

Body size in ecological networks

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Body size determines a host of species traits that can affect the structure and dynamics of food webs, and other ecological networks, across multiple scales of organization. Measuring body size provides a relatively simple means of encapsulating and condensing a large amount of the biological information embedded within an ecological network. Recently, important advances have been made by incorporating body size into theoretical models that explore food web stability, the patterning of energy fluxes, and responses to perturbations. Because metabolic constraints underpin body-size scaling relationships, metabolic theory offers a potentially useful new framework within which to develop novel models to describe the structure and functioning of ecological networks and to assess the probable consequences of biodiversity change.

Introduction

Across the biosphere, the largest metazoans (e.g. whales and giant sequoias) weigh over 21 orders of magnitude more than the smallest microbes [1,2] and, even within specific ecosystems, there is considerable variation in body mass among members of the same food web (Figure 1). In the Tuesday Lake food web, for instance, there are ten orders of magnitude difference in body mass between the smallest phytoplankton at the base of the web and the largest predatory fish at the top ([2,3]; Figure 1b). Because many life-history traits are correlated with body size, this variation can have potentially profound effects across multiple scales of biological organization, from the individual to the ecosystem [4–7] (Box 1). Within an ecosystem, species are linked to one another via a network of interspecific interactions (e.g. predator–prey feeding links or facilitation, among others) and fluxes of energy or matter (e.g. nutrients). It is still only relatively recently that the role of body size in structuring food webs and other ecological networks, such as host–parasitoid systems [8] and mutualistic webs (Box 2), has begun to be explored systematically [2,3,5,9,10]. Because food webs are by far the most familiar and intensively studied type of

ecological network, they form the primary focus of this article.

In most published ecological networks, each species is depicted as a single ‘node’, thus subsuming a large amount of biological information into an individual data point. This obscures many important ecological traits of a given

Glossary

Complexity: the product of the number of species, S , and connectance, C , within a food web [$SC = S(L/S^2) = L/S$]. Once thought to be destabilising, complexity is now believed to enhance stability if most links are weak (i.e. low interaction strength).

Connectance: the proportion of links (L) that are realised in a binary food web of S species ($C = L/S^2$).

Consumer: an organism that uses a given food resource.

Ecological network: a set of nodes (usually species) that are connected to one another via pairwise interactions (represented by links). Food webs are the most familiar ecological networks, with the links between species representing trophic interactions (i.e. fluxes of matter and energy).

Ecological stoichiometry: the study of the ratios of chemical (elemental, molecular, or nutrient) concentrations between consumers and resources (often in the form of carbon:nitrogen:phosphorus ratios).

Indirect effects: an effect of one species on another that occurs through links with one or more other species in a food web (e.g. trophic cascades, apparent competition).

Keystone species: Species that exert disproportionately strong effects within a community or ecosystem. Perturbations (e.g. changes in abundance) that affect keystone species typically propagate rapidly throughout the network.

Metabolic rate: the power required to sustain an organism (energy time⁻¹), comprising the rates of resource uptake from the environment and resource allocation to survival, growth and reproduction.

Mutualistic networks: networks of seed-eaters or pollinators, and their food resources, unlike traditional predator–prey food webs that comprise multiple trophic levels.

Niche models: a model whereby species diets are ordered hierarchically within a single (niche) dimension, with a subset of basal species that do not feed on other species. A niche value is assigned to each consumer species. Each consumer can feed on all species that fall within a range of niche values with a randomly chosen centre that is lower than the consumer’s own niche value.

Predator: a consumer that eats metazoans. A broader definition, in which all consumers (e.g. detritivores, herbivores) are defined as predators, is also occasionally employed by food web ecologists.

Stability: there are three definitions of stability in common use, all of which refer to the ability of a system to maintain its structure (e.g. the species complement within a food web) over time: (i) response to temporary (pulse) perturbations: ability to recover from small (local stability) and large (global stability) perturbations; rate of recovery (resilience); ability of non-equilibrium systems to recover (permanence). (ii) response to permanent (press) perturbations: resistance (degree of change in structure; for example, if the loss of a species does not result in secondary extinctions, the system is resistant with respect to species composition). (iii) internal stability (no perturbations): inverse of variability in population densities over time (variability can be internally and/or externally driven).

