

# Ecosystem ecology: size-based constraints on the pyramids of life

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**Biomass distribution and energy flow in ecosystems are traditionally described with trophic pyramids, and increasingly with size spectra, particularly in aquatic ecosystems. Here, we show that these methods are equivalent and interchangeable representations of the same information. Although pyramids are visually intuitive, explicitly linking them to size spectra connects pyramids to metabolic and size-based theory, and illuminates size-based constraints on pyramid shape. We show that bottom-heavy pyramids should predominate in the real world, whereas top-heavy pyramids indicate overestimation of predator abundance or energy subsidies. Making the link to ecological pyramids establishes size spectra as a central concept in ecosystem ecology, and provides a powerful framework both for understanding baseline expectations of community structure and for evaluating future scenarios under climate change and exploitation.**

## Ecological pyramids and size spectra: size-centric views of community structure

Understanding the processes that structure communities (see [Glossary](#)) in ecosystems is a fundamental goal in ecology. Elton laid the conceptual foundation for our understanding of these processes with two key observations: (i) interactions among organisms strongly shape the structure and function of communities; and (ii) the nature of these interactions is governed by both the identities and the sizes of the organisms involved [1]. Elton further noted the strong link between the position of organisms in food chains and their body sizes, and that larger organisms higher in food chains were less abundant than smaller ones lower down. To capture both phenomena, he introduced ecological pyramids as a way to represent the distribution of abundance and biomass among body sizes.

These first ecological pyramids were ‘pyramids of numbers’, where the ‘layers’ represented ‘bins’ of body size, and the width of the layers represented the abundance of all organisms within each size class. The pyramid

representation of communities quickly took hold in ecology and pyramids were re-expressed in terms of biomass [2], production, and eventually trophic level (Hutchinson, unpublished, in [3]). Subsequently, there was a rapidly adopted and persistent reframing of ecological pyramids so that the layers were defined by trophic level rather than by body-size class. This trophic representation of the ecological pyramid is now by far the most common form presented in ecological texts (e.g., [4–8]).

The shape of ecological pyramids qualitatively conveys rich information about the underlying ecological processes

### Glossary

**Community:** the biotic component of an ecosystem; organisms inhabiting a given geographic area and sharing a common resource base.

**Ecological pyramids:** graphs of relative abundance or biomass among body-size classes or trophic levels in ecological communities [1]. Elton originally described pyramids of abundance and body size in 1927 [1], but pyramids of biomass and trophic levels have been more prevalent since Lindeman introduced the trophic-level concept in 1942 [3].

**Predator:prey mass ratio (PPMR):** ratio of predator to prey mass measured at the individual level. At the community level, PPMR is the average mass of predators at trophic level  $n$  divided by the average mass of their prey at trophic level  $n-1$ .

**Size spectra:** linear regressions of body-mass class against either total abundance in each size class (abundance spectra) or total biomass in each size class (biomass spectra) of individuals, irrespective of species identity, typically on log axes. Hence, indeterminate-growing species, such as fishes, enter and grow through multiple mass classes throughout their life. Size spectra are one form of individual size distributions (ISD [66]).

**Size spectrum theory:** several models have been developed for understanding the slopes of size spectra [12,19,20,23]; here, we focus on the approach for calculating slopes based on the scaling of energy use with body size from metabolic theory and the loss of energy with trophic transfers [23–25], which elsewhere has been called the Energetic Equivalence Hypothesis with Trophic Transfer Correction [46].

**Subsidy:** energy from nonlocal production sources, external to the community being considered, that enters the community at trophic level at or above primary consumers.

**Transfer efficiency (TE):** production at trophic level  $n$  divided by the production at trophic level  $n-1$ .

**Turnover:** the rate at which biomass is replaced (turns over) in a community or part thereof (i.e., trophic level or body size class); typically expressed as the ratio of production:biomass (P:B) or the average lifespan in the assemblage of interest. Turnover time (the time required for biomass to be replaced in an assemblage) is the inverse of turnover rate.

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that drive ecosystem structure. Communities within ecosystems comprise individuals deriving their energy from a common basal pool. Therefore, the combination of the first and second laws of thermodynamics (conservation of energy and increasing entropy, respectively) with inefficient energy transfer from predators to prey, dictates that pyramids of production (integrated over time) must always be bottom heavy (Hutchinson, unpublished, in [3]). In other words, there is always greater production of primary producers compared with herbivores, and greater production of herbivores compared with primary carnivores, and so on. Elton suggested that pyramids of numbers and biomass should be bottom heavy [1], but this might not always be the case, because the shape of numbers and biomass pyramids depends on the relative rates at which biomass and energy move between size classes [9–11]. For example, biomass pyramids may have a narrower base than apex, a form known as an ‘inverted biomass pyramid’ (IBP) [3].

The size spectrum is an alternative representation of the distribution of abundance and biomass among body sizes that has been popular among aquatic ecologists for several decades [12,13]. Size spectra describe the relation between body size and abundance (abundance spectra) or biomass (biomass spectra), typically with abundance or body mass summed within logarithmic body-size bins [12]. Thus, similar to ecological pyramids, size spectra involve converting a continuous variable (e.g., body size or trophic position) into a category for ease of analysis. Also similar to ecological pyramids, size spectra represent a simple, powerful, and yet apparently distinct way of understanding and predicting community structure.

