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

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The authors declare no conflict of interest.
Abstract: Gleaners and exploiters (opportunists) are organisms adapted to feeding in nutritionally poor and rich environments, respectively. A trade-off between these two strategies – a negative relationship between the rate at which organisms can acquire food and 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 nanoflagellates to large mammals, belonging to both aquatic and terrestrial realms. Using data on the resource acquisition and assimilation rates in >500 species, we find no evidence of a trade-off across species. Instead, there is a positive relationship between maximum 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 well. Correcting for differences in body mass weakens but does not reverse the positive 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-exploiter trade-off. This pattern may reflect adaptation to variable versus stable, homogenous 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 and competitive dynamics in nature. A plausible target for study is the well-documented trade-off between growth rate and defence against predation, which can also drive the slow-fast gradient we observe here.

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 commonly-assumed 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.

Introduction

Trade-offs represent fundamental challenges that organisms face when acquiring and allocating resources to growth, defence and reproduction. If trade-offs did not exist, the equilibrium outcome would be a single ‘Darwinian demon’ (or a single species in ecological competition) that succeeds in all conditions. Because this contradicts both logic and patterns in nature, we know that trade-offs must exist (1–3). They are therefore a core assumption in 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 capacities for searching for food and for acquiring and processing food, called the gleaner-exploiter or gleaner-opportunist trade-off (7), or the oligotroph-copiotroph trade-off in microbial ecology (8, 9). This trade-off is expected because resources are limited, and there are high energetic and material costs associated with construction, maintenance, and operation of structures to search for and process food. Organisms living in low resource environments are expected to be gleaners that can rapidly search large areas or volumes for resources, i.e., they have a high maximum clearance rate (or attack rate in the terrestrial literature). Conversely, organisms in resource-rich environments are expected to be exploiters that ingest, assimilate, and process resources at high rates (high maximum ingestion rate). As the two strategies lead to greater relative success under different conditions, the gleaner-exploiter trade-off can enable coexistence between competing species when combined with spatial or temporal heterogeneity in resource availability (2, 10–13). This idea enjoys broad
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’ between attack rates and the conversion of prey into predator biomass’ (7). However, there is 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.

Here, we explore whether the gleaner-exploiter trade-off exists in eukaryotic heterotrophic 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 patterns across species here, though we briefly examine intraspecific variation as well.

Resource acquisition and consumption are measured in experiments that quantify the number 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 rate at which it can handle, ingest, and assimilate food (Fig. 1A). Holling type II, Holling type III and Ivlev functions all describe this saturating relationship, and they are all characterized by two parameters: the predator’s maximum ingestion ($I_{\text{max}}$) rate and its maximum clearance rate ($C_{\text{max}}$) (16). Increasing the maximum ingestion rate parameter improves performance under high-resource conditions. Increasing the maximum clearance rate parameter improves performance under low-resource conditions. The putative gleaner-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 also have high assimilation rates and support this with data. Hereafter we discuss ingestion and assimilation as a joint process.

To evaluate whether the gleaner-exploiter trade-off exists, we used $C_{\text{max}}$ and $I_{\text{max}}$ estimates 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 $I_{\text{max}}$.

**Results**

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

Specific $C_{\text{max}}$ and specific $I_{\text{max}}$ are also positively associated (Fig. 3A, SI Appendix Table S4),
contrary to the expectation of the gleaner-exploiter trade-off. In other words, size-correction
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 random effects account for most of the variation (conditional $R^2$ of 81%). However, the relationship remains robust across taxonomic groups and model specifications (Fig. 3, SI Appendix Fig. S3). Every taxonomic group investigated yielded a positive relationship (SI Appendix Fig. S3), so this is not driven by patterns in a subset of the data. Environment of origin (terrestrial/aquatic) and feeding dimensionality (surface/volume) have minimal effect on the relationship between $C_{\text{max}}$ and $I_{\text{max}}$, whether size-corrected or not (Fig. 3, SI Appendix Tables S7-S12).