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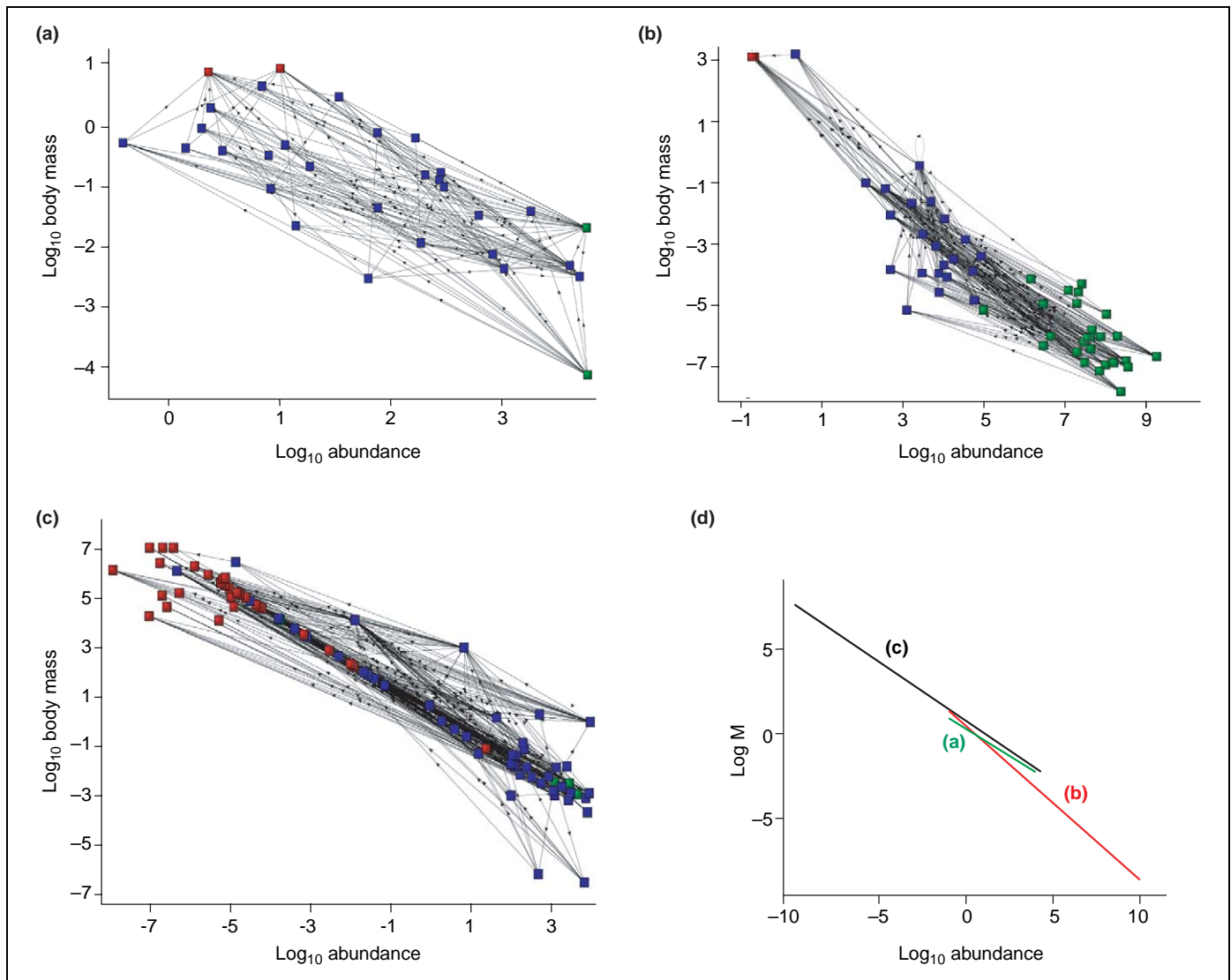