It is interesting to consider why the trophic-level version of ecological pyramids has been most popular among terrestrial ecologists, whereas size spectra, which are more closely allied to Elton’s original pyramids of body size, have been more widely adopted among aquatic ecologists. This difference may be due, in part, to differing views of the relative importance of body size versus taxonomic identity among terrestrial versus aquatic ecologists. The species niche concept has historically dominated in terrestrial ecology, probably because of the dominance of determinate growth among study organisms, whereby function changes little with size. Conversely, in aquatic systems, where indeterminate growth dominates and ontogenetic changes in diet are common, the concept of species belonging to a single niche or trophic level is less plausible and the size-based view has been more widely appreciated. However, the prevalence of ‘omnivory’ in food webs compels us to now consider explicitly the functional role of individual body size in ecosystem ecology (e.g., ([14]).

The slopes of size spectra describe the rate at which abundance (abundance spectra) or biomass (biomass spectra) change with increasing body size. These slopes are remarkably consistent in aquatic ecosystems; typically approximately  $-1$  and zero for abundance and biomass spectra, respectively [13,15,16]. Several models have been developed to explain these slopes, ranging from null stochastic models [17,18] to detailed process-based models of predator–prey interactions (e.g., [12,19–22]), to simpler bulk property models based on energy transfer [23–25].

These models share a common basis in recognizing that two key community characteristics determine size spectrum slopes: (i) the relation between predator and prey body sizes; and (ii) the efficiency of energy transfer from prey to predators. Drawing from terrestrial macroecology [26], recent theoretical and empirical work combined this knowledge with predictions from the energetic equivalence hypothesis and metabolic-scaling theory [10,24,27] to provide a way to estimate baseline size spectra: the size spectrum slopes that would be expected in the absence of human disturbance (Box 1).

Although the conceptual similarity between ecological pyramids and size spectra has been noted in passing (e.g., [10,28]), neither the quantitative link nor the implications were fully appreciated. Here, we reveal the quantitative link between ecological pyramids and size spectra, and in doing so, show how pyramid shape is constrained by the same characteristics that control size spectra slopes: transfer efficiency (TE) and the community-wide predator–prey mass ratio (PPMR; Box 2). We show how pyramid shape varies with TE and PPMR, and review available empirical estimates of TE and PPMR. Our review indicates that biomass pyramids are usually expected to be bottom heavy for communities that share a common resource base. We hypothesize that inverted biomass pyramids arise from census artefacts or energetic subsidies. Most estimates of community PPMR and TE, as well as the individual-level data required for size spectra, currently come from marine ecosystems, and these are our focus here. However, making the link between ecological pyramids and size spectra demonstrates that size spectra are not an oddity of aquatic ecology, but may be of central importance in ecosystem ecology, providing a size-based lens through which to understand metabolic constraints on pyramids.

### Translating between ecological pyramids and size spectra

Ecological pyramids and size spectra are alternative graphical and mathematical portrayals of the same information (Figure 1). The steps for converting both pyramids of numbers and biomass to the corresponding abundance or biomass spectra are identical (Figure 1), provided the pyramids are expressed in terms of body size (rather than trophic level). Conversion of a trophic level pyramid to the corresponding size spectrum requires the additional step of converting trophic level to body-size class (Figure 1). This conversion can be made if the relation between body size and trophic level is known (i.e., is equivalent to PPMR; Box 2).

The translation of ecological pyramids to size spectra illustrates how the slope of a given biomass (or abundance) spectrum directly reflects the overall shape of the corresponding biomass (or numbers) pyramid, with layers defined by body mass, and that the link for trophic pyramids depends on the community relation between trophic level and body size (PPMR; Figure 1, Box 2). Converting from ecological pyramids to size spectra illuminates size-based constraints on the shapes expected for ecological pyramids (as explained below). Conversely, converting from size spectra to ecological pyramids is a powerful method for visualizing the abstract concept of the size spectrum and the underlying parameter combinations (Box 3).

### Box 1. From single trophic-level energetic equivalence to size spectra

If all individuals in a community share a common resource base (i.e., feed at the same trophic level), energetic equivalence [26] predicts that energy use ( $E$ ) of different body-size classes is independent of body size ( $M$ ), meaning that  $E \propto M^0$  [67]. Given that total organism metabolic rate ( $MR$ ), which determines energy use, is known to scale as  $MR \propto M^{0.75}$  [68], the implications for the scalings of abundance ( $N$ ) and biomass ( $B$ ) with  $M$  are as follows:  $N$  should scale with  $M$  as  $N \propto M^{-0.75}$ , because  $E \propto M^0$  and  $E = MR \times N$ .  $B$  should scale with  $M$  as  $B \propto M^{0.25}$ , because  $B = M \times N$ , such that  $B \propto M^1 \times M^{-0.75} = M^{0.25}$  (Figure 1) [24].

