

Across ecosystem comparisons of size structure: methods, approaches and prospects

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Understanding how ecological communities are structured and how this may vary between different types of ecosystems is a fundamental question in ecology. We develop a general framework for quantifying size-structure within and among different ecosystem types (e.g. terrestrial, freshwater or marine), via the use of a suite of bivariate relationships between organismal size and properties of individuals, populations, assemblages, pair-wise interactions, and network topology. Each of these relationships can be considered a dimension of size-structure, along which real communities lie on a continuous scale. For example, the strength, slope, or elevation of the body mass-versus-abundance or predator size-versus-prey size relationships may vary systematically among ecosystem types. We draw on examples from the literature and suggest new ways to use allometries for comparing among ecosystem types, which we illustrate by applying them to published data. Finally, we discuss how dimensions of size-structure are interconnected and how we could approach this complex hierarchy systematically. We conclude: (1) there are multiple dimensions of size-structure; (2) communities may be size-structured in some of these dimensions, but not necessarily in others; (3) across-system comparisons via rigorous quantitative statistical methods are possible, and (4) insufficient data are currently available to illuminate thoroughly the full extent and nature of differences in size-structure among ecosystem types.

In his influential 1927 book, 'Animal ecology', Elton wrote 'size has a remarkably great influence on the organisation of animal communities' (p. 59, Elton 1927). He described a 'pyramid of numbers' (p. 68) where the numerical abundance of organisms are organised by their size, because 'the enemy is larger than the animal upon which it preys' (p. 62). These views have held remarkable resonance throughout the ecological literature, reflecting the importance of body size as a structural mechanism within and across many levels of organisation (Peters 1983, Kerr and Dickie 2001, Brown et al. 2004). Body size is arguably the most fundamental trait of an organism, determining numerous life history and physiological characteristics (Peters 1983, Brown et al. 2004). Size can therefore greatly influence the occurrence and consequences of the ecological interactions an organism takes part in (Brooks and Dodson 1965), which have important implications for patterns at the levels of populations and communities (Gaston and Lawton 1988, Lawton 1990, Petchey et al. 2008). However, variability in the importance of body size among different ecosystem types (i.e. freshwater, marine and terrestrial systems), and the mechanisms that give rise to this variation is less well understood.

Considerable research effort has gone into documenting general patterns in the organisation of ecosystems (Cebrian 1999, Shurin and Seabloom 2005, Shurin et al. 2006). For instance, the role of biodiversity in maintaining ecosystem functioning and community stability (McCann 2000, Loreau et al. 2001, Ives and Carpenter 2007), and the importance of energy flows and nutrient cycles are concepts commonly applied to all ecosystem types (Lindeman 1942, DeAngelis 1992). There is also an emerging consensus that biological mechanisms which govern the topological properties of ecological networks might be consistent across ecosystems (Dunne et al. 2002, Montoya and Sole 2002, Montoya et al. 2006, Petchey et al. 2008). At the same time, certain fundamental differences between ecosystem types have been stressed in the literature (Link 2002, Shurin et al. 2006). The relative importance of 'bottom-up' processes (e.g. nutrient limitation) versus 'top-down' processes (e.g. predation) in aquatic and terrestrial ecosystems, in particular, has received considerable attention (Cebrian 1999, 2004, Shurin and Seabloom 2005, Shurin et al. 2006). Differences in the functional consequences of organismal size have been suggested as a means to account for both the generalities and differences between ecosystem types (Shurin et al. 2006).

There is currently a dichotomy in the literature whereby aquatic ecosystems are generally viewed as being strongly size-structured, whereas this is typically not perceived to be the case for many terrestrial systems (Shurin et al. 2006) but see (Cohen et al. 2005, Stang et al. 2006, 2009). Feeding interactions in aquatic systems are often strongly driven by individual body size, rather than species identity (Brooks and Dodson 1965), because typically, gape-limited consumers feed on increasingly larger items as they grow (Jennings et al. 2001, Kerr and Dickie 2001). In terrestrial systems on the other hand, traits (e.g. abundance, phylogeny) other than size can often have greater influence on species interactions (Vazquez 2005, Shurin et al. 2006, Wiens 2010).