Figure 1. Food webs for (a) Broadstone Stream in England [10,15], (b) Tuesday Lake in the USA. [2,3,9,23], and (c) the Ythan Estuary in Scotland [40,54], showing trivariate relationships between log_{10} body mass (M), log_{10} abundance (N) and feeding links (*sensu* [2]). Arrows show the direction of energy flux, which is predominantly from smaller, more abundant species to larger, rarer species. Basal species are shown in green, intermediate species in blue and top species in red. Within the Ythan food web, empirical data for N were available for approximately one-third of the species in the web; the values for the remaining examples were estimated from general allometric relationships, but these species were excluded from the regression analysis of M versus N . Regression lines derived for each of the three MN plots are plotted together in (d) (a: $M=0.21-0.6N$, $r^2=0.53$; b: $M=0.62-0.91N$, $r^2=0.81$; c: $M=1.12-0.71N$, $r^2=0.84$), showing that within the abundance–body size phase space, real food webs are constrained to a specific area that is ultimately determined by metabolic constraints. Units of mass on the y-axes are given in milligrams and units of numerical abundance on the x-axis are given as the number of individuals m^{-2} in (a) and (c) and the number of individuals m^{-3} in (b). The food web data for (b) were produced by Stephen R. Carpenter [2].

species, including its population abundance, growth rate and productivity, as well as its spatial niche and its trophic, competitive and facilitative relationships with other members of the ecological network. All of these traits are correlated with body size (Table 1). Recently, metabolic theory has been invoked to explain the plethora of quarter-power allometric scaling relationships seen in nature (e.g. body-size versus each of home range size, nutrient cycling rates, numerical abundance and biomass production) and its proponents suggest that it will become as central to ecology as genetic theory is to evolutionary biology [5] (Box 1). Essentially, metabolic rate, which scales with body size (and temperature), appears to constrain biological processes, such as the flux of energy, at all levels of organization [5]. Because it captures so many aspects of the ecology of a species, body size provides a useful surrogate measure of the niche of each species

and, by extension, of entire ecological networks. Measuring body size might therefore offer a convenient way to collapse a suite of covarying species traits into a single dimension, without necessarily having to observe the traits directly. Here, we describe body-size effects in ecological networks through a scale of ascending complexity, from those that are manifested within species (i.e. individual nodes within the network) to those that are expressed at the scale of the entire network (summarized in Table 1).

Body-size effects within network nodes: ontogenetic shifts, cohort dominance and cannibalism

Variations in population-size distributions of individual species (i.e. nodes) can have effects that ramify through the wider network, especially if the nodes involved are keystone species and/or top predators (i.e. species that

Box 1. Allometries in food webs: the riddle of quarter-power scaling

Allometric scaling relationships pervade biological systems at multiple scales of organization [1,4,5]. The form of these relationships is (Eqn I)

$$Y = Y_0 M^b \quad [\text{Eqn I}]$$

where Y is some dependent variable, Y_0 is a normalization constant, M is body mass, and b is the scaling exponent. When $b \neq 1$, the relationship is called allometric, and plots as a curve on linear axes and as a straight line when taking the logarithms on both sides of the equation (Eqn II):

$$\log Y = \log Y_0 + b \log M \quad [\text{Eqn II}]$$

where b is the slope of the allometric relationship. Empirical values of b for different allometries are usually multiples of 0.25, as predicted by recently developed metabolic theory [5]. According to this theory, biological rates are ultimately determined by minimizing energy flow through a hierarchical network that is space filling and has invariant terminal end units. Thus, the number of capillaries (i.e. exchange surfaces) gives the total rate at which nutrients are supplied to tissues. Metabolic theory predicts that the distribution network will have a fractal-like architecture and that whole-organism metabolic rate (i.e. the power required to sustain an organism) should scale as $M^{3/4}$. Although some controversy exists around the universal form of the scaling of metabolism [55], a recent evaluation of published empirical data strongly supports the theoretical $M^{3/4}$ scaling [56]. The scaling of metabolism underpins the rest of predicted body-size allometries, which, in most cases, are also well supported by empirical measurements.

In Figure 1, we illustrate some commonly reported examples. The ingestion rates of consumers (g of ingested prey time^{-1}) and secondary production (g biomass produced time^{-1}) scale as whole-organism metabolism with $M^{3/4}$, such that the amount of food required per individual consumer is proportional to its metabolic rate and that a constant fraction of metabolism tends to be allocated to production [5,57]. The home-range size of animal species is predicted to scale as M^1 , and this is supported by field observations [58]. Species numerical abundance across trophic levels is predicted to scale as