In size-structured ecosystems, however, only the lowest trophic level exploits the basal resource pool directly, whereas larger consumers obtain energy indirectly from this basal resource pool by eating smaller prey. Given that the transfer of energy between predators and prey is inefficient, total energy use must decrease with body-size class and trophic level [3]. This rate of energy depreciation between trophic levels depends on TE and PPMR for the community [23,69]. These two parameters can therefore be used to estimate the scaling of biomass with abundance across trophic levels [24] or trophic continua [25], which are often more representative than are discrete trophic levels in real communities [70]. The expected scalings of  $E$ ,  $N$ , and  $B$  with  $M$  across trophic levels are then, respectively (Equations I–III and Figure 1):

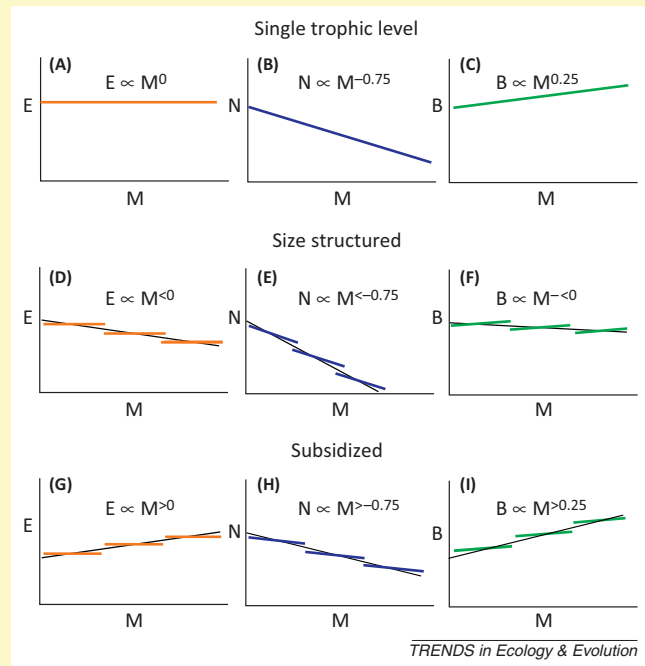
$$E \propto M^{\log(Te)/\log(PPMR)}, \quad \text{[I]}$$

$$N \propto M^{-0.75} \times M^{\log(Te)/\log(PPMR)}, \text{ and} \quad \text{[II]}$$

$$B \propto M^{0.25} \times M^{(\log Te)/\log PPMR} \quad \text{[III]}$$

Empirical testing of this model using well-sampled fish and invertebrate communities in the North Sea demonstrated a close fit between predicted and observed size spectrum slopes [25,27]. Furthermore, incorporating the metabolic effect of temperature on abundance, biomass, and production using the Boltzmann constant, popularized by the metabolic theory of ecology [10], enabled prediction of potential global fisheries production under a range of climate change scenarios [61]. If consumers at higher trophic levels and larger body sizes have

access to subsidies, then scaling exponents will be more positive than the size-structured expectations.



**Figure 1.** The scalings of energy use ( $E$ ), abundance ( $N$ ), and biomass ( $B$ ) with body-mass class ( $M$ ) for multiple species within a trophic level (A), and across multiple trophic levels (B,C). Loss of energy between trophic levels (or across trophic continua) with size-structured energy flow results in steeper scalings than the single-trophic level expectations (D–F), whereas subsidies may result in shallower scalings (G–I). All axes are logarithmic. Adapted from [24] (A–C).

### A size-based theory of pyramid shape

The shape of a biomass pyramid depends on the scaling of biomass ( $B$ ) with body mass ( $M$ ) (the biomass spectrum,  $B \propto M^x$ ), and, in particular, whether this relation has a positive or negative exponent  $x$  (i.e., whether the slope of the biomass spectrum is positive or negative). Biomass pyramids have broad bases and narrow apices when the scaling exponent  $x$  of the biomass spectrum is  $<0$ , and are inverted with narrower bases than apices when  $x > 0$  (Figure 2; Box 1). In turn, pyramid shape depends on

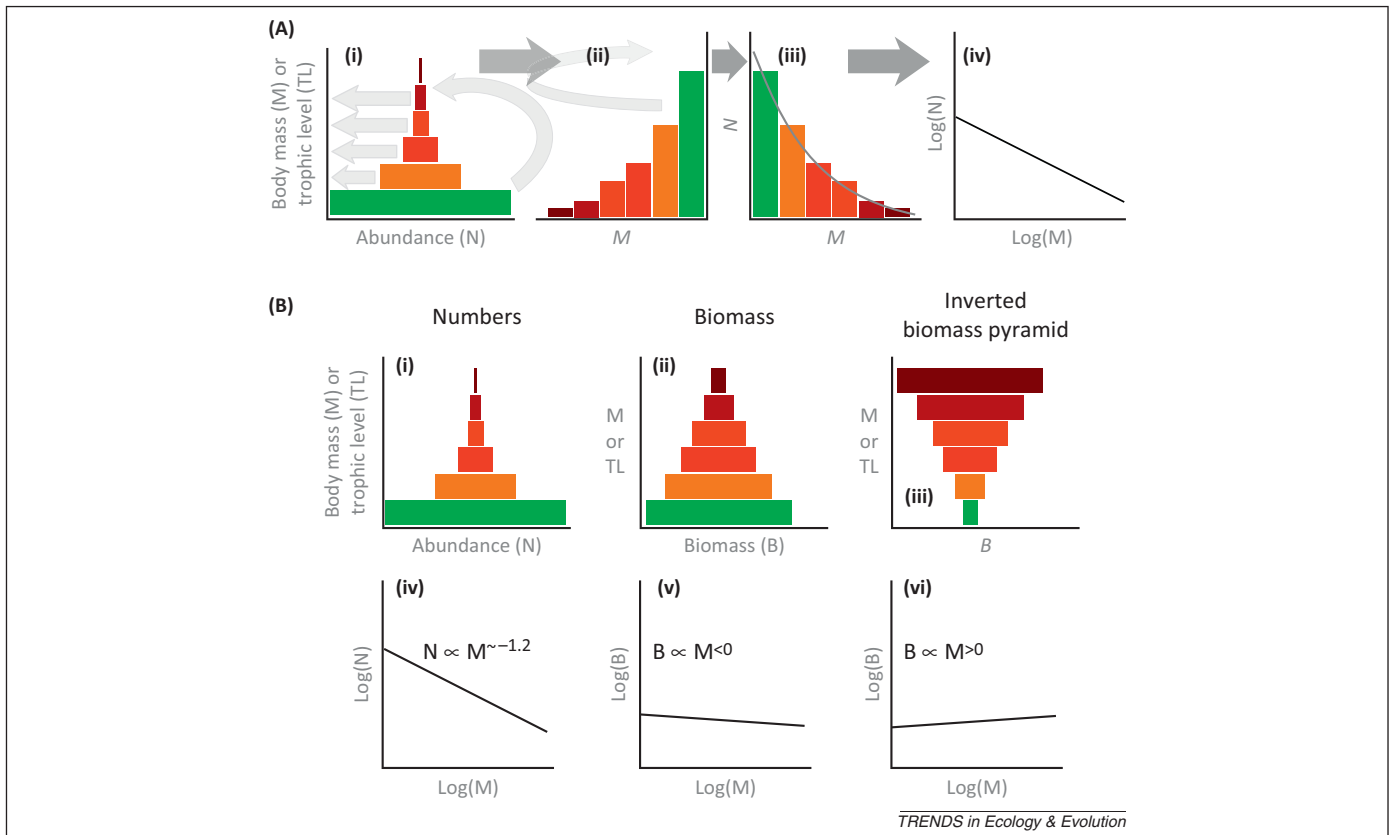
the parameters that control the size spectrum slope (TE and PPMR). Varying TE and PPMR demonstrates how biomass ( $B$ ) will scale with body-mass class ( $M$ ) and, thus, indicates the corresponding shapes of biomass pyramids (Figure 2). When predators are larger than their prey (i.e., PPMRs  $>1$ ), extreme combinations of TE and PPMR are required to invert the biomass pyramid (red domain in Figure 2). Conversely, bottom-heavy pyramids prevail (scaling exponents of  $<0$ ) for more realistic TE values ( $<0.125$ ) across a wide range of PPMR values (blue domain

