

#### Heterotrophic eukaryotes show a slow-fast continuum, not a gleaner-exploiter trade-off

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1	HETEROTROPHIC EUKARYOTES SHOW A FAST-SLOW CONTINUUM, NOT A GLEANER-
2	EXPLOITER TRADE-OFF
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11	
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18	
19	The authors declare no conflict of interest.
20	

21 Abstract: Gleaners and exploiters (opportunists) are organisms adapted to feeding in nutritionally poor and rich environments, respectively. A trade-off between these two 22 strategies - a negative relationship between the rate at which organisms can acquire food and 23 24 assimilate it – is a critical assumption in many ecological models. Here, we evaluate evidence for this trade-off across a wide range of heterotrophic eukaryotes from unicellular 25 nanoflagellates to large mammals, belonging to both aquatic and terrestrial realms. Using 26 data on the resource acquisition and assimilation rates in >500 species, we find no evidence 27 of a trade-off across species. Instead, there is a *positive* relationship between maximum 28 29 clearance rate and maximum ingestion rate. The positive relationship is not a result of lumping together diverse taxa; it holds within all sub-groups of organisms we examined as 30 well. Correcting for differences in body mass weakens but does not reverse the positive 31 32 relationship, so this is not an artefact of size-scaling either. Instead, this positive relationship represents a slow-fast gradient in the 'pace-of-life' that overrides the expected gleaner-33 exploiter trade-off. This pattern may reflect adaptation to variable versus stable, homogenous 34 35 environments and be the result of r-K selection. Other trade-offs must therefore shape ecological processes, and investigating them may provide deeper insights into coexistence 36 and competitive dynamics in nature. A plausible target for study is the well-documented 37 trade-off between growth rate and defence against predation, which can also drive the slow-38 fast gradient we observe here. 39

Significance statement: Organisms must allocate energy and resources to all basic life
functions, and this leads to inescapable trade-offs. These trade-offs govern the species
composition and functioning of ecosystems. We show that perhaps the most commonlyassumed trade-off in ecology – between relative performance at low and high resource (food)
levels – does not exist. Instead, species that do better at low resource levels also do better at
high resource levels. Models predicting how communities respond to environmental change

will need to be re-evaluated in light of this. Our results also imply that the most important
trade-off in nature is probably that between the ability to grow fast and survive the threat of
predation.

49

### 50 Introduction

Trade-offs represent fundamental challenges that organisms face when acquiring and 51 allocating resources to growth, defence and reproduction. If trade-offs did not exist, the 52 equilibrium outcome would be a single 'Darwinian demon' (or a single species in ecological 53 competition) that succeeds in all conditions. Because this contradicts both logic and patterns 54 in nature, we know that trade-offs must exist (1-3). They are therefore a core assumption in 55 56 ecological and evolutionary models, and they govern the composition and dynamics of biological communities (4-6). One commonly-assumed form is the trade-off between the 57 capacities for searching for food and for acquiring and processing food, called the gleaner-58 exploiter or gleaner-opportunist trade-off (7), or the oligotroph-copiotroph trade-off in 59 microbial ecology (8, 9). This trade-off is expected because resources are limited, and there 60 are high energetic and material costs associated with construction, maintenance, and 61 operation of structures to search for and process food. Organisms living in low resource 62 environments are expected to be gleaners that can rapidly search large areas or volumes for 63 resources, i.e., they have a high maximum clearance rate (or attack rate in the terrestrial 64 literature). Conversely, organisms in resource-rich environments are expected to be exploiters 65 that ingest, assimilate, and process resources at high rates (high maximum ingestion rate). As 66 67 the two strategies lead to greater relative success under different conditions, the gleanerexploiter trade-off can enable coexistence between competing species when combined with 68 spatial or temporal heterogeneity in resource availability (2, 10–13). This idea enjoys broad 69

70 acceptance in ecology and continues to shape the way we model ecological interactions and ecosystem processes (14, 15); it has even been discussed as the 'well-known trade-off 71 between attack rates and the conversion of prey into predator biomass' (7). However, there is 72 73 surprisingly little experimental or observational evidence that such a trade-off exists. This represents a major gap in our understanding of ecological processes and their drivers. 74 Here, we explore whether the gleaner-exploiter trade-off exists in eukaryotic heterotrophic 75 76 consumers. The gleaner-exploiter trade-off may be investigated both within and across species, and the patterns observed may be different at the two scales. We focus on exploring 77 78 patterns across species here, though we briefly examine intraspecific variation as well. Resource acquisition and consumption are measured in experiments that quantify the number 79 80 of prey consumed per predator per unit time, across gradients in prey density. This relationship is a saturating function because at high prey density the predator is limited by the 81 rate at which it can handle, ingest, and assimilate food (Fig. 1A). Holling type II, Holling 82 type III and Ivlev functions all describe this saturating relationship, and they are all 83 characterized by two parameters: the predator's maximum ingestion  $(I_{max})$  rate and its 84 maximum clearance rate  $(C_{max})$  (16). Increasing the maximum ingestion rate parameter 85 improves performance under high-resource conditions. Increasing the maximum clearance 86 rate parameter improves performance under low-resource conditions. The putative gleaner-87 88 exploiter trade-off can therefore be restated as a negative relationship between these parameters (Fig. 1 B, C). We make the assumption that organisms with high ingestion rates 89 also have high assimilation rates and support this with data. Hereafter we discuss ingestion 90 91 and assimilation as a joint process.

92 To evaluate whether the gleaner-exploiter trade-off exists, we used  $C_{\text{max}}$  and  $I_{\text{max}}$  estimates 93 from organisms ranging from unicellular nanoflagellates to large mammals, across a range of

terrestrial and aquatic systems. These data were obtained from measurements of functional response curves (Fig. 1A) compiled in two published data sets (16, 17) with more than 1400 estimates from > 500 species.  $C_{\text{max}}$  was expressed in dimensions of volume per time or area per time depending on whether the taxa scanned volumes or surfaces for prey. We refer to these as volume and surface feeders respectively. We analysed these  $C_{\text{max}}$  and  $I_{\text{max}}$  values as well as body mass-corrected versions that we call specific  $C_{\text{max}}$  and specific  $I_{\text{max}}$ .