Discussion

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

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).
Moreover, this pattern holds across a wide range of taxonomic groups, terrestrial and aquatic environments, and surface and volume feeders (Figs. 3, SI Appendix Fig. S3). The taxonomic groups in our dataset span a wide range of ecological strategies and life histories, yet none exhibits any sign of the expected trade-off. And despite dramatic differences between terrestrial and aquatic environments in food concentration, spatial and temporal heterogeneity in both environmental variability and food availability, the patterns we describe differ only to a small degree. In short, the absence of a trade-off is a general pattern, not driven by data imbalances or particular groups.

There is also a positive relation between affinity (~ clearance rate) and maximum uptake of solutes in unicellular osmotrophs (bacteria, phytoplankton) (SI Appendix Fig. S6) despite similar claims of a trade-off (20, 21), and this has a very mechanistic explanation. Both the affinity and the maximum uptake rate increase with the density of uptake sites (porters) on the cell surface (22) and a positive relation is therefore expected.

What does the positive relationship between acquisition and ingestion imply for our understanding of nature? It represents evidence for a dominant slow-fast gradient in organismal strategies (Figs. 1 D, E), and can be thought of as the outcome of r- vs K-selection (25–27). Indeed, the huge diversity of animal and plant life history strategies can to a large extent be explained by a slow-fast gradient in the ‘pace of life’ (28, 29). The pace-of-life syndrome is the result of a fundamental trade-off between current versus future reproduction. In other words, traits and behaviours that favour success in the short term come at the cost of longevity and success in future reproductive possibilities. Adaptation to different points along a gradient of environmental variability produces correlated clusters of traits and behaviours (26). Strong environmental variation that keeps population sizes low favours ‘fast’ life strategies that can rapidly reproduce and colonize ephemeral habitats.
‘Slow’ traits such as high competitive ability are favoured in stable environments, where population densities are large and density-dependent effects are strong.

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 taxonomic scale than the broad groups we examined. Although we cannot address this definitively across a wide range of taxa, our dataset does contain multiple estimates from a 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 rate (SI Appendix Fig. S4). In 5 of these species, we again find a positive relationship, consistent with our overall findings. In the 6th species, Scolothrips takahashii, we find a very weak and non-significant negative relationship [CIs: -0.42, 0.2]. This analysis is complicated by the existence of different life stages for some species, and the existence of unsuccessful individuals that gain few resources. This brings us to the second objection.

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
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
species (30), the focus of this paper. Species (generally speaking) can be expected to
reproduce themselves to the next generation and are not subject to the bias introduced by
low-fitness individuals in intraspecific comparisons. Additionally, this objection applies most
strongly to field populations; controlled lab studies are able to minimize variation in resource
availability. However, only 22 data points in our dataset are from field studies. Therefore, we
believe that the positive trait relationship across species cannot be attributed to this
mechanism.

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
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
demonstrated within a species (33). However, we can assess this indirectly. Ingesting and
assimilating food necessarily implies some somatic growth. If an organism has a high
ingestion rate and a low assimilation rate, it has a low resource-use efficiency and a relatively
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,
we can test our underlying assumption by checking for a positive association between
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
reasonably diverse dataset of 47 taxa (Fig. 4, SI Appendix Table S13).

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
taxonomic and trait range (see Methods). A gleaner-exploiter trade-off may occur at
intermediate taxonomic/phylogenetic scales (as we have accounted for variation at the
phylum and at the species level, however imperfectly. This appears unlikely to us. A more
plausible version of this argument is that specific clades, defined at intermediate taxonomic
scales such as Family or Class, exhibit a gleaner-exploiter trade-off. However, these would be
exceptions rather than a general rule, which is the focus of our argument.