### Box 2. The benefits of individual-level data

Several approaches have been used for examining relations between body mass and abundance in communities (reviewed in [66]). We have focused here on size spectra, which convey the same information as individual size distributions (ISDs). An important distinction that separates both size spectra and ISDs from other analyses of body mass–abundance relations is that, for size spectra and ISDs, body sizes are measured at the level of individuals rather than as species-level averages. Species-aggregated data can introduce bias into body mass–abundance relations [71,72] and are less appropriate for testing predictions from metabolic theory [10]. Similarly, use of species-level data can prevent clear and significant relations between body size and trophic level from being detected [71], and to spurious estimates of scaling coefficients based on PPMR [71,72]. These problems are most prominent when species have indeterminate growth, and when body mass and trophic level are strongly related (as in marine communities), but can be important even when indeterminate growth and size-based energy flow are less prominent (as for terrestrial food webs) [47,71,72]. As such, we strongly advocate for the collection of

individual-level body-size and trophic-level data wherever possible. To facilitate retrospective analyses of existing species-average data, we pragmatically suggest the consideration of whether species ontogenetic size change lies within one log unit. If so, the use of species-level mean sizes has been a useful way of yielding insightful results (e.g., [56,64]). Alternatively, a statistical sampling approach, based on empirical or estimated mean–variance relations of body size within species may be used (e.g., [65]).

Empirical estimates of community PPMR can be obtained from stomach content or stable isotope data [42]. In the crudest sense, samples of whole size classes are blended and the trophic level of a sample of the homogenate is estimated using stable isotope ratios [73]. Mean PPMR can then be calculated from the slope ( $\beta$ ) of the community relation between trophic level and body-mass class as:  $PPMR = e^{1/\beta}$  (when body mass classes are on a  $\log_e$  scale or  $PPMR = 10^{1/\beta}$  when on a  $\log_{10}$  scale [36]). An important future direction would be to propagate uncertainty in  $\beta$ , using, for example, the delta method, bootstrapping, or Bayesian methods.



**Figure 1.** From ecological pyramids to size spectra. **(A)** When beginning with a trophic-level (TL) pyramid, first convert TL to body mass ( $M$ ) to give an  $M$  pyramid. From the  $M$  pyramid, left-align  $M$  class layers and rotate  $90^\circ$  counter-clockwise (i to ii); flip the plot onto its vertical axis (ii to iii); express both axes on the log scale, to linearize (iii to iv). **(B)** Typical bottom-heavy pyramids of numbers ( $N$ ) (i) and biomass ( $B$ ) (ii), as well as an inverted biomass pyramid (IBP) (iii), along with the corresponding size spectrum representation for each configuration (iv–vi, respectively).

of Figure 2). Intermediate to these two situations, a scaling exponent of zero (broken line in Figure 2), implies that biomass is invariant across body sizes and trophic levels, resulting in a biomass ‘stack’ rather than a pyramid.

Pyramid shape has been previously explained by differences in turnover rates [usually expressed as production:biomass ratios (P:B) or generation lengths] between trophic levels [29,30]. However, this turnover-based explanation has led to some confusion regarding what pyramid configurations are realistic (e.g., [11,31]; Box 3) and it is not necessary to invoke turnover as an explanation. Although there is a pattern of varying turnover rates with trophic levels and body sizes, turnover is the proximate rather than the ultimate explanation for pyramid shape. Turnover rate is ultimately dictated by organismal metabolic rate, which is in turn determined by body size [3,29,30]. Fortunately, because P:B ratios (turnover rate) arise from metabolic rates, their scaling with body size, as  $P:B \propto M^{-0.25}$ , is both predicted by metabolic theory [10] and supported empirically [32–34]. Hence, varying turnover rate (P:B ratio) with size and trophic levels is implicitly and automatically accounted for in size spectrum theory [35].

