levels and community compartments; (3) trait  
436 information for the trophic species including at least their population-averaged body mass,  
437 their metabolic type and their movement type (see Supplementary metadata table for  
438 definitions); (4) information for each trophic link such as the type (e.g. predacious), the  
439 dimensionality (2D and 3D) and the classification (individual-based and non-individual-  
440 based) (see Supplement metadata table for definitions); (5) descriptors for the ecosystems  
441 such as the ecosystem type and the geographic location.

442 In our analyses, we focused on predatory (variable: `interaction.type`) and individual-  
443 based (variable: `interaction.classification`) interactions. The former excludes interactions of  
444 other types (e.g. herbivorous, detritivorous, parasitic, parasitoid), whereas the latter discards  
445 interactions of consumers attacking groups, swarms or films of resources (e.g. filter feeding,  
446 grazing). Some of the studies included in our database sampled the same ecosystem at  
447 different locations, resulting in replicated predator-prey species pairs<sup>29</sup>. To avoid  
448 pseudoreplication, each unique combination of taxonomy, life stage, and individual body  
449 mass for predator and prey species was included only once. After exclusion of interactions  
450 with missing variables, the resulting data included 88,197 unique predator-prey interactions  
451 among the original 222,151 feeding links.

452 First, we analyzed the reduced data for the relationship between the base-10  
453 logarithms ( $\log_{10}$ ) of predator and prey body masses [gram fresh mass]. We compared the fit  
454 of two ordinary least squares (OLS) regressions (either predator mass or prey mass as the  
455 dependent variable) to that of a major axis regression and a mixed-effects major axis  
456 regression including random effects on the intercept of the different studies (variable:  
457 `link.citation`). Traditional methods only allow to fit either major axis regressions or mixed  
458 models with random effects. Hence, our aim of comparing major axis regressions with and  
459 without random effects (i.e. random intercepts for each study) could only be achieved by  
460 realizing models that were fitted by Bayesian methods using the RStan package<sup>30</sup> (see  
461 supplementary statistical methods for details). Consistent with traditional major axis  
462 regressions, we minimized the sum of squared orthogonal distances of the observations

463 (x,y) to the regression line<sup>31</sup> instead of the vertical distance (y) as in OLS (model I)  
 464 regressions.

465         Second, we used Bayesian major axis models to compare the fit of the simple scaling  
 466 model to six models, whereby each included one co-variable: ecosystem type, predator or  
 467 prey metabolic type, predator or prey movement type or interaction dimensionality (see  
 468 Supplementary Table 2 for variables). Overall, the results were mostly consistent between  
 469 the mixed-effects and non-mixed models. The mixed-effects models fit the relationships  
 470 separately for each study. As the body-mass ranges within studies do not cover the entire  
 471 body-mass gradient and the number of data points within studies is much lower than in the  
 472 entire database, some of the fitted scaling relationships can become arbitrary as single  
 473 points can strongly affect the slope. Averaging across all slopes and all intercepts using  
 474 hierarchical approaches can lead to clusters of such arbitrary slopes, which can exert  
 475 substantial leverage on the average relationship across all studies. In our data, the clustering  
 476 remained even when using random intercepts and a fixed slope across all studies.  
 477 Therefore, the mixed-effects modelling of our data suffered from two limitations: (1) it loses  
 478 information about the overall trend across the whole database (i.e. none of the study-specific  
 479 scaling relationships spans the entire body-mass gradient), and (2) the joint mean slope and  
 480 intercept are affected by partially arbitrary slopes (data sets with few points). As both  
 481 regressions also yielded qualitatively similar results, we report the results of the non-mixed  
 482 major axis regressions in the manuscript (Figs. 3, 4) with comparisons to the fits of the mixed  
 483 major axis regressions in the supplement (Supplementary Figures 2-7). Model comparison  
 484 (based on their WAIC values, Watanabe-Akaike Information Criterion) of these seven  
 485 models (the simple model without co-variable and the six models with one co-variable each)  
 486 provided a ranking of their performance, and we used the model parameters to gain an  
 487 understanding of how they modify the relationship. In the analysis of predator-prey body-  
 488 mass scaling, we refrained from analyzing more complex models with interactions between  
 489 these co-variables for three reasons: (1) they imply impossible combinations (e.g. swimming  
 490 predators in terrestrial ecosystems), (2) their higher order interactions hamper the  
 491 mechanistic understanding of individual effects, and (3) their strong collinearity causes  
 492 interference between factors.

493         Third, we analyzed our database for the dependence of the predators' average  
 494 predator-prey body-mass ratios on predator traits (body mass, metabolic and movement  
 495 type) and ecosystem type. To avoid circularity in the statistical model (predator body mass in  
 496 both the dependent and independent variables), we fitted Bayesian major axis regressions  
 497 with  $\log_{10}$  prey mass as the dependent and  $\log_{10}$  predator mass as the independent variable  
 498 with the co-variables predator metabolic type, predator movement type, and ecosystem type.  
 499 We restructured the resulting predator-trait model equation to calculate the effect of the

500 independent and co-variables on predator-prey body-mass ratios. By discarding prey  
501 species traits, these analyses allow prediction of which predators in a community have the  
502 highest average body-mass ratios without knowledge of the predator-prey links.