This widely-held perception that there is a terrestrial–aquatic dichotomy in terms of the importance size-structuring is readily conceivable for several reasons. First, there are real and obvious differences in the physical structure of the habitats, such as the viscosity of the media, which have shaped how organisms function within it. Pelagic ecosystems have relatively little habitat heterogeneity and ‘body size refugia’ (i.e. organisms substantially larger or much smaller than a predator will typically escape predation by that predator) are often the principal means by which organisms can escape predation (Chase 1999). Terrestrial ecosystems tend to be more physically heterogeneous with more spatial refugia, though many benthic aquatic ecosystems (e.g. coral reefs or stream beds) also have diverse spatial refuges (Townsend and Hildrew 1994). Second, the relative importance of different

types of interaction (e.g. predation, competition, mutualism, parasitism) often differ between terrestrial and aquatic ecosystems. The communities in the latter group appear to be structured predominantly by predation, in which body size plays an important role (Woodward and Warren 2007, Barnes 2008). In terrestrial ecosystems, on the other hand, much pioneering food web work has focussed on host–parasitoid interactions (Holt and Lawton 1993, Rott and Godfray 2000), in which body size may still play a role (Memmott et al. 2000, Cohen et al. 2005) but species identity is typically seen as being of critical importance (Holt and Lawton 1993). Furthermore, in terrestrial systems plants are often modular and/or bigger than their consumers, therefore quantifying herbivory is much more complicated than in aquatic systems, where the majority of primary production is by single celled algae which are consumed in their entirety. Third, perspectives about the relative importance of body size versus taxonomic identity have been shaped by different historical traditions within the respective disciplines. It has generally been more common for aquatic ecologists to record the size of individuals, while terrestrial ecologists often focus on the taxonomic identity of individuals (details in Box 1); until recently relatively few ecologists have systematically recorded both (see Cohen et al. 2003 for an early example).

There is an emerging realisation that differences in size-structure among ecosystem types are, in reality, far more subtle and multi-faceted than the traditional aquatic–terrestrial divide. Moreover, we are now beginning to recognise that the

Box 1. The size of what?

The entity (e.g. individual, population, species, or size-class) for which size is quantified has implications for conceptualising, defining and quantifying size structure, and for interpreting the ecological meaning of the resultant patterns. Body size as an attribute of individuals is relatively unambiguous (at least at a given point in time) but researchers often speak of the body size of a species, which usually refers to some averaged or maximal attribute of the individuals within a species or population. The entities of interest have usually been taxonomic in terrestrial ecology (e.g. species) and size classes in marine ecology, and especially fisheries science; rarely are both examined in one ecosystem. This use of different entities hinders across-system comparisons and needs to be standardised. A clear example comes from recent studies that plot population density of the species in a local community against their average body masses (Cohen et al. 2003, Woodward et al. 2005b, Laver et al. 2010, O’Gorman and Emmerson 2010). This procedure contrasts with the individual size distribution approach (White et al. 2007), which depicts the distribution of individual body masses in a community, regardless of taxonomy. Approaches that combine both taxonomic and size-based entities require individual-level data, and it has been demonstrated in studies of body mass–abundance relationships (White et al. 2007, Reuman et al. 2008), predator–prey mass ratios (Woodward and Warren 2007), and body mass–trophic level relationships how aggregation into different entities can affect perceptions of size structure and subsequent conclusions. For example, Reuman et al. (2008) described how the slope of the abundance spectrum differed from the slope of the local size–density relationship (LSDR) for the same community food webs in a study of 149 food webs. The mechanisms that give rise to these relationships operate at different levels of organisation (i.e. the individual: abundance spectrum; or species average: LSDR).

In addition to differences ascribed to the type of entity being used, further divisions may arise via the choice of taxa (species, genera, families, etc., or a mixture), the use of functional groups (bacterivores, grazers) instead of taxa, or decisions to split species into ontogenetic stages. ‘Average body size’ can also be computed in many ways, including arithmetic- or geometric-mean body mass, median or modal body mass, or even using a qualitative ‘characteristic’ body size. Asymptotic body mass is often used in place of average body mass for species of indeterminate growth, and is commonly used in fisheries science (Andersen and Beyer 2006). Temporal and spatial scales over which averages are measured are often unspecified, and averages may be based on samples that are biased towards certain age classes or life stages. More explicit details often need to be provided as to what exactly is being measured in a given study. Thus, the general, often unaddressed, question that underpins any investigation of the importance of size in structuring communities is: ‘the size of what?’ It is critical that this is clearly defined, especially if comparisons are to be made across different studies and systems.