#### How can we parameterize size-based pyramids?

PPMRs can be estimated empirically from stomach content and/or stable isotope data (Box 2). TE has previously been empirically estimated using size-based stable isotope data [36]. However, this method depends on an assumed P:B

scaling ( $P:B = k.M^{-0.25}$ , where  $k$  is a normalizing constant) and there is considerable uncertainty regarding the constant in this scaling relation [27]. More robust TEs can be estimated using mass-balance models (e.g., [37,38]), and models that account for energy transfer at the individual level, including the probability of encountering prey, the probability of prey capture, and the gross growth efficiency [19,20]. It is important to emphasize here that, in the context of size spectra, PPMRs must be estimated at the individual rather than species level (Box 2) and, to date, most estimates for both this version of PPMR and TE come from marine foodwebs in the four-order-of-magnitude body-size range encompassed by most fishes (10 g–100 kg).

Community mean PPMRs and TEs consistently fall within surprisingly narrow ranges (Figure 2). On average, predators are two to three orders of magnitude heavier than their prey (mean PPMRs typically range between 100 and 3000) [36,39–41]. Energy transfer is inefficient, with 10–13% of prey converted into predator production (mean TEs typically fall between 0.1 and 0.13; [37,38,42]; right-hand side of Figure 2). Within this TE–PPMR range, biomass pyramids are not inverted (blue zone, Figure 2). Inverted biomass pyramids may occur under extreme ecological conditions, when mean PPMRs are close to 3000 (the upper end of the typical range) and transfer is efficient (mean TEs of 0.15 or more). These extremes do not occur in whole communities, but may sometimes occur for low trophic-level subsets of communities, such as in planktonic size classes. Indeed, inverted biomass pyramids often

**Box 3. The world before humans: measuring impacts and estimating baselines**

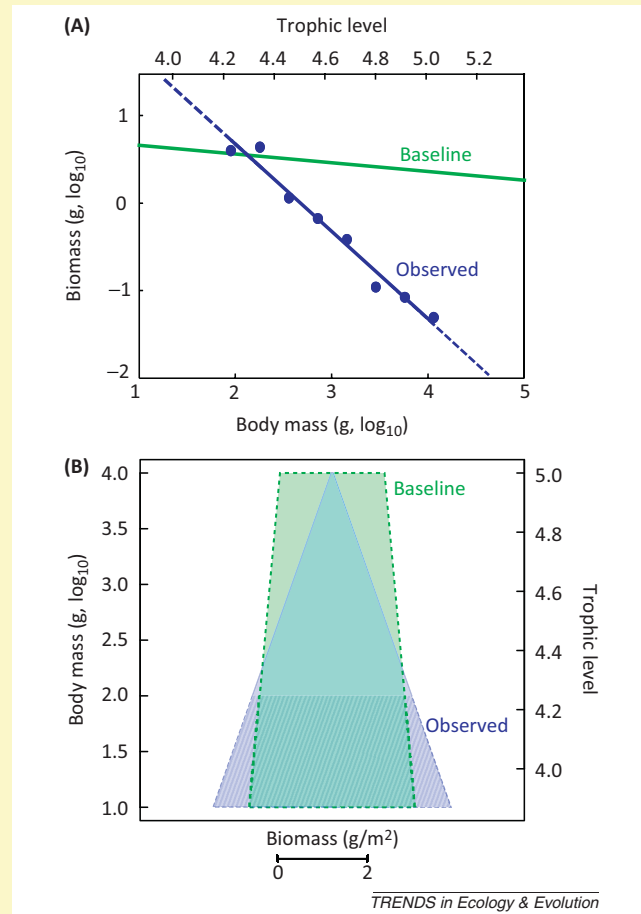
The loss of large-bodied predators, rise of mesopredators, and trophic cascades are a pervasive legacy of human activities in both terrestrial and marine ecosystems, recently termed ‘trophic downgrading’ [53]. Management objectives are hard to define without an understanding of what once was, and what has been lost. However, because hunting and overexploitation began long before scientific data collection, appropriate baselines against which to compare modern community structure are often unavailable [74,75]. Fortunately, size spectrum theory provides a unique method of predicting the structure of ecosystems before the impact of humans.

Previous attempts to estimate how ecosystems looked before humans led to surveys of animal biomass at remote locations. These studies recorded high biomasses of large-bodied predators on relatively pristine reefs in the Pacific Ocean [11] and Mediterranean Sea [31]. The authors concluded that inverted biomass pyramids (where large predators account for the majority of the standing biomass) may represent the baseline ecosystem state for nearshore marine ecosystems, and suggested that differences in turnover rate between small and large fish account for this pattern. Although it is certain that humans have caused a significant depletion of large-bodied predators across the oceans of the world, size-based constraints on trophic pyramids (see Figure 2 in main text) show that inverted pyramids are unlikely. Instead, these apparently inverted pyramids likely result from inflated abundance estimates [76–78] and/or from the aggregation of highly mobile predators that feed and assimilate energy from pelagic sources beyond the local reef ecosystem.