503         The accuracy of this approach was determined in a five-step cross-validation process.  
504 First, we chose one of the food webs (“test data”) and ranked its predators according to their  
505 empirical average body-mass ratios. Second, we ran the predator-trait regression model  
506 described above in the remaining database containing the other 289 food webs (“training  
507 data”) to predict the predators’ average body-mass ratios depending on their traits. Third, we  
508 calculated the proportion of predators that were correctly predicted by this “predator-trait  
509 model” (hereafter: accuracy) for a fraction  $x$  of the highest ranked predators of the test-data  
510 food web (hereafter: fraction of target predators). For example, a fraction of target predators  
511 of 0.1 implies that the 10% highest ranked predators (i.e. those with the highest average  
512 body-mass ratios) of the empirical “test data” are compared to the 10% highest ranked  
513 predators as predicted by the predator-trait model of the “training data”. An exemplary  
514 accuracy of 0.8 would indicate an 80% overlap between the two species lists. Fourth, this  
515 assessment of prediction accuracy was systematically replicated across a gradient in the  
516 fraction of target predators  $x$  between 5% and 95% (steps of 5%). Finally, these four steps  
517 were repeated for each of the 290 food webs independently to calculate the average  
518 accuracy across food webs depending on the fraction of target predators.

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526 organizing a prior version of the database.

## 527 Data availability

528 The data supporting the findings of this study (GATEWAY 1.0) are available at the iDiv data  
529 repository<sup>41</sup>.

530 **Code availability**

531 The R code of the statistical analyses is available as a supplement.

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619

## 620 Author contributions

621 U.B. developed the study design. All authors gathered, contributed or organized data. U.B.  
622 and B.R. carried out statistical analyses. M.R.H. made the figures. U.B. and A.C.I. wrote the  
623 first draft of the manuscript. All authors discussed the results and commented on the  
624 manuscript.

## 625 Competing interests

626 The authors declare no competing financial interests.  
627

628 **Table 1:** Comparison (Watanabe-Akaike Information Criterion, WAIC) of six predator-prey  
 629 body-mass scaling models with one co-variable. Bayesian major axis models (ma) as in Fig.  
 630 3 and Fig. 4 of the main manuscript and mixed Bayesian major axis models as in  
 631 Supplementary Figures 2-7.

Co-variable	Bayesian ma		Bayesian ma mixed	
	WAIC	Rank	WAIC	rank
Predator metabolic group	$2.414 \times 10^5$	1	$2.229 \times 10^5$	1
Predator movement type	$2.720 \times 10^5$	2	$2.520 \times 10^5$	2
Ecosystem type	$2.722 \times 10^5$	3	$2.566 \times 10^5$	4
Prey metabolic group	$2.807 \times 10^5$	4	$2.563 \times 10^5$	3
Interaction dimensionality	$2.818 \times 10^5$	5	$2.616 \times 10^5$	6
Prey movement type	$2.830 \times 10^5$	6	$2.605 \times 10^5$	5
None	$2.859 \times 10^5$	7	$2.657 \times 10^5$	7

632  
 633

## 634 Figure legends

635 **Fig. 1:** The global distribution of food webs in GATEWAY (GlobAl daTabasE of traits and  
636 food Web Architecture, GATEWAY version 1.0, see Supplement).

637 **Fig. 2:** Overall scaling of predator and prey body mass assessed by four regression  
638 methods (n=88,197). Ordinary least squares regression (OLS) of prey mass depending on  
639 predator mass (blue line), ordinary least squares regression of predator mass depending on  
640 prey mass (magenta line), Bayesian major axis regression (black line), mixed Bayesian  
641 major axis (ma) regression with random intercepts (green line). Bayesian regression  
642 parameters are the means of the posterior distributions. The dashed line indicates equal  
643 body masses of predator and prey for comparison. All body masses are gram fresh masses.  
644 See Supplementary Table 3 for model parameters. Our extensive statistical considerations  
645 hold that the Bayesian major axis regression (black line) is the most appropriate model.