#### 100 Results

C<sub>max</sub> and I<sub>max</sub> are strongly and positively related to each other (Fig. 2A, SI Appendix Table 101 S1), and this relation holds across taxonomy, habitats and feeding dimensionality (SI 102 Appendix Fig. S1). However, both rates are strongly associated with organism body mass; 103 larger individuals have higher clearance rates and can ingest more prey than small ones (Figs. 104 105 2 B, C, SI Appendix Tables S2 & S3). So the positive relationship between C<sub>max</sub> and I<sub>max</sub> simply reflects the size-scaling of traits expected from the metabolic theory of ecology. This 106 confounding effect of body mass can be addressed in three ways: (i) by including body mass 107 in the regression as a covariate (i.e. multiple regression), (ii) by first size-correcting the trait 108 estimates (i.e. divided by organismal body mass) and then regressing specific  $C_{\text{max}}$  and 109 110 specific  $I_{\text{max}}$  estimates against each other, or (iii) by calculating the residuals of the regressions of each of the traits against body mass, and regressing them against each other. 111 All three approaches gave us consistent results, so we present the results based on size-112 correction alone here, as this presentation is more familiar (see SI Appendix Tables S4-S6 and 113 Fig. S2 for results from all three approaches). 114

115 Specific  $C_{\text{max}}$  and specific  $I_{\text{max}}$  are also positively associated (Fig. 3A, *SI Appendix* Table S4), 116 contrary to the expectation of the gleaner-exploiter trade-off. In other words, size-correction 117 does not reveal a trade-off. The relationship between specific  $C_{\text{max}}$  and specific  $I_{\text{max}}$  is

relatively weak (marginal  $R^2$  of 12%), partly because the species and taxonomic group 118 random effects account for most of the variation (conditional  $R^2$  of 81%). However, the 119 relationship remains robust across taxonomic groups and model specifications (Fig. 3, SI 120 Appendix Fig. S3). Every taxonomic group investigated yielded a positive relationship (SI 121 Appendix Fig. S3), so this is not driven by patterns in a subset of the data. Environment of 122 origin (terrestrial/aquatic) and feeding dimensionality (surface/volume) have minimal effect 123 on the relationship between  $C_{\text{max}}$  and  $I_{\text{max}}$ , whether size-corrected or not (Fig. 3, SI Appendix 124 Tables S7-S12). 125

#### 126 Discussion

The assumption of a trade-off between capacities to acquire and process resources has played 127 a major role in the development of ecological theory, particularly in the context of species 128 coexistence and diversity (1, 2, 18). The logic behind this trade-off is simple. Resource 129 acquisition requires flagella, feeding appendages, a motor apparatus, and/or systems to sense, 130 search for and capture prey. Converting acquired food to energy requires a gut or specialized 131 cellular organelles to digest and assimilate it. Maintaining and operating these machineries 132 for acquisition and subsequent processing requires investments in material and energy. If a 133 larger capacity to acquire food is needed, the cost must be paid for by reducing allocation to 134 the machinery for processing, and vice versa. This trade-off has been demonstrated in a few 135 specific taxa (19). 136

However, our analysis here contradicts this expectation across a very large range of
eukaryotic heterotrophs. We find instead that the relationship between capacities to search for
and process resources is positive, even when adjusted to account for differences in body
mass. Surprisingly, organisms that efficiently search for resources when these are scarce are
also most effective at ingesting and utilizing resources when they are abundant (Figs. 2, 3).

142	Moreover, this pattern holds across a wide range of taxonomic groups, terrestrial and aquatic
143	environments, and surface and volume feeders (Figs. 3, SI Appendix Fig. S3). The taxonomic
144	groups in our dataset span a wide range of ecological strategies and life histories, yet none
145	exhibits any sign of the expected trade-off. And despite dramatic differences between
146	terrestrial and aquatic environments in food concentration, spatial and temporal heterogeneity
147	in both environmental variability and food availability, the patterns we describe differ only to
148	a small degree. In short, the absence of a trade-off is a general pattern, not driven by data
149	imbalances or particular groups.
150	There is also a positive relation between affinity (~ clearance rate) and maximum uptake of
151	solutes in unicellular osmotrophs (bacteria, phytoplankton) (SI Appendix Fig. S6) despite
152	similar claims of a trade-off (20, 21), and this has a very mechanistic explanation. Both the
153	affinity and the maximum uptake rate increase with the density of uptake sites (porters) on
154	the cell surface (22) and a positive relation is therefore expected.
155	What does the positive relationship between acquisition and ingestion imply for our
156	understanding of nature? It represents evidence for a dominant slow-fast gradient in
157	organismal strategies (Figs. 1 D, E), and can be thought of as the outcome of $r$ - vs $K$ -
158	selection (25–27). Indeed, the huge diversity of animal and plant life history strategies can to
159	a large extent be explained by a slow-fast gradient in the 'pace of life' (28, 29). The pace-of-
160	life syndrome is the result of a fundamental trade-off between current versus future
161	reproduction. In other words, traits and behaviours that favour success in the short term come
162	at the cost of longevity and success in future reproductive possibilities. Adaptation to
163	different points along a gradient of environmental variability produces correlated clusters of
164	traits and behaviours (26). Strong environmental variation that keeps population sizes low
165	favours 'fast' life strategies that can rapidly reproduce and colonize ephemeral habitats.

166	'Slow' traits such as high competitive ability are favoured in stable environments, where
167	population densities are large and density-dependent effects are strong.
168	There are four potential objections to our conclusions. (i) trade-offs may apply at an

intraspecific level but not an interspecific level, (ii) trade-offs may be concealed by variation
in resource acquisition (30), (iii) our assumption that – all else being equal – increases in
maximum ingestion rate are associated with increases in maximum assimilation rate may be
untrue, and (iv) we have not accounted for relatedness appropriately in our analyses. We
address these in turn.

We first consider the possibility that gleaner-exploiter trade-offs exist at a narrower 174 taxonomic scale than the broad groups we examined. Although we cannot address this 175 definitively across a wide range of taxa, our dataset does contain multiple estimates from a 176 177 small number of species. We therefore examined the 6 species for which we have 20 measurements or more of specific maximum clearance rate and specific maximum ingestion 178 rate (SI Appendix Fig. S4). In 5 of these species, we again find a positive relationship, 179 consistent with our overall findings. In the 6<sup>th</sup> species, *Scolothrips takahashii*, we find a very 180 weak and non-significant negative relationship [CIs: -0.42, 0.2]. This analysis is complicated 181 by the existence of different life stages for some species, and the existence of unsuccessful 182 individuals that gain few resources. This brings us to the second objection. 183

Intraspecific trade-offs may be concealed if variation in resource allocation between
individuals in a population is much smaller than variation in resource acquisition (3, 30–32).
Individuals within a population that acquire less resources also have fewer offspring on
average. Including these low-fitness individuals in analyses can drive a positive relationship
between traits at the population level; this is misleading because the strategies of the next
generation are determined by the individuals that have more offspring. Therefore, a more

190 careful examination would be needed to conclusively establish the absence of intraspecific trade-offs. However, this argument is much weaker when applied to comparisons across 191 species (30), the focus of this paper. Species (generally speaking) can be expected to 192 reproduce themselves to the next generation and are not subject to the bias introduced by 193 low-fitness individuals in intraspecific comparisons. Additionally, this objection applies most 194 strongly to field populations; controlled lab studies are able to minimize variation in resource 195 availability. However, only 22 data points in our dataset are from field studies. Therefore, we 196 believe that the positive trait relationship across species cannot be attributed to this 197 198 mechanism.