Ecosystem baselines, under current climate conditions, have been estimated for the heavily exploited North Sea, and for the oceans of the world using the size spectrum approach. In the North Sea, the ecosystem baseline size spectra were markedly less steep than the observed biomass-at-size, suggesting the largest size classes had been reduced by up to and over 99% [27]. The power of ecological pyramids for communicating ecosystem structure can be shown by presenting the North Sea size spectra as pyramids (Figure 1). This shows that, although the exploited community was characterized by a very bottom-heavy biomass pyramid, the baseline expectation approached a biomass ‘column’ with relatively high biomass expected in large size classes. Extrapolating beyond the range of body sizes sampled also illustrates how the pyramid representation can be useful for visualising release in smaller size-classes (Figure 1).

characterize planktonic assemblages, with the biomass of larger heterotrophic zooplankton outweighing that of smaller autotrophic phytoplankton [29,43]. However, such high TEs are unlikely to be representative of the whole-community mean, or of the mean for assemblages comprising larger body sizes and higher trophic levels [38,44]. Similarly, for more moderate TEs closer to the typical empirically observed range, extremely large PPMRs (>4000) are required for inverted biomass pyramids, which again may occur for subsets of the community with large body sizes, but are unlikely to be representative of the whole-community mean.

The general linearity of empirical size spectra (Box 4) and the strong agreement between predictions from size spectrum theory and empirical data supports the assumption of community-wide average values for transfer efficiency and predator:prey mass ratio [18,25,27,45]. However, recent work suggests that individual-level PPMR in fact increases with body size [44]. The authors point out that, because linear size spectra are empirically supported, this implies that TE must have a compensatory relation with PPMR,

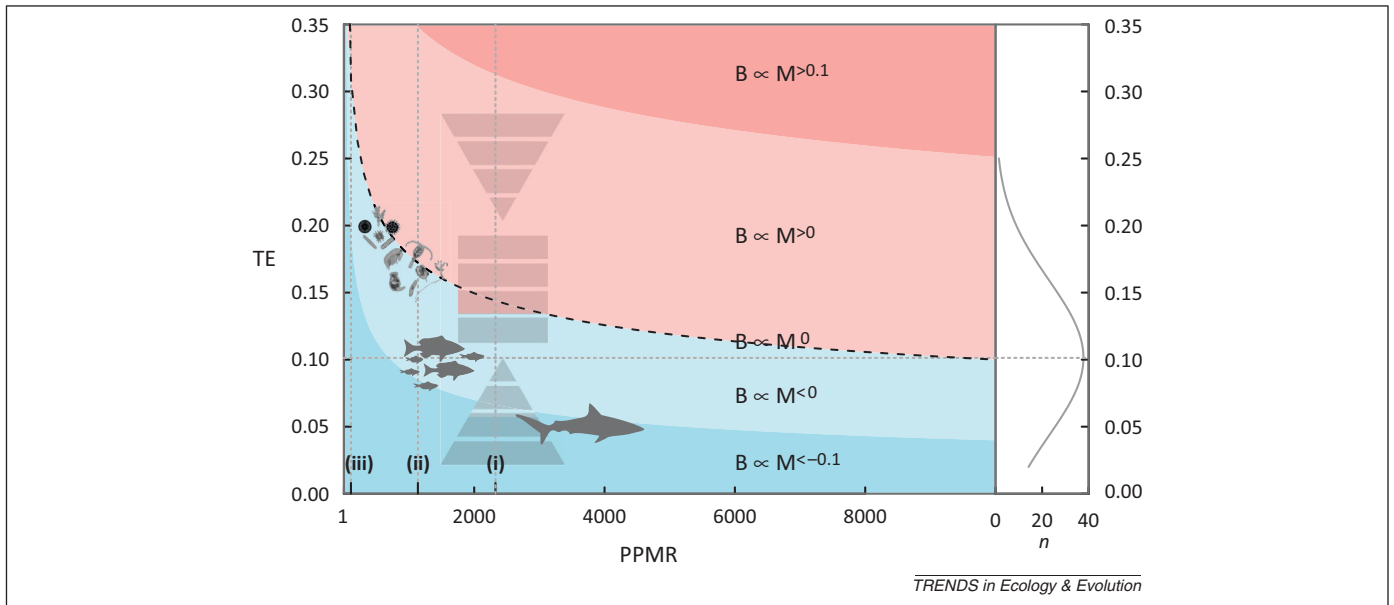


**Figure 1.** Re-expressing size spectra as biomass pyramids to understand baselines and community-scale impacts. (A) The observed (blue line and points) versus predicted baseline (green line) size spectra for the North Sea pelagic fish community can be re-expressed as biomass pyramids (B), highlighting the depletion of large-bodied community members. Extrapolating past the sampled range of body sizes (striped blue region) also illustrates how pyramids can convey release in small body sizes. Adapted from [27] (A).

such that it decreases with increasing body size [44]. This recent empirical finding is supported by a review of TE in marine foodwebs [38], which indicated that TE generally declines with increasing trophic level, with a mean of 0.13 from phytoplankton to zooplankton or benthic invertebrates, and 0.10 from zooplankton or benthic invertebrates to fish. Barnes *et al.* [44] calculated the corresponding TE values that would result, across the range of observed PPMRs, if a linear abundance spectrum with a ‘typical’ slope ( $\beta$ ) of  $-1.05$  was assumed (as  $TE = PPMR^{\beta+0.75}$ ). This approach for estimating TE could be used in future studies for which linear size spectra are observed, and PPMR has been quantified.