We have shown that there is no evident trade-off between acquisition and
ingestion/assimilation capacities across species; in other words, the gleaner-exploiter trade-off
does not exist. But some trade-off must exist, and our theoretical understanding of
ecological processes relies on understanding its nature. Our work therefore suggests that
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,
competitive ability, colonization, abiotic tolerances, and others), one of the best documented
is that between foraging and predation risk (34). Foraging inevitably leads to elevated
exposure to predation in both terrestrial (35) and aquatic (36) organisms. Intriguingly, this
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
high resource concentrations come at the cost of greater risk of predation. ‘Slow’ strategies
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
resources (acquisitive-conservative or leaf economic spectrum) seen in plants: species that
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).
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.

**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.

**Data**

*Data sources and description.*

The Kiørboe and Hirst dataset (16) focusses on aquatic organisms, specifically pelagic ones. It provides 873 estimates of $C_{\text{max}}$, 337 estimates of $I_{\text{max}}$, and 151 cases where both parameters were estimated simultaneously in the same species. The taxa encompass heterotrophic protists (nanoflagellates, dinoflagellates, ciliates), crustaceans (copepods, krill), chaetognaths, tunicates (salps), planktivorous fish, and gelatinous plankton (Cnidaria and Ctenophores).

The Uiterwall et al. dataset (17) focusses on heterotrophic eukaryotes. It includes organisms from both aquatic and terrestrial environments, ranging in size from microscopic flagellates to large mammals. The aquatic groups present includes insects in addition to all those in the Kiørboe and Hirst dataset. The terrestrial taxa are primarily insects and arachnids, but also
include birds, mammals, and reptiles. It therefore includes taxa from the Kiørboe and Hirst dataset, but contains many more data points (2083).

Data processing steps.

1. 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.

2. The two data sets expressed body mass in different units. To make the two datasets 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 $Q_{10}$ 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 $C_{\text{max}}$ values had a correlation of 0.98, while the same comparison for $I_{\text{max}}$ values yielded a correlation of 0.97, making any such changes relatively unimportant.

4. We calculated mass-corrected maximum ingestion rates and maximum clearance rates by dividing the values by the species’ body mass.

Data exclusion rules.

1. Cases without temperature information from (17) were excluded.

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 were volume feeders (3D environment). However, in some cases, predator-prey interactions were classified as occurring in a 2.5D environment in (17), e.g., insects crawling on whole plants or spiders on webs. These data were excluded as they are difficult to interpret and compare with observations in 2- and 3-dimensional space.

5. When specific maximum ingestion rates are plotted against body mass, there is a 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., organisms consuming more than 1000 times their own body mass per day. These values are highly implausible, and so the data almost certainly represent errors. They were therefore excluded.

6. We excluded all points from a single study (Palanichamy 1983) that (17) noted were of poor quality.

7. Data from a few studies were present in both datasets. Because some of the source studies themselves represented compilations of earlier datasets, we could not simply exclude cases where the source paper was identical. To be conservative, we excluded 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 and maximum specific ingestion rate were available.

**Analysis.**

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

**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 our dataset arose from measurements on just 510 species. Points from the same species are expected to be more similar to each other than those from other species. The same argument applies to closely-related species. We addressed this by using linear mixed effects models with random effect terms (details in Model fitting subsection) for species identity and for taxonomic group. These taxonomic groups broadly corresponded to phyla, with the exception of varied protists that were grouped together for simplicity and model robustness. The taxonomic groups we used were: Arthropods, Chaetognaths, Chordates, Ciliates, Cnidarians, Crustaceans, Ctenophores, Dinoflagellates, Molluscs, Platyhelminths, Rotifers, Tardigrades, and Other Protists. We note that this non-independence could also be addressed through a phylogenetic regression framework, but the gains from the additional complexity are expected to be 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, evolutionary jumps in trait value, and other features expected across this broad 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
dataset does not exist. As our results were robust to a variety of different modelling
approaches, we believe this is unlikely to alter our conclusions.