199 Thirdly, we may be incorrect in our assumption that maximum ingestion rates and maximum assimilation rates are positively associated, and therefore in our consequent decision to treat 200 201 these as a single process. A direct test of this across species is unfortunately not possible because of a lack of data on assimilation rates, although this has in one case been 202 demonstrated within a species (33). However, we can assess this indirectly. Ingesting and 203 assimilating food necessarily implies some somatic growth. If an organism has a high 204 ingestion rate and a low assimilation rate, it has a low resource-use efficiency and a relatively 205 206 low growth rate. In contrast, a high ingestion rate and a high assimilation rate implies a high resource-use efficiency and a high growth rate (in the presence of sufficient food). Therefore, 207 208 we can test our underlying assumption by checking for a positive association between 209 maximum specific ingestion rates and specific growth rates (or alternatively, a lack of association with resource-use efficiencies). We find support for this assumption in a small but 210 reasonably diverse dataset of 47 taxa (Fig. 4, SI Appendix Table S13). 211

Finally, our use of random effects for species and for high-level taxonomic groups (broadly
corresponding to phyla) is an imperfect proxy for non-independence due to phylogenetic
relatedness. At present, the data and methods available are insufficient to fit an appropriate

evolutionary model that accounts for the complexities of trait evolution across this broad 215 taxonomic and trait range (see Methods). A gleaner-exploiter trade-off may occur at 216 intermediate taxonomic/phylogenetic scales (as we have accounted for variation at the 217 phylum and at the species level, however imperfectly. This appears unlikely to us. A more 218 plausible version of this argument is that specific clades, defined at intermediate taxonomic 219 scales such as Family or Class, exhibit a gleaner-exploiter trade-off. However, these would be 220 exceptions rather than a general rule, which is the focus of our argument. 221 We have shown that there is no evident trade-off between acquisition and 222 ingestion/assimilation capacities across species; in other words, the gleaner-exploiter trade-223 off does not exist. But some trade-off must exist, and our theoretical understanding of 224 ecological processes relies on understanding its nature. Our work therefore suggests that 225 226 other trade-offs deserve more attention, both empirical and theoretical. Out of the wide variety of putative trade-offs that relate important biological traits (predation rates, defence, 227 competitive ability, colonization, abiotic tolerances, and others), one of the best documented 228 is that between foraging and predation risk (34). Foraging inevitably leads to elevated 229 exposure to predation in both terrestrial (35) and aquatic (36) organisms. Intriguingly, this 230 231 trade-off can contribute to the emergence of the fast-slow gradient we observe in our data (37–39). 'Fast' life history strategies that lead to acquiring more resources at both low and 232 high resource concentrations come at the cost of greater risk of predation. 'Slow' strategies 233 234 that are poor at resource acquisition at all resource concentrations therefore benefit from lower mortality. This pattern resembles the trade-off between acquisition and conservation of 235 resources (acquisitive-conservative or leaf economic spectrum) seen in plants: species that 236 237 acquire nutrients and grow slowly are better at conserving these by avoiding predation and tissue losses. This similarly leads to a slow-fast continuum among plants (31, 40, 41). 238

The fundamental foraging-predation risk trade-off may therefore be a more important determinant of the composition and seasonal succession of biological communities than the gleaner-exploiter trade-off. Much remains unknown about how it influences community dynamics and ecosystem processes (42), and its implications deserve further investigation. The slow-fast gradient in the pace of life represents an additional, interesting dimension of biological variation, but one that is unlikely to directly contribute to patterns of coexistence.

245

#### 246 Material and methods

We synthesized two data sets of resource assimilation and acquisition measurements
compiled from the literature (16, 17) Both compilations are mainly composed of data from
laboratory experiments, but a few field experiments (n=22) are included in (17). We describe
the datasets and processing steps taken below.

251 **Data** 

252 *Data sources and description.* 

The Kiørboe and Hirst dataset (16) focusses on aquatic organisms, specifically pelagic ones. 253 It provides 873 estimates of  $C_{\text{max}}$ , 337 estimates of  $I_{\text{max}}$ , and 151 cases where both parameters 254 were estimated simultaneously in the same species. The taxa encompass heterotrophic 255 protists (nanoflagellates, dinoflagellates, ciliates), crustaceans (copepods, krill), chaetognaths, 256 tunicates (salps), planktivorous fish, and gelatinous plankton (Cnidaria and Ctenophores). 257 The Uiterwall et al. dataset (17) focusses on heterotrophic eukaryotes. It includes organisms 258 from both aquatic and terrestrial environments, ranging in size from microscopic flagellates 259 to large mammals. The aquatic groups present includes insects in addition to all those in the 260 Kiørboe and Hirst dataset. The terrestrial taxa are primarily insects and arachnids, but also 261

include birds, mammals, and reptiles. It therefore includes taxa from the Kiørboe and Hirstdataset, but contains many more data points (2083).

264 *Data processing steps.* 

Uiterwaal et al. (17) estimated a handling time parameter (time per unit resource
 consumed) by fitting a Holling type II function to data on foraging rate as a function
 of resource availability. We converted handling time to maximum ingestion rate by
 taking its inverse, thereby expressing it in dimensions of mass per time.

- 269 2. The two data sets expressed body mass in different units. To make the two datasets
  270 comparable, we converted carbon mass to fresh weight by assuming a carbon content
- of 10 % of the wet mass (43) i.e. carbon mass was multiplied by a factor of 10.
- 3. To enable comparison, all estimates were temperature-corrected to reflect their
- estimated value at 15 °C, assuming a Q<sub>10</sub> of 2.8 (44). Temperature-correction is
- somewhat questionable in the case of warm-blooded animals, but (i) these represented
- a very small number of individuals (27 mammals, 20 birds) and (ii) across the dataset,
- $log_{10}$ -transformed uncorrected and temperature-corrected  $C_{max}$  values had a correlation
- of 0.98, while the same comparison for  $I_{\text{max}}$  values yielded a correlation of 0.97,
- 278 making any such changes relatively unimportant.
- 4. We calculated mass-corrected maximum ingestion rates and maximum clearance ratesby dividing the values by the species' body mass.
- 281 *Data exclusion rules.*
- 1. Cases without temperature information from (17) were excluded.

283 2. Cases where there were no estimates of the mass of individual prey were excluded

- except for the model and plot of the absolute clearance rate and ingestion rate against
- each other (Fig. 2).

- 3. Most species were aquatic or terrestrial, but 2 species were listed as being of 'mixed'
  habitat. These were excluded.
- 4. Most terrestrial organisms were surface feeders (2D environment), while most aquatic 288 289 were volume feeders (3D environment). However, in some cases, predator-prev interactions were classified as occurring in a 2.5D environment in (17), e.g., insects 290 crawling on whole plants or spiders on webs. These data were excluded as they are 291 difficult to interpret and compare with observations in 2- and 3-dimensional space. 292 5. When specific maximum ingestion rates are plotted against body mass, there is a 293 294 cloud of points that separates clearly from the bulk of the data (SI Appendix Fig. S5). These points have unrealistically high specific ingestion rates, exceeding  $10^3 d^{-1}$ , i.e., 295 organisms consuming more than 1000 times their own body mass per day. These 296 297 values are highly implausible, and so the data almost certainly represent errors. They were therefore excluded. 298
- 6. We excluded all points from a single study (Palanichamy 1983) that (17) noted were
  of poor quality.
- 301 7. Data from a few studies were present in both datasets. Because some of the source
  302 studies themselves represented compilations of earlier datasets, we could not simply
  303 exclude cases where the source paper was identical. To be conservative, we excluded
  304 all species from (17) that were also present in (16) before merging.