**Base over apex: inverted biomass pyramids in subsidized parts of ecosystems**

Inverted pyramids appear to occur in subcommunities that are subsidized with additional energy and materials, such as in detritivorous communities and with aggregations of wide-ranging predators. This pattern has also been noted in lakes, with inverted biomass pyramids generally



**Figure 2.** The shape of ecological pyramids depends upon the predator:prey mass ratio (PPMR) and transfer efficiency (TE). Biomass pyramids are ‘bottom heavy’ when  $B \propto M^{-0.1}$  (blue shading) and ‘inverted’ when  $B \propto M^{0.1}$  (pink shading). Biomass stacks occur when  $B \propto M^0$  (black broken line), with biomass invariant across body masses. The right vertical axis shows the distribution of TEs from marine food web models (mean = 0.101, s.d. = 0.058, [37]) with the horizontal dotted gray line indicating the mean. The vertical dotted gray lines represent the only available estimates of community-wide PPMR (i, demersal fish in the Western Arabian Sea [79]; ii, North Sea fish [27]; iii, entire North Sea food web [25]). Organism silhouettes illustrate TE and PPMR combinations observed or suggested for subsets of food webs (fish and sharks [44], both ‘bottom heavy’, and plankton [34,38], spanning from bottom heavy to inverted).

#### Box 4. Assumptions and limitations of the size spectrum approach

The general assumptions of size-based analyses have been described in detail elsewhere (e.g., [12,42]), but specific assumptions involved with estimating community PPMR and with estimating baseline size spectra slopes deserve attention here (also see [24,36,45]). Estimating PPMR from stable isotope data assumes that fractionation of  $\delta^{15}\text{N}$  is consistent across trophic levels. Available evidence suggests that this assumption is generally valid [24,45], but future studies that seek to estimate empirically PPMR should include sensitivity analyses for the effect of varying fractionation rates on PPMR estimates or explicitly account for uncertainty in PPMR (Box 2). Similarly, the effect of variation in TE about the estimated value used in models should be made explicit.

A key assumption in using the size spectrum approach to generate baseline estimates of community structure using empirical estimates of PPMR is that it is insensitive to the anthropogenic processes that have driven communities away from their baseline structure. This assumption is likely valid and is supported by available evidence from the North Sea [47,80], but should be tested in future studies in other systems.

It is also important to note that the TE–PPMR model for estimating size spectrum slopes provides an estimate of the equilibrium expectation that would be realized under steady-state conditions. Natural environmental fluctuations and human disturbance will lead to deviations from equilibrium. So, although the time-averaged view of the size spectrum should conform to equilibrium expectations, the ‘snapshot’ view is a sample that can be nonlinear and have unexpected slope and intercept parameters. For example, in real marine food webs, production is pulsed rather than constant, resulting in a seasonal wave of production that travels through the size spectrum [81]. Similarly, human impacts such as fishing also disturb the equilibrium state, and simulation models indicate that this will result in ‘waves’ that propagate through the size spectrum and nonlinearities [82]. However, the simplified expectations of linear spectra and steepened slopes following fishing are supported empirically [27,83,84].

indicative of allochthonous input from terrestrial vegetation [9]. Although there are few empirical estimates of TE and PPMR for communities and ecosystems other than aquatic pelagic, one study estimated PPMR for a marine benthic detritivore and filter-feeder community [45], and body mass–abundance relations in soil detritivore communities have been extensively documented [46–48]. These sources of information suggest that, in both aquatic and terrestrial ecosystems, detritivorous and filter-feeding communities are characterized by PPMRs of  $<1$ , indicating that larger-bodied individuals feed at lower trophic levels than do smaller members of the community. PPMRs of  $<1$  result in inverted biomass pyramids; in the North Sea, this yields a biomass spectrum slope of 0.48 [45] for benthic invertivores (consumers of benthic invertebrates), whereas in soil foodwebs, abundance spectrum slopes are consistently shallower than  $-0.75$  (implying biomass spectrum slopes of  $>0.25$ ) [46]. Although one could infer from the latter that the predictions of size spectrum theory were not supported by the data for soil food webs if assuming PPMRs of  $>1$ , PPMRs in detritivorous soil foodwebs are likely to be fractional ( $<1$  and greater than zero), in which case observed scalings would have been compatible with theoretical predictions. From these observations, we hypothesize that subsidized ecosystem compartments, where larger consumers have access to more production than do smaller members of the community, exhibit inverted biomass pyramid slices.

#### Escaping the constraints of size-based energy flow

A related mechanism may operate at much broader scales, whereby large highly mobile consumers essentially ‘self subsidize’, by accessing production from multiple local biomass pyramids, hence escaping the constraints of energy availability at local scales. Indeed, limited energy