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
substantially different predictions because of the way residuals are calculated in
standard regression fitting; regression slopes are biased towards zero. Standardized
Major Axis (SMA) regression is a solution to this problem, although it tends to
produce slope estimates that are biased upwards in realistic conditions (48).
Unfortunately, it is presently not possible to do SMA regression with random effects,
to our knowledge. As we believe the latter to address a more important problem for
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
introduced by avoiding SMA regression is in the direction of making our analyses
more conservative.

Model fitting.

Most results in the paper are based on linear mixed effects models with log_{10}-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.

Model checking.
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 intercepts for species only, random intercepts for species and taxonomic group, random intercepts for species and taxonomic group plus random slopes for taxonomic group). These sets of models gave slightly different parameter estimates, but no analysis led to a different conclusion. We therefore present the results from the models we believe to be most appropriate: linear mixed effects models with random intercepts for species and taxonomic group in addition to random slopes for taxonomic group identity. In one case, the model returned a singular fit. Deeper investigation using Bayesian hierarchical models with weakly informative priors showed that these had negligible influence on parameter estimates and inferences. We present the Bayesian hierarchical model results in this case.

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.

**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.

**Data Availability.**

Data and code for all analyses and plots will be uploaded on GitHub.
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**Figure legends**

**Fig. 1.** A typical functional response curve relating resource uptake rate to resource concentration (**A**). The functional response curve is characterized by two parameters, the maximum ingestion rate ($I_{\text{max}}$), and the maximum clearance rate ($C_{\text{max}}$, also known as $F_{\text{max}}$ or attack rate). $C_{\text{max}}$ is the initial slope of the curve and is equal to the maximum volume or area that the consumer can clear for resources per unit time. $I_{\text{max}}$ is the uptake rate at which the curve saturates. The variation in functional response curves between species implied by a gleaner-opportunist trade-off (**B**) and the consequent negative relationship between $C_{\text{max}}$ and $I_{\text{max}}$ (**C**). In contrast, the variation in functional response curves between species implied by a fast-slow gradient in the ‘pace of life’ (**D**) and the consequent positive relationship between $C_{\text{max}}$ and $I_{\text{max}}$ (**E**). Colours of dots in (**C**) and (**E**) refers to the corresponding curves in (**B**) and (**D**).

**Fig. 2.** The relationships between $C_{\text{max}}$, $I_{\text{max}}$ and body mass. $C_{\text{max}}$ and $I_{\text{max}}$ are strongly positively associated (**A**) (marginal $R^2 = 72\%$, conditional $R^2 = 96\%$), but this relationship reflects their strong dependence on body mass (**B**, **C**) (marginal $R^2 = 64\%$ & $72\%$, conditional $R^2 = 94\%$ & $92\%$, for $C_{\text{max}}$ and $I_{\text{max}}$, respectively). The size-dependence of both traits is close to isometric based on OLS regression, but accounting for non-independence with random effects for species and taxonomic group identity reduces the slopes to 0.75 for $I_{\text{max}}$ and 0.6 for $C_{\text{max}}$. Black lines represent across-group patterns captured in the models by fixed effects, while grey lines represent taxonomic group-level variation captured with random slopes and intercepts. Species-level variation is also captured by random intercepts. Variation in the relationships across environments (aquatic/terrestrial) and feeding dimension (surface/volume feeders) is minimal, and is shown in Appendix SI Fig. S1.
Fig. 3. Specific $C_{\text{max}}$ (i.e. size-corrected $C_{\text{max}}$) is positively related to specific $I_{\text{max}}$. 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 within-group 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 by group identity.

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 group variation was ignored, because only 6 groups were present, and 3 of those had fewer than 3 points.
Gleaner–opportunist trade–off

Resource concentration

Fast–slow continuum

Ingestion rate

$C_{\text{max}}$

$I_{\text{max}}$

$C_{\text{max}}$
Specific $I_{\text{max}}$ (m$^2$ or m$^3$.mg$^{-1}$.day$^{-1}$) vs. Specific $C_{\text{max}}$ (mg.mg$^{-1}$.day$^{-1}$).