After removing data according to the above criteria, we were left with 2457 data points with 2114 estimates of maximum clearance rate, 1392 estimates of maximum ingestion rate, and 1206 cases where both rates were estimated in the same species. 1206 is therefore the sample size for our primary results about the relationship between the two traits, although the regressions of the individual traits against body size had more (details in Appendix tables).

We additionally had 47 data points for which estimates of both specific growth rate andmaximum specific ingestion rate were available.

312 Analysis.

313 Details of all models fitted are in Tables S1-S13.

314 *Modelling approach.* 

Relationships between pairs of continuous variables can be addressed well through a
regression framework. However, the present dataset possesses features that ordinary least
squares (OLS) regression is not well-suited to.

1. Non-independence of points due to taxonomic relatedness. The 2457 data points in 318 our dataset arose from measurements on just 510 species. Points from the same 319 species are expected to be more similar to each other than those from other species. 320 The same argument applies to closely-related species. We addressed this by using 321 322 linear mixed effects models with random effect terms (details in Model fitting subsection) for species identity and for taxonomic group. These taxonomic groups 323 broadly corresponded to phyla, with the exception of varied protists that were grouped 324 together for simplicity and model robustness. The taxonomic groups we used were: 325 Arthropods, Chaetognaths, Chordates, Ciliates, Cnidarians, Crustaceans, Ctenophores, 326 Dinoflagellates, Molluscs, Platyhelminths, Rotifers, Tardigrades, and Other Protists. 327 We note that this non-independence could also be addressed through a phylogenetic 328 regression framework, but the gains from the additional complexity are expected to be 329 330 limited unless an accurate evolutionary model is fit i.e. one that takes into account correlated trait evolution, variation in evolutionary rates across the phylogeny, 331 evolutionary jumps in trait value, and other features expected across this broad 332 333 phylogenetic and taxonomic range. This remains technically challenging despite

substantial advances in recent years (45-47), and the data required to do so across our 334 dataset does not exist. As our results were robust to a variety of different modelling 335 approaches, we believe this is unlikely to alter our conclusions. 336 337 2. Many of the relationships we investigate here are reversible, in the sense that either variable could be plotted on the X-axis. However, switching the axes leads to 338 substantially different predictions because of the way residuals are calculated in 339 standard regression fitting; regression slopes are biased towards zero. Standardized 340 Major Axis (SMA) regression is a solution to this problem, although it tends to 341 342 produce slope estimates that are biased upwards in realistic conditions (48). Unfortunately, it is presently not possible to do SMA regression with random effects, 343 to our knowledge. As we believe the latter to address a more important problem for 344 345 our analysis, we did not use SMA. As our primary conclusion is that the relationship is not negative and SMA regression estimates are more steeply positive, any bias 346 introduced by avoiding SMA regression is in the direction of making our analyses 347 more conservative. 348

#### 349 *Model fitting*.

Most results in the paper are based on linear mixed effects models with log<sub>10</sub>-transformed rates and body mass estimates. The models used both (i) random intercepts for species identity, and (ii) random intercepts and slopes for group identity.

For the relationship between specific growth rate and maximum specific ingestion rate (Fig. 4), only 2 out of the 47 points belonged to the same species and very few taxonomic groups were represented, making a mixed-effects model unsuitable. OLS regression was used in this case instead.

357 Model checking.

358 As a test of robustness, we fit all models (except that in Fig. 4) with OLS regression, SMA regression, and linear mixed effects models with different random effects structures (random 359 intercepts for species only, random intercepts for species and taxonomic group, random 360 intercepts for species and taxonomic group plus random slopes for taxonomic group). These 361 sets of models gave slightly different parameter estimates, but no analysis led to a different 362 conclusion. We therefore present the results from the models we believe to be most 363 appropriate: linear mixed effects models with random intercepts for species and taxonomic 364 group in addition to random slopes for taxonomic group identity. In one case, the model 365 returned a singular fit. Deeper investigation using Bayesian hierarchical models with weakly 366 informative priors showed that these had negligible influence on parameter estimates and 367 inferences. We present the Bayesian hierarchical model results in this case. 368

We used two common metrics for assessing the variance explained in mixed models, the marginal  $R^2$  and conditional  $R^2$  (49). The marginal  $R^2$  quantifies the variance explained by the fixed effects alone, while the conditional  $R^2$  quantifies the variance explained by the full model, i.e., fixed and random effects jointly.

373 *Tools used.* 

We used the R statistical environment v. 3.6.2, along with the packages *dplyr* and *janitor* for data handling, *lmodel2* for SMA regression, *lme4* for mixed-effects modelling, *rstanarm* for Bayesian hierarchical modelling, *MuMIn* for estimates of variance explained in the mixed models, *pbkrtest* for mixed model hypothesis testing, *ggplot2*, *ggtext* and *cowplot* for plotting, and *sjPlot* for generating tables.

#### 379 Data Availability.

380 Data and code for all analyses and plots will be uploaded on GitHub.

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388	Refe	rences		
389	1.	Smith SL, et al. (2016) Flexible phytoplankton functional type (FlexPFT) model: size-		
390		scaling of traits and optimal growth. J Plankton Res 38(4):977–992.		
391	2.	Abrams PA (2004) When Does Periodic Variation in Resource Growth Allow Robust		
392		Coexistence of Competing Consumer Species ? <i>Ecology</i> 85(2):372–382.		
393	3.	Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3(3):259–268.		
394	4.	Tilman D (1990) Constraints and Tradeoffs: Toward a Predictive Theory of		
395		Competition and Succession. <i>Oikos</i> 58(1):3–15.		
396	5.	Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annu Rev Ecol		
397		<i>Syst</i> 31:343–366.		
398	6.	Vincent TL., Scheel D, Brown JS, Vincent T. (2012) Trade-Offs and Coexistence in		
399		Consumer-Resource Models. Am Nat 148(6):1038–1058.		
400	7.	Gibert JP, Yeakel JD (2019) Eco-Evolutionary Origins of Diverse Abundance,		
401		Biomass, and Trophic Structures in Food Webs. Front Ecol Evol 7(February):1-11.		
402	8.	Fredrickson AG, Stephanopoulos G (1981) Microbial competition. Science (80-)		
403		213(4511):972–979.		
404	9.	Koch AL (2001) Oligotrophs versus copiotrophs. <i>BioEssays</i> 23(7):657-661.		
405	10.	Adler FR (1990) Coexistence of two types on a single reource in discrete time. J Math		
406		<i>Biol</i> :695–713.		
407	11.	Armstrong RA, McGehee R (1980) Competitive Exclusion. Am Nat 115(2):151–170.		
408	12.	Smith HL (1981) Competitive Coexistence in an Oscillating Chemostat. SIAM J Appl		
409		Math 40(3):498–522.		

