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Biomass competition connects individual and community scaling patterns

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Both metabolism and growth scale sublinearly with body mass across species. Ecosystems show the same sublinear scaling between production and total biomass, but ecological theory cannot reconcile the existence of these nearly identical scalings at different levels of biological organization. We attempt to solve this paradox using marine phytoplankton, connecting individual and ecosystem scalings across three orders of magnitude in body size and biomass. We find that competitive interactions determined by biomass slow metabolism in a consistent fashion across species of different sizes. These effects dominate over species-specific peculiarities, explaining why community composition does not affect respiration and production patterns. The sublinear scaling of ecosystem production thus emerges from this metabolic density-dependence that operates across species, independently of the equilibrium state or resource regime. Our findings demonstrate the connection between individual and ecosystem scalings, unifying aspects of physiology and ecology to explain why growth patterns are so strikingly similar across scales.

Ecosystems show remarkable regularities that suggest that their functioning is bound by common organising principles[1–4]. One of these regularities is the sublinear scaling between biomass production and total biomass, which follows a power law (often near ¾) that is independent of the ecosystem considered[3]. Different ecosystems thus grow at similar rates mainly determined by their total biomass, independently of species size and composition. These size-independent patterns are at odds with the sublinear scaling of metabolism with size observed for individual organisms, and their origin remains unclear[3,5,6]. Recent work shows that the sublinear scaling of ecosystem production can emerge if populations of different species themselves grow sublinearly[7]. However, the apparent incompatibility between ecosystem-level and individual-level scalings remains unresolved[7–9].

Why are the two scalings incompatible? Across most taxa, individual metabolism and growth scale sublinearly with body mass following a power law with an exponent $\beta < 1$[6,10,11] (Fig. 1a). This sublinear scaling implies that, while larger organisms have greater metabolic (or growth) rates in an absolute sense, they consume less energy per unit mass compared to smaller organisms (valid for any scaling $\beta < 1$). Therefore, the size of organisms should affect the functioning of populations and communities. Two systems (populations or communities) of equal biomass density but different size composition should not have the same metabolism or growth: a system composed of smaller organisms should respire/grow faster than a system of larger organisms if $\beta < 1$ (and the other way around if $\beta > 1$). Since ecosystem metabolism and production increase with total biomass at a similar rate ($\alpha \sim ¾$)[1,3], the metabolic theory of ecology would predict that this pattern results from changes in species size[12]: ecosystems of larger biomass should be dominated by larger organisms that have lower metabolism per unit mass[5]. However, empirical data do not support this explanation as size structure is nearly invariant across ecosystems (or does not change sufficiently to explain this ecosystem pattern)[3,5]. An alternative hypothesis is that sublinear scaling in ecosystems is a consequence of density-dependent processes that slow production as biomass accumulates[3,7,8,13]. But how these processes operate to control biomass growth in such a consistent way across species and ecosystems – positing a common underlying mechanism – remains unknown.

We attempt to solve this puzzle by overcoming a limitation of the metabolic theory of ecology. It is often assumed that metabolism-size relationships of organisms in isolation hold for these same organisms in communities, but this assumption has little empirical support[13–16]. Competition for resources alters energy use, and many species reduce

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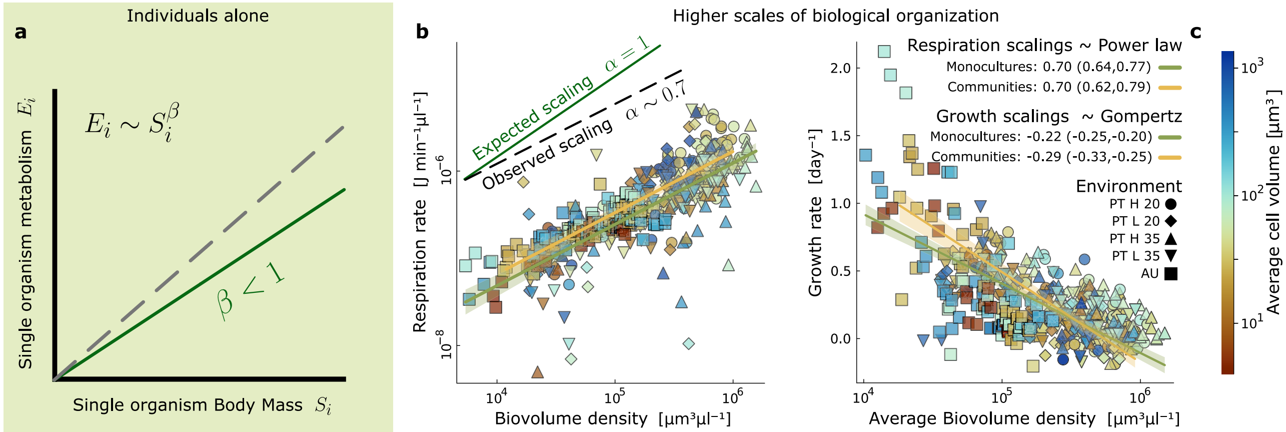