degree to which body size is an important property of ecosystems is likely to fall somewhere along a continuum rather than a discrete category (i.e. size-structured or not). This view is leading towards the development of a more refined set of questions regarding the extent and nature of body size in structuring ecological communities, including: what are the dominant axes of variation in the size-structuring of communities; are communities distributed continuously or are they aggregated along these axes by ecosystem type; and what empirical data and analytical methods can we employ to answer these questions?

The aim of this paper is to develop a conceptual but statistically viable framework to address these questions, and to provide a brief review of the literature regarding the importance of allometric relationships at different levels of ecological organisation (a comprehensive review of the literature is beyond the scope of this study). We then conclude with a series of examples in which we explore the possible mechanisms that might drive similarities or differences in size structure between different types of ecosystems and define how these may be explored quantitatively with data.

The axes of size structure

There are numerous allometric relationships that describe how an ecological variable scales with organismal size. For example, allometries of metabolic rate (Peters 1983, Brown et al. 2004), population abundance (Damuth 1981, Cyr et al. 1997, Reuman et al. 2008), interaction strength (Emmerson and Raffaelli 2004, Wootton and Emmerson 2005, Berlow et al. 2009), and trophic level (Jennings et al. 2001, Jonsson et al. 2005) have been described and reflect properties of individuals, populations, pair-wise interactions and ecological networks (Woodward et al. 2005b, Ings et al. 2009). Each of these allometries represents a measure of the influence of size at a different level of ecological organisation: each relationship depicts size structure in a different way.

There are many synthetic frameworks which emphasise the importance of body size for determining the structure and dynamics of ecological systems (Brooks and Dodson 1965, Peters 1983, Gaston and Lawton 1988, Lawton 1990, Brown et al. 2004). For example the metabolic theories of Brown et al. (2004) and Peters (1983) demonstrate how the body size dependence of metabolic rate influences the fluxes of energy and materials over multiple levels of ecological organisations, whereas Gaston and Lawton (1988) consider the influence of size on population dynamics and subsequent community level patterns of abundance and species richness. However, none of these conceptual or theoretical frameworks have yet attempted to draw comparisons across ecosystems of the relative influence of body size. Here we attempt to do just this, by establishing a new framework from which we can approach the analysis of across ecosystem comparisons of size structure.

An objective characterization of the relative importance of body size as a determinant of the structure of ecological communities from different ecosystem types (e.g. oceanic, coastal, estuarine, stream, lacustrine, savannah–grassland, rainforest, tundra) is crucial because it aids our understanding of how disturbances (e.g. species extinctions) might propagate

throughout the rest of the community (e.g. secondary extinctions). Furthermore, prior knowledge of the relative size structure of different ecosystem types could aid policy makers and management strategists to identify and protect the particular aspects of ecosystems that are fundamental for the architecture of the communities, and those that might be particularly vulnerable to future environmental change (Petchey and Belgrano 2010).

A strong allometric relationship (steep slope and high r^2 of the log-log linear relationship between the variable of interest and body mass) indicates that size is relatively important for the ecological variable of interest and a weaker relationship indicates that size is less important. Comparing the relative strengths, slopes, or elevations (i.e. intercepts) of allometric relationships among ecosystem types is a quantitative method for investigating the degree of size-structuring and how it varies among communities. Put another way, we suggest that comparing the relative importance of size for determining aspects of community structure at different levels of organisation and between different ecosystem types can be achieved by assessing statistical variation in the strength, slope, or elevation of specific allometries (e.g. log-species average body size versus log-population density for all species in a community). Essentially, the response variable in each of the many allometric relationships that could describe aspects of community structure can be considered to represent axes of size structure. Quantitative differences between ecosystems can be assessed for each of these axes, by adopting an analysis of co-variance or a linear mixed effects modelling framework (Bolker et al. 2009). Furthermore, these axes of size structure can be combined with other response variables to form a multi-dimensional representation of community size-structure (Fig. 1): it should therefore be possible to quantify the variation in size-structure among and within communities within this multivariate allometric framework statistically. For instance, canonical correspondence analysis (CCA) could be applied to community-level data where the similarities (and therefore clustering within multi-dimensional space) between different ecosystems are determined by one 'axis' of size structure (e.g. the mass-abundance slope) assumed to be the principal axis of variation (this can be determined a priori by applying principal components analysis). The CCA can then be 'constrained' by ecosystem type (e.g. marine, terrestrial or freshwater) as well as by other axes of size structure that have been measured (e.g. the mean predator-prey body mass ratio). Such an analysis will provide a quantitative measure (i.e. F-ratio and p-value in a permutation test) of whether the axis of size structure of interest differs between ecosystem types and also which other axes of size structure can significantly explain variation in this variable.