410	13.	Grover JP (1991) Resource Competition in a Variable Environment : Phytoplankton
411		Growing According to Monod 's Model. Am Nat 138(4):811-835.
412	14.	Klauschies T, Gaedke U (2020) Nutrient retention by predators undermines predator
413		coexistence on one prey. Theor Ecol 13(2):183-208.
414	15.	Follows MJ, Dutkiewicz S (2011) Modeling Diverse Communities of Marine
415		Microbes. Ann Rev Mar Sci 3(1):427–451.
416	16.	Kiørboe T, Hirst AG (2014) Shifts in mass scaling of respiration, feeding, and growth
417		rates across life-form transitions in marine pelagic organisms. Am Nat 183(4):E118-30.
418	17.	Uiterwaal SF, Lagerstrom IT, Lyon SR, DeLong JP (2018) Data paper: FoRAGE
419		(Functional Responses from Around the Globe in all Ecosystems) database: a
420		compilation of functional responses for consumers and parasitoids. <i>bioRxiv</i>
421		(December):43.
422	18.	Kneitel JM, Chase JM (2004) Trade-offs in community ecology : linking spatial scales
423		and species coexistence. Ecol Lett 7:69-80.
424	19.	Chase JM, Wilson WG, Richards SA (2001) Foraging Trade-Offs and Resource
425		Patchiness Theory and Experiments. Ecol Lett 4:304–312.
426	20.	Brandenburg KM, et al. (2018) Intraspecific trait variation and trade-offs within and
427		across populations of a toxic dinoflagellate. <i>Ecol Lett</i> 21(10):1561–1571.
428	21.	Fernandez VI, Yawata Y, Stocker R (2019) A Foraging Mandala for Aquatic
429		Microorganisms. ISME J 13(3):563–575.
430	22.	Fiksen Ø, Follows MJ, Aksnes DL (2013) Trait-based models of nutrient uptake in
431		microbes extend the Michaelis-Menten framework. Limnol Oceanogr 58(1):193-202.

432	23.	Litchman E, Edwards KF, Klausmeier CA (2015) Microbial resource utilization traits
433		and trade-offs: implications for community structure, functioning, and biogeochemical
434		impacts at present and in the future. Front Microbiol 06(19):3685-3688.
435	24.	Meyer JR, Gudelj I, Beardmore R (2015) Biophysical mechanisms that maintain
436		biodiversity through trade-offs. Nat Commun 6:1-7.
437	25.	MacArthur R., Wilson E. (1967) The Theory of Island Biogeography. (Princeton
438		University Press, Princeton).
439	26.	Wright J, Bolstad GH, Araya-Ajoy YG, Dingemanse NJ (2019) Life-history evolution
440		under fluctuating density-dependent selection and the adaptive alignment of pace-of-
441		life syndromes. <i>Biol Rev</i> 94(1):230–247.
442	27.	Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. Trends Ecol Evol
443		17(10):462–468.
444	28.	Healy K, Ezard THG, Jones OR, Salguero-Gómez R, Buckley YM (2019) Animal life
445		history is shaped by the pace of life and the distribution of age-specific mortality and
446		reproduction. Nat Ecol Evol 3(8):1217–1224.
447	29.	Salguero-Gómez R, et al. (2016) Fast-slow continuum and reproductive strategies
448		structure plant life-history variation worldwide. Proc Natl Acad Sci 113(1):230-235.
449	30.	van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: Their
450		influence on variation in life history tactics. Am Nat 128(1):137–142.
451	31.	Agrawal AA (2020) A scale-dependent framework for trade-offs, syndromes, and
452		specialization in organismal biology. <i>Ecology</i> 101(2):1–24.
453	32.	Houle D (1991) Genetic covariance of fitness correlates: What genetic correlations are
454		made of and why it matters. Evolution (N Y) 45(3):630–648.

455	33.	Olijnyk AM, Nelson WA (2013) Positive phenotypic correlations among life-history
456		traits remain in the absence of differential resource ingestion. Funct Ecol 27(1):165-
457		172.
458	34.	Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a
459		review and prospectus. Can J Zool 68(4):619-640.
460	35.	Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in
461		terrestrial systems. Behav Ecol Sociobiol 60(4):457-464.
462	36.	Kiørboe T, Jiang H, Goncalves RJ, Nielsen LT, Wadhwa N (2014) Flow disturbances
463		generated by feeding and swimming zooplankton. Proc Natl Acad Sci 111(32):11738-
464		11743.
465	37.	Réale D, et al. (2010) Personality and the emergence of the pace-of-life syndrome
466		concept at the population level. Philos Trans R Soc B Biol Sci 365(1560):4051-4063.
467	38.	Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D (2018) Pace-of-life syndromes:
468		a framework for the adaptive integration of behaviour, physiology and life history.
469		Behav Ecol Sociobiol 72(3). doi:10.1007/s00265-018-2473-y.
470	39.	Debecker S, Stoks R (2019) Pace of life syndrome under warming and pollution:
471		integrating life history, behavior, and physiology across latitudes. Ecol Monogr
472		89(1):1–22.
473	40.	Wright IJ, et al. (2004) The worldwide leaf economics spectrum. Nature
474		428(6985):821–827.
475	41.	Sartori K, et al. (2019) Leaf economics and slow-fast adaptation across the geographic
476		range of Arabidopsis thaliana. Sci Rep 9(1):1–12.
477	42.	Mariani P, Andersen KH, Visser AW, Barton AD, Kiørboe T (2013) Control of

478		plankton seasonal succession by adaptive grazing. Limnol Oceanogr 58(1):173-184.
479	43.	Kiørboe T (2013) Zooplankton body composition. Limnol Oceanogr 58(5):1843–1850.
480	44.	Hansen PJ, Bjørnsen PK, Hansen BW (1997) Zooplankton grazing and growth:
481		Scaling within the 2-2,-µm body size range. <i>Limnol Oceanogr</i> 42(4):687–704.
482	45.	Revell LJ, et al. (2018) Comparing evolutionary rates between trees, clades and traits.
483		Methods Ecol Evol 9(4):994–1005.
484	46.	Mazel F, et al. (2016) Improving phylogenetic regression under complex evolutionary
485		models. <i>Ecology</i> 97(2):286–293.
486	47.	Davies TJ, Regetz J, Wolkovich EM, McGill BJ (2019) Phylogenetically weighted
487		regression: A method for modelling non-stationarity on evolutionary trees. Glob Ecol
488		<i>Biogeogr</i> 28(2):275–285.
489	48.	Smith RJ (2009) Use and misuse of the reduced major axis for line-fitting. Am J Phys
490		Anthropol 140(3):476–486.
491	49.	Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R 2 from
492		generalized linear mixed-effects models. Methods Ecol Evol 4(2):133-142.
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Fig. 1. A typical functional response curve relating resource uptake rate to resource 497 concentration (A). The functional response curve is characterized by two parameters, the 498 maximum ingestion rate ( $I_{max}$ ), and the maximum clearance rate ( $C_{max}$ , also known as  $F_{max}$  or 499 attack rate).  $C_{\text{max}}$  is the initial slope of the curve and is equal to the maximum volume or area 500 that the consumer can clear for resources per unit time.  $I_{\text{max}}$  is the uptake rate at which the 501 curve saturates. The variation in functional response curves between species implied by a 502 gleaner-opportunist trade-off (B) and the consequent negative relationship between  $C_{\text{max}}$  and 503  $I_{\text{max}}$  (C). In contrast, the variation in functional response curves between species implied by a 504 fast-slow gradient in the 'pace of life' (D) and the consequent positive relationship between 505  $C_{\text{max}}$  and  $I_{\text{max}}$  (E). Colours of dots in (C) and (E) refers to the corresponding curves in (B) and 506 507 (D).