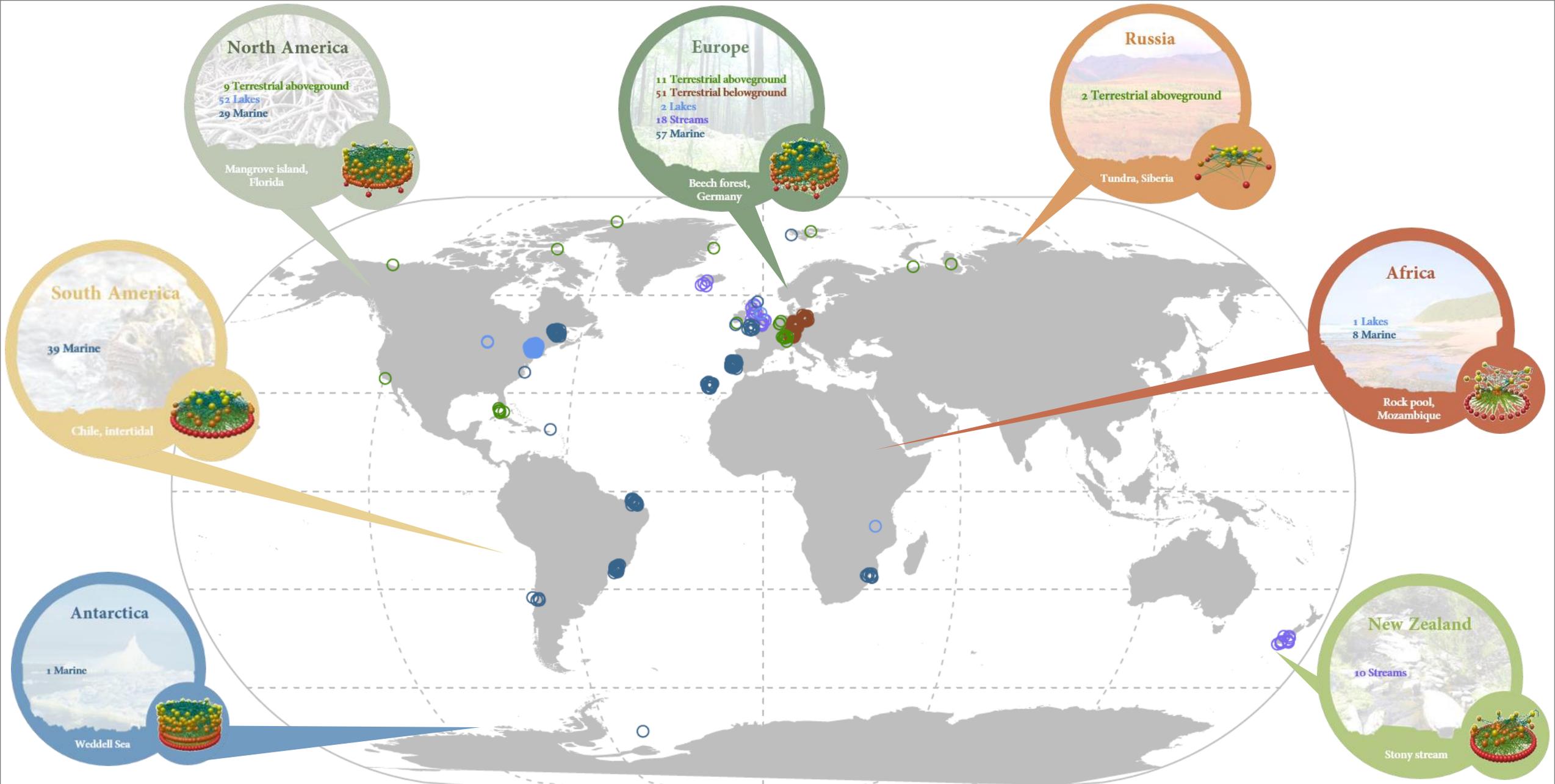
646 **Fig. 3:** Species' traits constrain the scaling of  $\log_{10}$  predator body mass with  $\log_{10}$  prey body  
647 mass (n=88,197): **(a)** predator metabolic type, **(b)** prey metabolic type, **(c)** predator  
648 movement type, **(d)** prey movement type. Solid black lines represent the overall scaling  
649 relationship, and the colored lines show the relationships for subgroups. Bayesian  
650 regression parameters are the means of the posterior distributions. Dashed lines indicate  
651 equal body masses of predator and prey for comparisons. See Supplementary Table 3 for  
652 model parameters.

653 **Fig. 4:** Ecosystem characteristics constrain the scaling of  $\log_{10}$  predator body mass with  
654  $\log_{10}$  prey body mass (n=88,197): **(a)** ecosystem type, **(b)** interaction dimensionality. Solid  
655 black lines represent the overall scaling relationship, and the coloured lines show the  
656 relationships for the subgroups. Bayesian regression parameters are the means of the  
657 posterior distributions. Dashed lines indicate equal body masses of predator and prey for  
658 comparisons. See Supplementary Table 3 for model parameters.

659

660 **Fig. 5:** The predator-trait model predicts the target predators with the highest body-mass  
661 ratios across different ecosystem types (color code) (n=7296). **(a)** Observed versus  
662 predicted average body-mass ratios characterize the goodness of fit ( $R^2=0.633$ ,  
663  $RMSE=0.914$ ). Dashed diagonal line shows where observations and predictions are  
664 identical. **(b)** Accuracy (proportion of correct predictions) in an out-of-sample food web  
665 depending on the fraction of target predators to be predicted. The diagonal line characterizes  
666 predictions when predators are chosen at random. Grey area corresponds to an exemplary

667 fraction of the 25% of the predators with the highest body-mass ratios. See Supplementary  
668 Figure 8 for variation in accuracy across the individual food webs.



● terrestrial aboveground  
 ● terrestrial belowground  
 ● lakes  
 ● streams  
 ● marine