**A** shows the relationship for aquatic and terrestrial species.

**B** further divides the data into Surface feeders and Volume feeders.

**C** illustrates the overlap of aquatic and terrestrial species categories.
Supplementary Information for

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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, *Scolothrips 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$^{-1}$·d$^{-1}$) for nitrogen and specific maximum uptake rate ($V_{\text{max}}$, µmol N·µmol C$^{-1}$·d$^{-1}$) of nitrogen for phytoplankton belonging to different taxa. Note that affinity and $V_{\text{max}}$ 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 $V_{\text{max}}$ and the half saturation constant, the two parameters reported by Litchman et al. (2007). The regression line shown is $\log_{10}(\alpha) = 0.036 + 0.89 \log_{10}(V_{\text{max}})$, $R^2 = 0.74$. 
Bibliography for figures


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:** \( \log_{10}(C_{\text{max}}) \)

**Predictor variables:**

(a) *Fixed effects:* \( \log_{10}(I_{\text{max}}) \)

(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

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<th>Estimates</th>
<th>CI</th>
<th>( p )</th>
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<td>(Intercept)</td>
<td>-3.51</td>
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<td>0.30 – 0.73</td>
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**Random Effects**

- \( \sigma^2 \) = 0.28
- \( \tau_{00} \) species = 0.84
- \( \tau_{00} \) group = 1.21
- \( \tau_{11} \) group,\( \log_{10}(I_{\text{max}}) \) = 0.10
- \( \rho_{01} \) group = -0.32
- ICC = 0.90
- \( N_{\text{species}} \) = 361
- \( N_{\text{group}} \) = 13

Observations = 1206

Marginal \( R^2 \) / Conditional \( R^2 \) = 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: \( \log_{10}(\text{body mass}) \)
(b) Random intercepts: species, taxonomic group
(c) Random slopes: taxonomic groups have different \( \log_{10}(C_{\text{max}}) \) vs. 
\( \log_{10}(\text{body mass}) \) slopes

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<td>0.45 – 0.76</td>
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Random Effects

- \( \sigma^2 \): 0.31
- \( \tau_{00} \) species: 0.85
- \( \tau_{00} \) group: 0.67
- \( \tau_{11} \) group,\( \log_{10}(\text{body mass}) \): 0.05
- \( \rho_{01} \) group: 0.07
- ICC: 0.85
- \( N \) species: 453
- \( N \) group: 13

Observations: 2114

Marginal \( R^2 \) / Conditional \( R^2 \): 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.

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

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

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<td>0.64 – 0.86</td>
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**Random Effects**

\( \sigma^2 \) 0.46
\( \tau_{00} \) species 0.74
\( \tau_{00} \) group 0.29
\( \tau_{11} \) group.\( \log_{10}(\text{body mass}) \) 0.02
\( \rho_{01} \) group 0.50
ICC 0.72
N species 378
N group 13

**Observations** 1392
Marginal \( R^2 \) / Conditional \( R^2 \) 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 \texttt{lmer}() and so we instead present results from a Bayesian hierarchical model here. This model was fit with \texttt{rstanarm}() and used weakly informative priors. Quantitative results of the \texttt{lmer}() and \texttt{rstanarm}() fits were very similar, but the Bayesian hierarchical model results are more robust in this case.