508

Fig. 2. The relationships between  $C_{\text{max}}$ ,  $I_{\text{max}}$  and body mass.  $C_{\text{max}}$  and  $I_{\text{max}}$  are strongly 509 positively associated (A) (marginal  $R^2 = 72\%$ , conditional  $R^2 = 96\%$ ), but this relationship 510 reflects their strong dependence on body mass (B, C) (marginal  $R^2 = 64\% \& 72\%$ , 511 conditional  $R^2 = 94\%$  & 92%, for  $C_{max}$  and  $I_{max}$ , respectively). The size-dependence of both 512 traits is close to isometric based on OLS regression, but accounting for non-independence 513 with random effects for species and taxonomic group identity reduces the slopes to 0.75 for 514  $I_{\text{max}}$  and 0.6 for  $C_{\text{max}}$ . Black lines represent across-group patterns captured in the models by 515 fixed effects, while grey lines represent taxonomic group-level variation captured with 516 517 random slopes and intercepts. Species-level variation is also captured by random intercepts. Variation in the relationships across environments (aquatic/terrestrial) and feeding dimension 518 (surface/volume feeders) is minimal, and is shown in Appendix SI Fig. S1. 519

Fig. 3. Specific  $C_{max}$  (i.e. size-corrected  $C_{max}$ ) is positively related to specific  $I_{max}$ . This positive relationship (A) holds across species and groups (black line, representing fixed effects in the model) and also within all taxonomic groups examined (grey lines, captured in the model by random slope and intercept terms). Variation between habitats has little effect on the relationship (B), and the same is true for feeding dimensionality (C). Note that withingroup patterns (random effects) are not shown in B & C for clarity but were accounted for in the model. *Appendix SI* Fig. S3 shows an alternate visualisation of 3A with points coloured

528 by group identity.

529

530 Fig. 4. Higher specific maximum ingestion rates are associated with higher maximum

specific growth rates (p < 0.001,  $R^2 = 0.42$ ). This used an OLS regression and taxonomic

532 group variation was ignored, because only 6 groups were present, and 3 of those had fewer

533 than 3 points.

Gleaner-opportunist trade-off

Fast-slow continuum









### **Supplementary Information for**

#### HETEROTROPHIC EUKARYOTES SHOW A FAST-SLOW CONTINUUM, NOT A GLEANER-EXPLOITER

#### TRADE-OFF

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Fig. S1. The relationships between  $C_{\text{max}}$ ,  $I_{\text{max}}$  and body mass, across habitats and feeding dimensionality. Here within-group patterns are not depicted for clarity except in A and D (thin grey lines), though it is captured in the models. There is very limited variation in these relationships across environments (aquatic/terrestrial) and feeding dimensionality (surface/volume feeders).



Fig. S2. Residual analysis. Residuals from the regressions between  $C_{\text{max}}$  and body mass, and  $I_{\text{max}}$  and body mass are regressed against each other, and they are weekly but positively related to one another ( $R^2 = 0.05$ , p < 0.001). This result is not sensitive to the extreme points on either axis. The regressions against body mass accounted for species- and taxonomic group- level variation in the data with random effects, so the residuals here have accounted for this variation. Therefore, we used an OLS regression in this case.



Fig. S3. Specific  $C_{\text{max}}$  (i.e. size-corrected  $C_{\text{max}}$ ) is positively related to specific  $I_{\text{max}}$  in all taxonomic groups we modelled (the thin grey lines).



Fig. S4. Specific  $C_{\text{max}}$  is positively related to specific  $I_{\text{max}}$  even at an intraspecific level. We investigated the 6 species for which we had 20 or more measurements to understand whether the gleaner-exploiter trade-off appears at an intraspecific level. In 5 of the 6 species here, the regressions show a positive relationship, consistent with across-species patterns and contrary to the trade-off expectation. The sole exception, *Scolothripe takahashii* (panel E), shows a weak, non-significant negative relationship. While this does constitute evidence against a trade-off at the intraspecific level, it is relatively weak evidence, as discussed in the main text.



Fig. S5. Maximum ingestion rate (A) and specific maximum ingestion rate (B) as functions of body mass for the data in the Uiterwaal et al. data set (1). The blue points are observations where the estimated specific maximum ingestion rates exceeds  $10^3 d^{-1}$ . These data were excluded from the analyses.



Fig. S6. Relation between specific affinity ( $\alpha$ , L.µmol C<sup>-1</sup>.d<sup>-1</sup>) for nitrogen and specific maximum uptake rate ( $V_{max}$ , µmol N.µmol C<sup>-1</sup>.d<sup>-1</sup>) of nitrogen for phytoplankton belonging to different taxa. Note that affinity and Vmax have been normal per unit carbon, and not biomass as was done for the eukaryotes. However, these should produce very similar results. The data were compiled by Litchman et al. (2), and the affinity was computed here as the ratio of the  $V_{max}$  and the half saturation constant, the two parameters reported by Litchman et al. (2007). The regression line shown is  $\log_{10} (\alpha) = 0.036 + 0.89 \log_{10} (V_{max})$ ,  $R^2 = 0.74$ .

## **Bibliography for figures**

- Uiterwaal SF, Lagerstrom IT, Lyon SR, DeLong JP (2018) Data paper: FoRAGE (Functional Responses from Around the Globe in all Ecosystems) database: a compilation of functional responses for consumers and parasitoids. *bioRxiv* (December):43.
- Litchman E, Klausmeier CA, Schofield OM, Falkowski PG (2007) The role of functional traits and trade-offs in structuring phytoplankton communities: Scaling from cellular to ecosystem level. *Ecol Lett* 10(12):1170–1181.

## Table S1. Regression results for maximum clearance rate against maximum ingestion rate.

Note that p-values depicted here are not entirely accurate because of technical challenges

associated with calculating degrees of freedom in mixed models.