Recent studies have compared specific allometries among different local communities (Reuman et al. 2008, 2009a, 2009b), but to date none that we are aware of have used the multivariate approach that we propose. Here we highlight allometries at different levels of ecological organisation, from individuals, to populations and assemblages, interactions, and ultimately to ecological networks, all of which could be analysed using this framework. We provide details of allometries at each level of organisation, explain how they can be used as axes of size-structure to compare among ecosystem

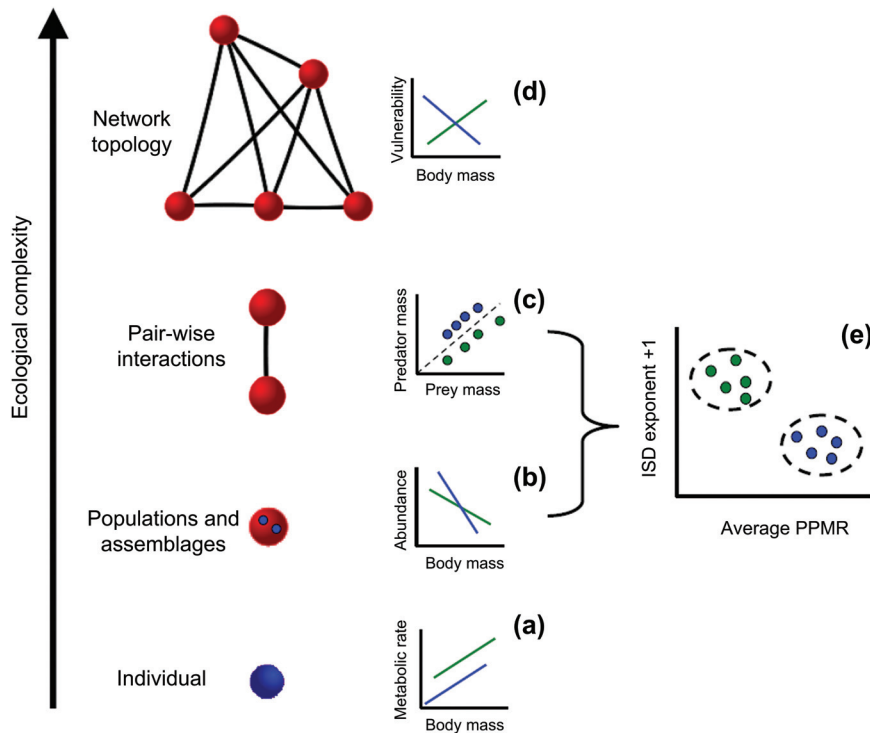


Figure 1. Schematic representation of the conceptual framework for investigating variation in the size structure of ecosystems. Size structure is manifested in allometries at multiple levels of ecological complexity, from (a) individuals, (b) populations and assemblages, (c) pair-wise interactions, and (d) the whole community or network. The strength (e.g. the r^2), slope or elevation of each allometry represents an axis of size-structure. Differences among ecosystems, (here denoted in a simplified but instructive example by green lines for terrestrial ecosystems and blue lines for aquatic ecosystems) can be tested for using analysis of covariance or simply differences in the slope, elevation, or coefficient of variation (r^2). For example, the elevation of the metabolism-mass relationship in (a) might be significantly different in a lake relative to a savannah grassland. Axes of size structure can then be combined across levels of complexity to create a multidimensional phase space in which ecosystem types can be placed to search for clustering (e). Here PPMR is the average predator to prey body mass ratio in a local community food web and ISD stands for the individual size distribution. ISD exponent + 1 is comparable to the classical un-normalized abundance spectrum slope (Reuman et al. 2008).

types, and present preliminary findings. We then synthesize across the axes of size-structure by illustrating how theoretical models can be used to link allometries across scales of ecological organisation. Finally, we identify some empirical and theoretical gaps for future research to fill.