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

**Predictor variables:**

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<td>0.39</td>
<td>0.20 – 0.67</td>
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**Random Effects**

| \( \sigma^2 \) | 0.33 |
| \( \tau_{00} \space \text{species} \) | 0.89 |
| \( \tau_{00} \space \text{group} \) | 0.12 |
| \( \tau_{11} \space \text{group.}\log_{10}(\text{specific } I_{\text{max}}) \) | 0.08 |
| \( \rho_{01} \space \text{group} \) | 0.37 |
| ICC | 0.77 |
| \( N \space \text{species} \) | 361 |
| \( N \space \text{group} \) | 13 |
| Observations | 1206 |
| Marginal R\(^2 \) / Conditional R\(^2 \) | 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 $\log_{10}(\text{body size})$

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

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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:** \( \log_{10}(C_{\text{max}}) \)

**Predictor variables:**

(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

<table>
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<th>Estimates</th>
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<th><em>p</em></th>
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<td>-3.97 – -2.94</td>
<td>&lt;0.001</td>
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<td>( \log_{10}(I_{\text{max}}) )</td>
<td>0.34</td>
<td>0.17 – 0.52</td>
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<tr>
<td>( \log_{10}(\text{body mass}) )</td>
<td>0.32</td>
<td>0.26 – 0.39</td>
<td>&lt;0.001</td>
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**Random Effects**

| \( \sigma^2 \) | 0.28 |
| \( \tau_{00} \) species | 0.66 |
| \( \tau_{00} \) group | 0.54 |
| \( \tau_{11} \) group.\( \log_{10}(I_{\text{max}}) \) | 0.06 |
| \( \rho_{01} \) group | -0.21 |
| ICC | 0.85 |
| N species | 361 |
| N group | 13 |
| Observations | 1206 |
| Marginal R\(^2\) / Conditional R\(^2\) | 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:** \( \log_{10}(C_{\text{max}}) \)

**Predictor variables:**

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

<table>
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<td>habitat [Terrestrial]</td>
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<td>( \log_{10}(\text{body mass}) \times \text{habitat [Terrestrial]} )</td>
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**Random Effects**

| \( \sigma^2 \) | 0.31 |
| \( \tau_{00} \text{ species} \) | 0.81 |
| \( \tau_{00} \text{ group} \) | 0.65 |
| \( \tau_{11} \text{ group.} \log_{10}(\text{body mass}) \) | 0.06 |
| \( \rho_{01} \text{ group} \) | 0.01 |
| ICC | 0.85 |
| \( N \text{ species} \) | 453 |
| \( N \text{ group} \) | 13 |

Observations 2114

Marginal \( R^2 \) / Conditional \( R^2 \) 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:** $\log_{10}(C_{\text{max}})$

**Predictor variables:**

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

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<th>CI</th>
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<td>0.41 – 0.73</td>
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<tr>
<td>dimension [Volume feeders]</td>
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<tr>
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<td>-0.05 – 0.10</td>
<td>0.479</td>
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**Random Effects**

- $\sigma^2$: 0.31
- $\tau_{00}$ species: 0.77
- $\tau_{00}$ group: 0.59
- $\tau_{11}$ group.$\log_{10}(\text{body mass})$: 0.04
- $\rho_{01}$ group: 0.30
- ICC: 0.84
- N species: 453
- N group: 13

**Observations**: 2114

**Marginal R$^2$/Conditional R$^2$**: 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: \( \log_{10}(I_{\text{max}}) \)

Predictor variables:

(a) Fixed effects: \( \log_{10}(\text{body mass}), \text{habitat}, \log_{10}(\text{body mass}) \times \text{habitat} \)

(b) Random intercepts: species, taxonomic group

(c) Random slopes: taxonomic groups have different \( \log_{10}(I_{\text{max}}) \) vs. \( \log_{10}(\text{body mass}) \) slopes

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<td>-0.57 – 0.16</td>
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Random Effects

\( \sigma^2 \) 0.46

\( \tau_{00} \) species 0.70

\( \tau_{00} \) group 0.31

\( \tau_{11} \) group,\( \log_{10}(\text{body mass}) \) 0.02

\( \rho_{01} \) group 0.73

ICC 0.72

N species 378

N group 13

Observations 1392

Marginal R\(^2\) / Conditional R\(^2\) 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: $\log_{10}(I_{\text{max}})$