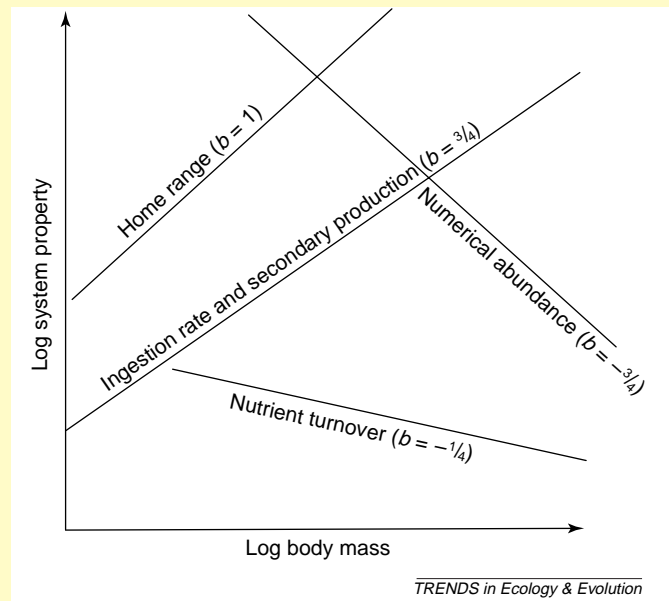


Figure 1. Examples of commonly observed allometric scaling relationships between body mass (M) and a range of system properties. Both axes are on log scales and the slopes are denoted by b .

M^{-1} , whereas it scales as $M^{-3/4}$ within single trophic levels using a common energy source [5]. The average rate of turnover of common elements (e.g. carbon or oxygen) and of some important nutrients (e.g. phosphorus) scales as $M^{-1/4}$, although the extent to which whole-body stoichiometry is determined by metabolic rate and whether or not it scales allometrically with body size needs further investigation [5,33–35].

tend to be both large and strong interactors [11]). An extreme example of this phenomenon comes from shallow lakes, where cycles of cohort dominance arising from temporal shifts in intraspecific size distributions can have catastrophic effects on populations of predatory fish at the

top of the food web [12]. The dominant predators of many piscivorous fish species, such as perch *Perca fluviatilis* and pike *Esox lucius*, are often larger conspecifics. In these systems, strong between-cohort cannibalistic and/or competitive interactions have the potential to induce

Box 2. Mutualistic networks: pollinators, seed-eaters and forbidden fruit

Food webs are not the only type of ecological network, although they are the most familiar. Mutualistic interactions such as pollination and seed dispersal are common [59], but such networks are rarely studied to a similar depth as is true of 'traditional' food webs [60]. The role of body size in plant–animal mutualistic webs remains relatively unexplored, in spite of obvious constraints on nodes and links (e.g. large consumer species are often rarer than small species, but they can transport more propagules over greater distances). The suggestion that large species are more likely to be lost from a food web than are smaller species [61] also seems to hold for mutualistic networks: for example, in the Canary Islands, the giant tortoises *Geochelone* spp. and giant lizards have all gone extinct, whereas the smaller (<0.5 m in length) *Gallotia* spp. lizard species still persist [62]. Similar examples of higher extinction rates of large-bodied seed-eaters and pollinators can be found among Gomphotheres (extinct relatives of modern elephants) from the Neotropics [63], and among birds [64] and reptiles [65] from oceanic islands. Because body-size distributions in mutualistic networks are skewed toward small species, the potential for functional redundancy [66] decreases with increasing body size. Thus, the extirpation of large species can result in the loss of mutualistic partners for several hundred plant species, causing dramatic

shifts in network topology. This is especially evident in insular networks such as oceanic islands, where 'mutualistic widow' plant species (e.g. the large-seeded *Mimulus maximus*) are common [67].

Most frugivore and pollinator species interact with a restricted subset of the plant species pool [68]. Mismatches owing to differences in body size, or in the size of relevant body parts, between species pairs can make mutualistic links physically 'forbidden': for instance, in a web containing 16 frugivores and 17 plant species, 24% of the missing links were ascribed to size effects [60]. Mutualistic webs are often characterized by truncated linkage distributions, such that the most connected species are less connected than predicted by a power-law model, and link mismatches have been suggested as a cause of this truncation [60,69].

At present, scattered information about mutualistic networks suggests that body size is an important determinant of the characteristics of links (e.g. the number and strength of realized links) and nodes (e.g. population size and vulnerability to extinction) in a way that mirrors many of the patterns reported in 'traditional' food webs. A major challenge now is to develop an equivalent body of theory that can explore the implications of body size on the structure and functioning of these ecological networks.