Fig. 1 | Respiration and growth scale sublinearly with total biovolume across monocultures and communities with no effect of species size. a The respiration and growth of individual organisms scale sublinearly ($\beta < 1$) with body size across most taxa: $E_i \sim S_i^{\beta}$. **b** This sublinear scaling at the individual level should affect the respiration and growth of monocultures and communities. In particular, total metabolism should increase linearly with total biomass for all monocultures since they are composed of organisms of similar size: $E \sim \sum_i^N S_i^{\beta} \sim N\bar{S}^{\beta} = B\bar{S}^{\beta-1}$ (expected scaling ~ B) because the total number of organisms $N = B/\bar{S}$. Instead, total respiration (**b**) and growth (**c**) scale sublinearly with biovolume even if species size varies by three orders of magnitude. Note that growth is analysed against the geometric mean of biovolume ln-transformed but plotted on a $\log_{10}$ scale for consistency. Lines (**b**, **c**) represent the fit value from the model and 95% confidence interval. Symbols refer to the geographic location (AU = Australia, PT = Portugal), light (High vs Low) and salinity (35 vs 20 ppt). Source data are provided as a Source Data file.

their respiration rate in denser populations[17–23]. We provide a formal account of how these density-dependent processes affect organismal metabolism, biomass production, and their scaling with body size. We explore both metabolism and growth because, while they are correlated, it is unclear which one drives the other[24]. By doing so, we demonstrate that the effect of competition on organismal metabolism is the key to reconciling individual and ecosystem scalings.

We base our assessment on marine phytoplankton, a system of global importance for primary production[25,26]. The size diversity of this system allows us to explore scaling relationships across three orders of magnitude in body size[27] at different scales (individuals, populations, species pairs, communities), measuring metabolism as both respiration and photosynthesis. To demonstrate the generality of our findings we use geographically separate and independent phytoplankton communities (Australia, AU[20] and Portugal, PT), and measure them under a total of five environmental conditions in the laboratory. In each location, we source five species from local culture collections and grow them alone (monocultures) or together (communities). In the first location (AU), we also test all pairs of species and grow all cultures under ideal conditions of light (115 μmol photons m^{-2} s^{-1}) and salinity (35 ppt). In the second location (PT), we grow cultures under four combinations of light (High vs Low, corresponding to 60 and 30 μmol photons m^{-2} s^{-1}, respectively) and salinity (35 vs 20 ppt), creating a range of suboptimal environments. We start all cultures from a small biovolume of phytoplankton (a proxy for biomass, obtained as the product of cell volume and cell number); we then track changes in cell size, biovolume density, growth, and metabolism (photosynthesis, respiration) from exponential to stationary phase. These data allow us to evaluate the effects of individual size on community functioning and quantify the effect of biomass competition on metabolism across growth phases and environments.

Results

Organismal size does not affect metabolism and growth at higher scales of organisation

Organismal respiration scales sublinearly with size across species, including phytoplankton[26]. Therefore, we would predict that species of different sizes (or communities with different size structures) should function at different rates. The effect of size should be particularly obvious for monocultures since all phytoplankton cells in a population have a similar size: total population respiration should scale linearly with total biovolume and with a size-dependent slope (intercept on a log-log scale, Fig. 1a, b).

Contrary to this prediction, we find that phytoplankton cell size does not influence total respiration rates even if species vary in size by three orders of magnitude ($F_{1,\ 95} = 0.77$; $p = 0.38$). Instead, total respiration scales sublinearly with total biovolume across monocultures and communities ($\alpha \sim 0.70$, obtained by fitting a power law; Fig. 1b), with values that are consistent with those observed in terrestrial and aquatic ecosystems[1,3]. Similarly, we find no effect of species size on total growth rate ($F_{1,\ 518} = 1.21$; $p = 0.27$), which declines with increasing biovolume with slopes ~ − 0.25 (− 0.22 for monocultures and − 0.29 for communities, calculated by fitting a Gompertz curve; Fig. 1c). Cell size also does not influence the sublinear scaling of total photosynthesis with biovolume ($F_{1,91} = 0.42$, $p = 0.52$; Supplementary Fig. 1a).

Importantly, we do not wish to provide a specific scaling exponent that is valid for all systems because the environment affects these relationships[28]. Geographic location, level of organisation and environmental conditions affected both intercepts and scaling exponents (see Supplementary Note 1, Supplementary Figs. 1–3 and Supplementary Tables 1–3). However, cell size does not explain this variability. Even when accounting for both differences between species and environments, scaling exponents and intercepts do not correlate with cell size (Supplementary Fig. 4 and Supplementary Table 5). So, while the environment affects scaling patterns and we cannot exclude species-specific differences, total biovolume (not individual size) appears the primary driver of population/community metabolism and growth (Fig. 1 and Supplementary Fig. 5).

Our simplified phytoplankton system, therefore, shows the same incompatibility between individual- and community-level scalings observed for other systems[3,13,28–30]. These two sublinear scalings seem incompatible because community metabolism (or growth) can be independent of species size only if individual metabolism scales isometrically (not sublinearly) with body size[13].

Resolving the paradox: the coexistence of sublinear and isometric scaling at the individual level

Here, we demonstrate, first mathematically and then empirically, that sublinear and isometric scaling at the individual level can coexist