### **Response variable:**

 $\log_{10}(C_{\max})$ 

(a) Fixed effects:	$\log_{10}(I_{\max})$
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $\log_{10}(C_{\text{max}})$ vs.
	$\log_{10}(I_{\rm max})$ slopes

		log10(Cmax)	
Predictors	Estimates	CI	р
(Intercept)	-3.51	-4.222.80	<0.001
$\log_{10}(I_{\max})$	0.52	0.30 - 0.73	<0.001
Random Effects			
$\sigma^2$	0.28		
$\tau_{00 \text{ species}}$	0.84		
$ au_{00 \ group}$	1.21		
$\tau_{11 \text{ group.log10}(Imax)}$	0.10		
ρ01 group	-0.32		
ICC	0.90		
N species	361		
N group	13		
Observations	1206		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.408 / 0.	.944	

**Table S2. Regression results for maximum clearance rate against body mass.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

## **Response variable:** $\log_{10}(C_{\text{max}})$

Predictor	variables:

(a) Fixed effects:	log <sub>10</sub> (body mass)
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $\log_{10}(C_{\text{max}})$ vs.
	log10(body mass) slopes

		log10(Cmax)	
Predictors	Estimates	CI	р
(Intercept)	-3.69	-4.243.14	<0.001
log <sub>10</sub> (body mass)	0.60	0.45 - 0.76	<0.001
Random Effects			
$\sigma^2$	0.31		
$\tau_{00 \text{ species}}$	0.85		
$\tau_{00}$ group	0.67		
$\tau_{11}$ group.log10(body mass)	0.05		
ρ01 group	0.07		
ICC	0.85		
N species	453		
N group	13		
Observations	2114		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.497 / 0.	.927	

**Table S3. Regression results for maximum ingestion rate against body mass.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

log<sub>10</sub>(body mass) slopes

### **Response variable:** $\log_{10}(I_{\text{max}})$

Predictor variables:	
(a) Fixed effects:	log <sub>10</sub> (body mass)
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}(I_{max})$ vs.

		log10(Imax)	
Predictors	Estimates	CI	р
(Intercept)	-0.32	-0.74 - 0.10	0.133
log10(body mass)	0.75	0.64 - 0.86	<0.001
Random Effects			
$\sigma^2$	0.46		
$\tau_{00}$ species	0.74		
$\tau_{00}$ group	0.29		
$\tau_{11}$ group.log10(body mass)	0.02		
ρ01 group	0.50		
ICC	0.72		
N species	378		
N group	13		
Observations	1392		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.682 / 0.	.911	

**Table S4. Maximum clearance rate and maximum ingestion rate are positively related to each other even after accounting for body size, demonstrated using our first method.** Here we size-corrected all estimates of maximum clearance rate and maximum ingestion rate by dividing them by organismal body mass, in mg. These new *specific* maximum clearance rate and *specific* maximum ingestion rate estimates were then regressed against each other. Note that in this case, we were faced with fitting problems (singular fits) using *lmer(*) and so we instead present results from a Bayesian hierarchical model here. This model was fit with *rstanarm(*) and used weakly informative priors. Quantitative results of the *lmer(*) and *rstanarm(*) fits were very similar, but the Bayesian hierarchical model results are more robust in this case.

#### **Response variable:**

 $\log_{10}(\text{specific } C_{\text{max}})$ 

(a) Fixed effects:	$\log_{10}(\text{specific } I_{\text{max}})$
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}$ (specific $C_{max}$ ) vs.
	$\log_{10}(\text{specific } I_{\text{max}}) \text{ slopes}$

	log10(specific Cmax)		
Predictors	Estimates	CI (95%)	
(Intercept)	-3.19	-3.502.94	
log <sub>10</sub> (specific <i>I</i> <sub>max</sub> )	0.39	0.20 - 0.67	
Random Effects			
$\sigma^2$	0.33		
$\tau_{00 \text{ species}}$	0.89		
$\tau_{00 \text{ group}}$	0.12		
τ <sub>11</sub> group.log10(specific Imax)	0.08		
ρ01 group	0.37		
ICC	0.77		
N species	361		
N group	13		
Observations	1206		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.124 / 0.	.799	

Table S5. Maximum clearance rate and maximum ingestion rate are positively related to each other even after accounting for body size, demonstrated using a second method. Here, we first calculated the residuals from the regressions between  $C_{\text{max}}$  and body mass, and between  $I_{\text{max}}$  and body mass. We then regressed these results against each other. As random effects were accounted for in the original regressions from which the residuals were obtained, there was no need for random effects here and so we used OLS regression instead.

#### **Response variable:** Residuals from regression of $\log_{10}(C_{\text{max}})$ vs $\log_{10}(\text{body size})$

(a) Fixed effects:	Residuals from regression of $log_{10}(I_{max})$ vs $log_{10}(body size)$
(b) Random intercepts:	none
(c) Random slopes:	none

	Residuals from $C_{\max}$ size regression		
Predictors	Estimates	CI	р
(Intercept)	0.01	-0.02 - 0.04	0.411
Residuals from $I_{\text{max}}$ size regression	0.17	0.13 - 0.21	<0.001
Observations	1206		
$R^2 / R^2$ adjusted	0.051 / 0.051		

**Table S6. Maximum clearance rate and maximum ingestion rate are positively related to each other even after accounting for body size, demonstrated using a third method.** Here we used a multiple regression with body mass as a covariate. *p*-values in this table are more accurate because they were assessed using a more conservative F-test, based on the Kenward-Roger approximation for the denominator degrees of freedom.

### **Response variable:** $\log_{10}(C_{\text{max}})$

(a) Fixed effects:	$\log_{10}(I_{\text{max}})$ , $\log_{10}(\text{body mass})$
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $\log_{10}(C_{\text{max}})$ vs.
	$\log_{10}(I_{\text{max}})$ slopes

		log <sub>10</sub> (C <sub>max</sub> )	
Predictors	Estimates	CI	р
(Intercept)	-3.45	-3.972.94	<0.001
$\log_{10}(I_{\max})$	0.34	0.17 - 0.52	<0.001
log <sub>10</sub> (body mass)	0.32	0.26 - 0.39	<0.001
Random Effects			
$\sigma^2$	0.28		
$\tau_{00 \text{ species}}$	0.66		
$\tau_{00 \text{ group}}$	0.54		
$\tau_{11 \text{ group.log10}(Imax)}$	0.06		
ρ <sub>01</sub> group	-0.21		
ICC	0.85		
N species	361		
N group	13		
Observations	1206		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.617 / 0.	.943	

**Table S7. Regression results for maximum clearance rate against body mass and habitat.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

### **Response variable:**

 $\log_{10}(C_{\text{max}})$ 

(a) Fixed effects:	log10(body mass), habitat, log10(body size) * habitat
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}(C_{max})$ vs.
	log10(body mass) slopes

		log10(Cmax)	
Predictors	Estimates	CI	р
(Intercept)	-3.71	-4.253.16	<0.001
log10(body mass)	0.58	0.42 - 0.75	<0.001
habitat [Terrestrial]	0.23	-0.17 - 0.62	0.263
log10(body mass) * habitat [Terrestrial]	0.16	0.04 - 0.28	0.011
Random Effects			
$\sigma^2$	0.31		
$\tau_{00 \text{ species}}$	0.81		
$\tau_{00}$ group	0.65		
$\tau_{11}$ group.log10(body mass)	0.06		
ρ01 group	0.01		
ICC	0.85		
N species	453		
N group	13		
Observations	2114		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.497 / 0.	.927	