Table 1. Examples of relationships between body size and ecological traits, and the potential implications for the structure and/or dynamics of ecological networks^a

Trait and relationship with body size [+/-]	Within nodes	Between nodes	Network	Refs
Number of size-classes (~cohorts) [+]	Potential for cannibalism and/or cohort dominance	Potential ontogenetic reversals of trophic status	Potential for intraguild predation, self-damping and feeding loops increases towards top of the web	[15,24]
Numerical abundance [-]	More small than large individuals	Prey are more abundant and are smaller than predators	Trophic pyramid of abundance	[2,9,10,15,23]
Trophic status [+]	Larger individuals are more carnivorous	Prey are smaller than predators	Assimilation efficiency increases towards top of the web	[10,15]
Diet width [+(-)]	Diet widths expand during ontogeny	High diet overlap among similar-sized species; size constraints on feeding links	Nested vertical hierarchy of feeding niches; size-delimited 'subwebs' within the community web	[15]
Secondary production [+]	Larger individuals are more productive	Production:biomass (PB) ratios are lower for predators than prey	PB ratios decline towards the top of the web	[10]
Nutrient cycling rate [-]	Larger individuals immobilize nutrients for longer	Larger species have slower return times for nutrients; consumer-driven resource dynamics	Stoichiometric imbalances between resources and consumers	[5,33]
Species richness [-]	n/a	Small species have more potential competitors and predators	Triangular food webs; greater redundancy at lower trophic levels	[22,70]

^aExamples of some of the consequences of these relationships are given in order of increasing scale of organization, from intraspecific (within-node) effects, to effects on pairwise consumer–resource feeding links (between-nodes), to effects that are manifested at the scale of the entire food web (network).

population crashes and the consequent loss of top predators can, in turn, affect the strength and distribution of interspecific interactions in the wider food web. Ultimately, this can induce large-scale ecosystem regime shifts, such as the switch from plant-dominated to algal-dominated lakes [12,13].

Such extreme examples of cohort dominance are most likely to be exhibited by species that can continue to increase in size considerably after the onset of sexual maturation (e.g. many reptiles and fishes). However, even species that must reach a fixed size and/or life stage before they can reproduce (e.g. many insects) can also show pronounced ontogenetic (developmental) shifts in their diet, resource use and trophic position, as displayed by *Tribolium* flour beetles in laboratory systems [14]. This species exhibits three types of cannibalism (adults eat both eggs and pupae, and larvae eat eggs), creating what is, in effect, a single-species food web with four nodes and three links that typically displays chaotic population dynamics. Although such size-driven intraspecific variations in basic trophic structure are being documented increasingly, the implications of ontogenetic and seasonal shifts in body-size distributions for the dynamics of entire food webs are still largely unknown (but see [10,15]).

Body size and patterns in food web structure

Predators are usually between one and three orders of magnitude larger than their prey in terms of body mass (e.g. [2,3,15]) and, although there are some notable exceptions (e.g. host–parasite and some host–parasitoid systems, pack hunters and baleen whales), this general biological phenomenon illustrates the links between the trophic structure of whole communities and body size [5]. Inevitably, if any given species assemblage is put together with the simple constraint that all predators must feed on

a certain size range of prey, the resultant food web will display non-random structure. Within a food web, if the potential diet of a given predator is defined as a subset of the next largest predator's diet, then a 'nested hierarchy' of dietary niches will result, as is widely observed in nature (e.g. [15–17]). For instance, in the Broadstone Stream macroinvertebrate food web (Box 1; Figure 1a), as predator size increases, progressively larger prey species are added faster than smaller species are dropped, so that the largest predator eats virtually all the prey species consumed by the smaller predators [15]. This hierarchical ordering of feeding niches is a central component of the recent 'niche models' that have so successfully reproduced many of the complex topological patterns seen in real food webs, including the prevalence of generalism and omnivory, from a relatively simple set of rules (e.g. [18–20]). If community niche space can be collapsed into a single axis, as suggested by these models, and if that axis is body size, then characterizing the size distribution within a food web will capture much of the biologically meaningful variation in a relatively straightforward manner. For example, Jennings *et al.* [21] showed that \log_2 body mass explained 93% of the variation in trophic level (as defined by $\delta^{15}\text{N}\%$ derived from stable isotope analysis) among 15 fish communities in the North Sea.