availability at local scales may have driven the evolution of increasing space use and increasing PPMR among larger-bodied species and size classes; many of the largest animals are wide-ranging herbivores (elephants) or filter-feeders (baleen whales, and whale sharks). Size spectra clearly illustrate that escaping local size-based energy flow is necessitated by decreasing energy availability with increasing body size and trophic level, such that there is insufficient energy left to support minimum viable local populations of large-bodied predators at the thin end of the size spectrum wedge. Hence, we hypothesize that, at some point, size-based predation must become energetically unfeasible, driving the largest consumers to escape the constraints of local size-based energy flow. Such escapes will be necessary to access sufficient energy to support minimum viable populations at low widely dispersed densities (due to large body size). Jennings [42] suggested that such escapes happen at system-dependent body-size thresholds. The more recent finding of Barnes *et al.* [44] instead suggests that the relation between trophic level and body size is in fact continuous and probabilistic, but nonlinear, such that marine organisms in the largest body-size classes (100–1000 kg) have a greater likelihood of feeding with much higher PPMR than the rest of the community (PPMR = 14 000 at 1000 kg versus 1500 at 100 g). There are two ways to escape the tyranny of low energy availability at the largest size classes: (i) the largest predators must be able to feed at sufficiently expansive spatial scales with strategies that may be viewed as skimming the tops of multiple spatially discrete local biomass pyramids, as typified by sharks, tunas, and wolves; or (ii) the alternate solution is to evolve extreme PPMR and sieve the bottom of widely dispersed and seasonally variable pyramids, as typified by elephants, baleen whales, basking and whale sharks, and mobulid rays. Even though wide-ranging predators may be present locally within the census frame and appear to be part of an inverted biomass pyramid, in this situation they in fact represent the spatially constrained tip of a biomass pyramid with a larger-than-censused base (or multiple smaller spatially discrete pyramids).

This emphasizes the importance of being mindful of the spatial and temporal scales at which production occurs when seeking to understand the processes that shape assemblages [49,50]. In the context of classical communities that share a common resource base, the scales of censusing should align with, and lie within, the community and ecosystem boundaries of local energy production. If members of an assemblage obtain production at different scales (e.g., predator aggregations) and one tries to interpret the structure of the assemblage with models that assume a common resource base, this may lead to a misleading picture of the processes responsible for observed community structure (e.g., differences in turnover time between trophic levels being invoked to explain apparent inverted biomass pyramids in the case of predator aggregations, Box 3). One possible solution is to sample hierarchically with progressively larger sample frames for wider ranging animals [50,51].

### Implications and future directions

By revealing the link between ecological pyramids and size spectra, we show that they are two sides of the same ecological coin. By demonstrating their interchangeability,

we are compelled to suggest that size spectrum theory be viewed as a mainstream approach to understanding ecosystem ecology alongside ecological pyramids. Ecological pyramids have not yet outlived their usefulness because, once scaled with appropriate quantitative axes (which have often been lacking) and parameterized using size spectrum theory, they provide a powerful way of visualizing the structure of ecological communities and the impact of human activities upon them (Box 3). Importantly, reverting to Elton's original size-based view of pyramids resolves uncertainty over how and when inverted biomass pyramids may occur in real single- and multitrophic level communities and sheds light on the types of ecological pyramid that likely existed before historical depletions of large predators (Box 3 [52,53]).

Within a trophic level, greater biomass occurs at increasing body-size classes. Biomass may also increase with body size for highly efficient low trophic-level subcommunities (i.e., plankton). However, across multiple trophic levels and for increasingly large-bodied communities, our review of the current knowledge of realistic ranges for PPMRs and TEs indicates that inverted biomass pyramids are highly unlikely. Instead, we hypothesize that inverted biomass pyramids may occur in two situations. First, in subsidized community subsets, such as detritivorous sediment and soil communities. Second, in 'island' communities, where there may be spatial mismatch between the scale of sampling (around islands, haul-out beaches, or waterholes) and the scale of production (wider ocean or entire savannah), resulting in some members of the community being 'subsidized' by sources of energy produced elsewhere that would ordinarily be unavailable to the rest of the local community. This provides another avenue for questioning and understanding the important role that subsidies play in structuring food webs [54–56], and the role that large-mobile consumers play in linking production pools [57,58], a role that may have been disrupted by historical reductions of predators [52]. Empirical tests of these mechanisms using stable isotopes, microchemistry, and other tools to elucidate production sources and trophic positions in real communities will be a fruitful avenue for future research (e.g., [58]). Although size spectra and ecological pyramids provide a useful tool for diagnosing subsidies at assemblage scales, ecologists need to be cautious in applying food web and community concepts to parts of food webs that may not satisfy the underlying assumptions of the conceptual models being used.

Given the increasing understanding of the importance of size-based processes in terrestrial as well as aquatic ecosystems, and accompanying calls to collect data that are suitable for a wide variety of analyses (i.e., size-based, trophic, or taxonomic; for example see [59,60]), exploring the nexus and unification of size-based, trophic, and taxonomic perspectives seems to be an important goal. Linking size spectra with trophic pyramids is an important step in this direction, and illustrates that size spectra are widely applicable for understanding constraints on community structure across ecosystems.

Size spectrum theory represents a powerful framework for understanding constraints on community structure that can be used to understand both historic baselines

and future scenarios under climate change (Box 3, [61]). Size spectra are also useful for generating null hypotheses against which empirical data can be compared to identify departures that are worth investigating further [62]. The full potential of the approach can be evaluated as data are collected from a wider range of communities on land and in the sea, and as key assumptions are tested (Box 4). Two types of data are needed: body mass–abundance data, ideally with body mass measured at the individual level (as opposed to species-level averages), and community-wide size-based stable isotope estimates of predator:prey mass ratio (Box 2). Such data are available for relatively few ecosystems at present but collecting these data should be a priority [60,63]. Even in the absence of such data, approximate conversions from species-averaged to size-based representations can be made (e.g., [64,65]; Box 2).

By linking ecological pyramids with size spectrum theory, we reconcile two foundational and previously divergent ecological theories to reveal the size-based constraints to the pyramids of life. This provides a fruitful, visually intuitive, and pragmatic approach both for measuring and communicating the ecosystem consequences of global change, as well as for guiding conservation management goals and targets.

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