**Table S8. Regression results for maximum clearance rate against body mass and feeding dimensionality.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

### **Response variable:** 10

 $\log_{10}(C_{\max})$ 

(a) Fixed effects:	log10(body mass), dimension, log10(body size) * dimension
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $\log_{10}(C_{\text{max}})$ vs.
	log <sub>10</sub> (body mass) slopes

		log10(Cmax)	
Predictors	Estimates	CI	р
(Intercept)	-3.00	-3.562.44	<0.001
log10(body mass)	0.57	0.41 - 0.73	<0.001
dimension [Volume feeders]	-0.85	-1.090.61	<0.001
log10(body mass) * dimension [Volume feeders]	0.03	-0.05 - 0.10	0.479
Random Effects			
$\sigma^2$	0.31		
$\tau_{00 \text{ species}}$	0.77		
$\tau_{00  \text{group}}$	0.59		
$\tau_{11 \text{ group.log10(body mass)}}$	0.04		
ρ01 group	0.30		
ICC	0.84		
N species	453		
N group	13		
Observations	2114		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.524 / 0.	.926	

**Table S9. Regression results for maximum ingestion rate against body mass and habitat.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

### **Response variable:**

 $\log_{10}(I_{\text{max}})$ 

(a) Fixed effects:	log10(body mass), habitat, log10(body mass) * habitat
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}(I_{max})$ vs.
	log10(body mass) slopes

		log <sub>10</sub> (I <sub>max</sub> )	
Predictors	Estimates	CI	р
(Intercept)	-0.32	-0.76 - 0.11	0.143
log <sub>10</sub> (body mass)	0.79	0.67 - 0.90	<0.001
habitat [Terrestrial]	-0.20	-0.57 - 0.16	0.274
log <sub>10</sub> (body mass) * habitat [Terrestrial]	-0.15	-0.260.04	0.010
Random Effects			
$\sigma^2$	0.46		
τ <sub>00</sub> species	0.70		
$\tau_{00}$ group	0.31		
$\tau_{11}$ group.log10(body mass)	0.02		
ρ01 group	0.73		
ICC	0.72		
N species	378		
N group	13		
Observations	1392		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.684 / 0.	.912	

Table S10. Regression results for maximum ingestion rate against body mass and feeding dimensionality. Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

# **Response variable:**

 $\log_{10}(I_{\text{max}})$ 

(a) Fixed effects:	log <sub>10</sub> (body mass), dimension, log <sub>10</sub> (body mass) * dimension
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $\log_{10}(I_{\text{max}})$ vs.
	log <sub>10</sub> (body mass) slopes

		log <sub>10</sub> ( <i>I</i> <sub>max</sub> )	
Predictors	Estimates	CI	р
(Intercept)	-0.40	-0.87 - 0.07	0.092
log10(body mass)	0.70	0.56 - 0.84	<0.001
dimension [Volume feeders]	0.11	-0.17 - 0.39	0.449
log <sub>10</sub> (body mass) * dimension [Volume feeders]	0.08	-0.01 - 0.18	0.089
Random Effects			
$\sigma^2$	0.46		
$\tau_{00}$ species	0.71		
$\tau_{00 \text{ group}}$	0.28		
$\tau_{11}$ group.log10(body mass)	0.02		
ρ01 group	0.63		
ICC	0.72		
N species	378		
N group	13		
Observations	1392		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.688 / 0.	.911	

**Table S11. Regression results for specific maximum clearance rate against specific maximum ingestion rate and habitat.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

### **Response variable:**

 $\log_{10}(\text{specific } C_{\text{max}})$ 

(a) Fixed effects:	$log_{10}$ (specific $I_{max}$ ), habitat, $log_{10}$ (specific $I_{max}$ ) * habitat
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}(specific C_{max})$ vs.
	$\log_{10}(\text{specific } I_{\text{max}}) \text{ slopes}$

	log <sub>10</sub> (specific C <sub>max</sub> )		
Predictors	Estimates	CI	р
(Intercept)	-3.36	-3.683.05	<0.001
$log_{10}(specific I_{max})$	0.43	0.25 - 0.62	<0.001
habitat [Terrestrial]	0.76	0.47 - 1.05	<0.001
log <sub>10</sub> (specific I <sub>max</sub> ) * habitat [Terrestrial]	-0.11	-0.26 - 0.04	0.141
Random Effects			
$\sigma^2$	0.33		
$\tau_{00}$ species	0.80		
$\tau_{00 \text{ group}}$	0.18		
τ <sub>11</sub> group.log10(specific Imax)	0.05		
ρ01 group	0.67		
ICC	0.76		
N species	361		
N group	13		
Observations	1206		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.188 / 0.8	305	

**Table S12. Regression results for specific maximum clearance rate against specific maximum ingestion rate and feeding dimensionality.** Note that p-values depicted here are not entirely accurate because of technical challenges associated with calculating degrees of freedom in mixed models.

### **Response variable:**

 $\log_{10}(\text{specific } C_{\text{max}})$ 

(a) Fixed effects:	$log_{10}(specific I_{max})$ , dimension, $log_{10}(specific I_{max}) * dimension$
(b) Random intercepts:	species, taxonomic group
(c) Random slopes:	taxonomic groups have different $log_{10}$ (specific $C_{max}$ ) vs.
	log <sub>10</sub> (specific I <sub>max</sub> ) slopes

	log10(specific Cmax)		
Predictors	Estimates	CI	р
(Intercept)	-2.67	-3.022.32	<0.001
log <sub>10</sub> (specific <i>I</i> <sub>max</sub> )	0.39	0.20 - 0.58	<0.001
dimension [Volume feeders]	-0.72	-0.930.51	<0.001
log <sub>10</sub> (specific <i>I</i> <sub>max</sub> ) * dimension [Volume feeders]	-0.01	-0.14 - 0.12	0.909
Random Effects			
$\sigma^2$	0.33		
$\tau_{00 \text{ species}}$	0.79		
$\tau_{00 \text{ group}}$	0.18		
τ <sub>11</sub> group.log10(specific Imax)	0.05		
ρ01 group	0.90		
ICC	0.76		
N species	361		
N group	13		
Observations	1206		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.172 / 0.	.800	

**Table S13. Specific growth rate increases with increases in specific maximum ingestion rate, consistent with our assumption.** We used OLS regression for this analysis and neglected group-level variation, as only 5 groups were represented and 3 of them had 2 points or less. One species was represented twice, all other measurements were on distinct species.

rate)

### **Predictor variables:**

(a) <i>Fixed effects</i> :	
(b) Random intercepts:	
(c) Random slopes:	

log<sub>10</sub>(specific *I*<sub>max</sub>) none none

	log10(specific growth rate)		
Predictors	Estimates	CI	р
(Intercept)	-0.42	-0.560.29	<0.001
log <sub>10</sub> (specific <i>I</i> <sub>max</sub> )	0.58	0.37 - 0.78	<0.001
Observations	47		
$R^2 / R^2$ adjusted	0.415 / 0.402		