Ultimately, however, if the size disparities between predators and prey at the extremes of the size spectrum become sufficiently large, perceptual and/or handling constraints will prevent these links from being realized: in other words, large vertebrate predators (e.g. sharks) are unlikely to feed directly on meiofauna (e.g. protozoa). Thus, body-size distributions might at least partially compartmentalize food webs so that although feeding hierarchies might exist within 'subwebs', perhaps delimited by multimodal humps within the community size

spectrum (e.g. microbes, meiofauna, macrofauna and megafauna), non-adjacent subwebs might have relatively few (and weak) direct connections between them. Supporting evidence has come recently from studies of benthic stream food webs that include three unimodal portions of the community size spectrum (diatoms, meiofauna and macroinvertebrates), and which have lower connectance than is typical of food webs that are restricted to more truncated portions of the size spectrum [22]. Similarly, the Tuesday Lake pelagic food web contains three size-delimited compartments, comprised of phytoplankton, zooplankton and fishes, respectively [23] (Figure 1b).

Body size and temporal scaling of food webs

Most published food webs are constructed from summary data, which can obscure potentially important seasonal and ontogenetic changes. Although such data have provided valuable insights into the size-dependent structuring of natural systems (e.g. trivariate relationships between body size, abundance and food web structure [2,3,10]; Figure 1), this assumption of constancy of food web structure is rarely, if ever, true: individual growth rates vary within and among species and over time. These changes can give rise to complex seasonal shifts in consumer–resource body size ratios that can alter the strength, or even direction, of feeding links, resulting in temporally variable food webs (e.g. [10,15]). Seasonal ontogenetic changes in diet, driven by shifts in the relative sizes of species, appear to account for many of the intraguild ‘feeding loops’ seen in real food webs (e.g. large instars of caddisfly larvae preying upon alderfly larvae, which themselves eat small instars of caddisfly larvae [10]). Indeed, the main determinant of the trophic position of a predator within a food web is often its (variable) size, rather than its (fixed) taxonomic identity (e.g. [10,13,15]). Exploring the consequences of size-driven shifts in trophic status in a simple manner represents a major challenge for ecological modelling because such shifts often introduce high levels of uncertainty and destabilize the dynamics of existing models [24]. Even the simple case of two predator species that prey on one another depending on their size class (e.g. large sea-stars feeding on small crabs and large crabs eating small sea-stars), can make traditional models extremely unstable. Nonetheless, feeding loops such as these are common in many systems, which, contrary to model predictions, also appear to be dynamically stable over many generations [10]. The use of more realistic functions to describe food-size niches and the incorporation of actual size distributions of species within a community into more refined models will undoubtedly provide important new insights, and greater efforts are now being made to document size-related interactions at the individual, rather than species, scale [8].

Body size and spatial scaling of food webs

Food webs are often viewed as discrete entities within clearly delimited spatial boundaries. In reality, however, the distribution of nodes and links varies spatially and the boundaries between food webs can be blurred [25]. Body size has a key role in determining how these spatial effects

are manifested. For instance, home range or territory size tends to increase with body size (Box 1; Figure 1) and, as a result, many systems contain certain species, such as avian top predators, whose foraging area spans several otherwise seemingly discrete ‘food webs’ [26].

Although the scaling of resource demand with body size provides one potential explanation of this pattern, recent analyses suggest that other spatial effects, such as the fractal properties of the environment, might also be important. The scaling of both the physical structure of habitats and the spatial patterns of resource distributions can be described in terms of their fractal dimension – a measurement of the way in which the extent of a habitat or resource changes at different scales of spatial resolution. Such a measure should reflect the differences in the way species of different sizes experience their environment and, because each species samples space at a particular scale of resolution, body size is a crucial determinant of the availability of food and resources that it perceives. For instance, the environment experienced by benthic meiofaunal species, such as rotifers and copepods living among the sand grains in a stream, is different from that experienced by the caddisfly larvae or amphipods living among the gravel and cobbles, and different again from that experienced by the brown trout swimming over the stream bed. Not only do the environments available to them differ in extent, but the amounts of these environments that they can exploit also differ. Within a spatial context, ‘resources’ (e.g. proteins, nutrients) can be viewed as being nested within ‘food’ (e.g. individual prey items for predators or soil solutions for plants), which is, in turn, nested within habitats. If distributions of resources, food and habitats are self-similar over multiple spatial scales, as is the case for East African mammalian herbivores and Minnesota savanna plants, their spatial patterning can be described by simple scaling laws derived from fractal geometry [27]. Fractal patterns of resource distribution might force different sizes and types of organism to exploit their environment in different ways. This could determine not only the size of home ranges of individual species, but also, by extension, spatial patterns of species diversity and body size within assemblages [27,28]. Essentially, this formalises earlier ideas that diversity is determined by the availability of spatial niches and that coexisting species cannot partition space infinitely.