Predictor variables:

(a) Fixed effects: $\log_{10}(\text{body mass})$, $\log_{10}(\text{body mass})$ * $\text{dimension}$

(b) Random intercepts: species, taxonomic group

(c) Random slopes: taxonomic groups have different $\log_{10}(I_{\text{max}})$ vs. $\log_{10}(\text{body mass})$ slopes

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Random Effects

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<tr>
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<td>N group</td>
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Observations 1392

Marginal $R^2$ / Conditional $R^2$ 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:** \( \log_{10}(\text{specific } C_{\text{max}}) \)

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

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<td>( \log_{10}(\text{specific } I_{\text{max}}) )</td>
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<td>habitat [Terrestrial]</td>
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<td>( \log_{10}(\text{specific } I_{\text{max}}) ) * habitat [Terrestrial]</td>
<td>-0.11</td>
<td>-0.26 – 0.04</td>
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**Random Effects**

| \( \sigma^2 \)          | 0.33     |
| \( \tau_{00} \) species | 0.80     |
| \( \tau_{00} \) group   | 0.18     |
| \( \tau_{11} \) group, \( \log_{10}(\text{specific } I_{\text{max}}) \) | 0.05     |
| \( \rho_{01} \) group   | 0.67     |
| ICC                      | 0.76     |
| \( N_{\text{species}} \) | 361      |
| \( N_{\text{group}} \)  | 13       |
| Observations             | 1206     |
| Marginal R\(^2\) / Conditional R\(^2\) | 0.188 / 0.805 |
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:** \( \log_{10}(\text{specific } C_{\text{max}}) \)

**Predictor variables:**
- **Fixed effects:** \( \log_{10}(\text{specific } I_{\text{max}}), \) dimension, \( \log_{10}(\text{specific } I_{\text{max}}) \) * dimension
- **Random intercepts:** species, taxonomic group
- **Random slopes:** taxonomic groups have different \( \log_{10}(\text{specific } C_{\text{max}}) \) vs. \( \log_{10}(\text{specific } I_{\text{max}}) \) slopes

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<td>-3.02 – -2.32</td>
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<td>( \log_{10}(\text{specific } I_{\text{max}}) )</td>
<td>0.39</td>
<td>0.20 – 0.58</td>
<td>&lt;0.001</td>
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<td>dimension [Volume feeders]</td>
<td>-0.72</td>
<td>-0.93 – -0.51</td>
<td>&lt;0.001</td>
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<tr>
<td>( \log_{10}(\text{specific } I_{\text{max}}) ) * dimension [Volume feeders]</td>
<td>-0.01</td>
<td>-0.14 – 0.12</td>
<td>0.909</td>
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**Random Effects**

| \( \sigma^2 \) | 0.33 |
| \( \tau_{00} \) species | 0.79 |
| \( \tau_{00} \) group | 0.18 |
| \( \tau_{11} \) group.*\( \log_{10}(\text{specific } I_{\text{max}}) \) | 0.05 |
| \( \rho_{01} \) group | 0.90 |
| ICC | 0.76 |
| N species | 361 |
| N group | 13 |
| Observations | 1206 |
| Marginal R\(^2\) / Conditional R\(^2\) | 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.

**Response variable:** \( \log_{10}(\text{specific growth rate}) \)

**Predictor variables:**
- (a) \textit{Fixed effects}: \( \log_{10}(\text{specific } I_{\text{max}}) \)
- (b) \textit{Random intercepts}: none
- (c) \textit{Random slopes}: none

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Estimates</th>
<th>CI</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.42</td>
<td>-0.56 – -0.29</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>( \log_{10}(\text{specific } I_{\text{max}}) )</td>
<td>0.58</td>
<td>0.37 – 0.78</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Observations 47

\( R^2 / R^2 \) adjusted 0.415 / 0.402