It seems logical that fractal models of resource use by organisms with different body sizes (e.g. [27]) could be extended still further to predict the spatial dimension of entire food webs, which could be viewed as a hierarchy of interconnected networks. This perspective envisages food webs as networks that are connected to one another at larger (i.e. geographical) scales by the movement of individuals of (usually larger) species, whereas these networks are compartmentalised at smaller scales into spatially localized subwebs delimited by the range of movement, or habitat associations, of smaller species. If such nested spatial patterns are common, then identifying and counting ‘natural’ units of ecological networks, in terms of the area required to support the population of the largest species in a system, might be a sensible way to delimit food web boundaries [29].

In addition to these general spatial scaling effects, trophic interactions within any given food web can also be influenced by more subtle and system-specific interactions between body size and space, such as the generation of spatial refugia that can mediate otherwise strong predator impacts and prevent the extirpation of prey species. Examples include rock crevices used by smaller, more vulnerable prey [30]; increased tolerance of hypoxic habitat patches by smaller species [31]; and ontogenetic shifts in habitat use [32].

Ecological stoichiometry, ecosystem fluxes and body size

Each trophic link within a food web describes not only the ingestion of individuals by other individuals (the community perspective), as described above, but also the associated flux of biomass, energy, nutrients and trace elements between consumers and resources (the ecosystem perspective). There are explicit connections between these two perspectives: individuals must expend metabolic energy to maintain concentration gradients across their body surfaces, to acquire nutrients and to excrete waste products, and the chemical composition of most species differs markedly from that of their environment [33]. Consequently, food webs that simply describe population parameters without being constrained explicitly by thermodynamics or chemistry (i.e. via mass balance of elements) might overlook important fluxes of energy or nutrients [34,35].

Homeostatic constraints force each consumer species to keep the elemental ratios (e.g. carbon:nitrogen:phosphorus) in its body tissues within certain narrow limits, which vary with taxonomy, trophic status and body size. For instance, vertebrates require more phosphorus than do invertebrates to produce skeletal structures, and plants have a higher and more variable carbon content than do their consumers [5]. Recent studies of the consequences of elemental or molecular stoichiometric imbalances between consumers and resources have revealed that nutrient availability can be driven by the population dynamics of consumers [33]. Low turnover rates among large predators might, for example, restrict the availability of limiting nutrients to the lower trophic levels by creating bottlenecks in nutrient fluxes.

Because trophic status and longevity usually increase with body size – whereas the opposite is true for measures of abundance, growth and turnover [1,5] – the potential for stoichiometric imbalances to occur is linked implicitly to the distribution of body sizes within a food web. Recent data suggest that imbalances in carbon:nitrogen:phosphorus ratios between consumers and resources are widespread, and can even extend beyond ecosystem boundaries [36,37]. As an example, Pacific salmon species are among the largest members of many North American stream ecosystems and, following their return to freshwater from the sea, their post-spawning carcasses represent a significant pool of otherwise scarce nutrients and trace elements [36–38]. These inputs span the boundaries of the marine, freshwater and terrestrial food webs: brown bears *Ursus arctos* transport marine-derived nitrogen

from salmon carcasses into the surrounding riparian streamside vegetation [36–38].

Body size, interaction strength and cascading extinctions

Entire nodes and their associated links can be lost from, or added to, ecological networks, particularly if the system is perturbed in some way. Recently, there has been much theoretical and some empirical evidence to support the view that complex (i.e. real) food webs that contain many species and links can be dynamically stable, if most species interactions are weak (i.e. predators have small *per capita* effects on prey species) (reviewed in [39]). Strong interactions, by contrast, can lead to cascading extinctions that destabilize food webs, as has occurred repeatedly on oceanic islands following the introduction of exotic predator species that members of the resident prey assemblage have not coevolved with. There is increasing evidence that the strengths of species interactions are closely related to the distribution of body sizes: Emmerson *et al.* [40] have shown recently that interaction strength scales with the body-size ratio of predator and prey raised to some power b [$a_{ij} \sim (M_j/M_i)^b$], where M is body mass and a_{ij} is the interaction coefficient, which is defined as the *per capita* effect of species j (the predator) on species i (the prey). Consequently the body sizes of the component members of a food web can determine the propagation of disturbances and, ultimately, the dynamic stability of the entire system [40,41].

If the size spectrum of a community is altered via some perturbation, as is often the case (e.g. overfishing [42]; acidification [43]; species extinctions [44]; invasions of new species [45]), this could have potentially profound impacts on community stability and ecosystem functioning [11,40]. For example, abrupt declines of the populations of harbour seals *Phoca vitulina*, Northern fur seals *Callorhinus ursinus*, Steller sea lions *Eumetopias jubatus* and sea otters *Enhydra lutris* in the North Pacific Ocean appear to have resulted from increased predation by killer whales *Orcinus orca* that had previously preyed on the great whales before industrial whaling severely reduced the numbers of the latter [45]. The invasion of a large, strongly interacting predator to these coastal food webs appears to have triggered collapses of the in-shore otter and pinniped populations. The crashes in the populations of these smaller predators have induced explosions in sea urchin numbers, leading to increased grazing pressure being exerted on kelp.

In general, perturbations often have disproportionately strong negative effects on larger species, which also tend to be strong interactors [11]. If the average body size of a top predator in a community is reduced (e.g. because of harvesting), then the predator–prey size ratio will decline and this should, in theory, reduce the strength of trophic interactions (i.e. effects of predators on prey). It is important, however, to bear in mind which trophic levels are being considered: the removal of large, well-defended, primary consumers from a food web without the concurrent loss of predators could increase the average interaction strength (e.g. [46]), thus potentially reducing the dynamic stability of the system. If, by contrast, species are lost from the top of the food web, the relative

importance of weaker interactions will increase, and this could have stabilizing effects on the remainder of the assemblage (e.g. [47]). Size-biased, non-random species loss therefore has important implications for the risk of cascading secondary extinctions [47–52] and the loss of functional diversity from ecosystems [11,50,53].

Summary and future directions

All natural ecosystems contain networks of species that are connected to one another (e.g. via food webs) and that perform different functional roles in the system (e.g. herbivores, predators, detritivores, frugivores or pollinators). Ecosystem processes and community structure are often inextricably linked, as revealed by (usually) positive biodiversity–ecosystem functioning relationships [53]. However, because species and their associated functions are currently being lost at an unprecedented rate, the need for an improved understanding of the role of body size in structural–functional relationships is pressing, particularly because species losses are highly non-random with respect to body size (e.g. [11]).

Metabolic theory [5] has been proposed as a suitable framework within which to develop such an integrated structural–functional approach because basal metabolic rate affects pattern and process via allometric scaling relationships across multiple levels of biological organization (Table 1). By integrating such metabolic-based scaling relationships with ecological stoichiometric techniques, it might be possible to draw more explicit links between the biological, chemical and physical constraints that mould natural systems. Although body size (and its associated correlates) is by no means the only ecological trait of note, and metabolic theory is not a ‘unifying theory of everything’, we can capture a significant proportion of the ecologically relevant characteristics of an ecosystem by considering body-size parameters and allometric relationships in future studies. The challenge now is for empiricists to produce highly resolved food webs that are quantified in terms of population dynamics, energetics and chemical fluxes, and for theoreticians to develop new and more realistic size-based models, so that these emerging ideas can be explored and tested more rigorously (Box 3).

Box 3. Outstanding questions

- Can metabolic theory be applied to predict the structure and dynamics of complex ecological networks?
- Can communities be collapsed into a single ‘niche-dimension’ related to body size?
- Can allometric scaling relationships provide a simple means of linking food-web topology and dynamics?
- What are the consequences of variations in body size over time and space for the structure and dynamics of ecological networks?
- Can food webs be described as hierarchies of spatially nested networks?
- How do body size distributions affect the flux of nutrients and create stoichiometric imbalances, and what effect does this have on food webs?
- How do selective extinctions of large-bodied species affect ecological networks, and what are the biogeographical consequences of size-biased species loss?

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