Individuals

A wealth of research has established allometric relationships between body mass and numerous physiological and ecological characteristics of individuals (e.g. growth rate, ingestion rate, metabolic rate) (Peters 1983). A simple equation ($B \sim b_0 M^y$) links an individual's body mass (M) to its metabolic rate (B). This approximate scaling relationship was thought to span 22 orders of magnitude from the smallest unicellular organisms to the largest metazoans but (Peters 1983, Brown et al. 2004) despite the central tendency for a common exponent ($y = 3/4$) there exists considerable variation in the elevation, b_0 , among metabolic groups (e.g. endotherms and ectotherms). For example, for a 1 kg organism, the metabolic rate of an endotherm is on average about 29 times that of a similar-sized ectotherm (Peters 1983). However, very recent work suggests that although the $3/4$ power scaling of metabolism may be a common feature for metazoans, protists and

prokaryotes often have linear (i.e. $y = 1$) and super-linear (i.e. $y > 1$) mass-metabolism scaling respectively (DeLong et al. 2010). If ubiquitous, these fundamental differences in metabolism between evolutionary groups are likely to have important consequences for the multitude of ecologically relevant allometries that stem from the mass-metabolism relationship (Brown et al. 2004, DeLong et al. 2010).

Because metabolism determines the rate at which organisms acquire, store and turn over resources (Brown et al. 2004), differences in the intrinsic metabolic capacity of endotherms and ectotherms have important implications for how size influences the structure of different ecosystem types, especially as endothermic taxa are generally more prevalent in terrestrial than in aquatic systems (Shurin et al. 2006). Differences in the taxonomic composition of local communities raises the possibility that the local relationships between individual body size and metabolic rate might differ significantly between ecosystem types and from the global ones that are more often studied (White et al. 2007, Reuman et al. 2008). This would enable comparison among ecosystem types by quantifying variation in the elevation (i.e. the intercept) or the slope of the local log body mass-log metabolism relationship (a fundamental allometric axis) among ecosystems (Fig. 1a). Statistical variation in this relationship between ecosystems could

then be compared using ANCOVA, treating body mass as the covariate, metabolic rate as the dependent variable and ecosystem type as the factor.

The generality of body size–metabolism relationships are not restricted to heterotrophs. For instance, mass specific growth rates of primary producers scale negatively with their body mass or diameter (Nielsen et al. 1996, Niklas and Enquist 2001). However, unlike in heterotrophs, where body size–metabolism relationships have different elevations (b_0) and slopes (y) between metabolic groups, the growth rate of all plants has been described by a single allometric formula, which spans 20 orders of magnitude in body mass (Niklas and Enquist 2001). Furthermore, both the nitrogen and phosphorus concentration of photosynthetic tissues from unicellular algae to trees tend to be negatively related to the diameter of the plant (Nielsen et al. 1996). These studies highlight the potential ubiquity of body mass scaling of fundamental physiological and ecological characteristics of primary producers in both aquatic and terrestrial ecosystems.

It has long been recognised that aquatic and terrestrial ecosystems differ principally in the body size of their primary producers (Lindeman 1942). Unicellular phototrophs dominate aquatic primary production, whereas large trees and grasses dominate the terrestrial realm (Shurin and Seabloom 2005, Shurin et al. 2006). Correspondingly, recent evidence suggests that the elemental stoichiometry (C:N:P) of primary producers differs between aquatic and terrestrial ecosystems and, as might be expected from their size, aquatic producers typically have higher concentrations of internal nitrogen and phosphorus than their terrestrial counterparts (Cebrian and Lartigue 2004). Given the critical mass-specific variation in growth rate, turnover time and nutritional quality between large and small primary producers we might expect to see considerable differences between aquatic and terrestrial ecosystems in terms of the efficiency of herbivory, secondary production and biomass structure (Gasol et al. 1997, Cebrian 1999).

Individual-level allometries, therefore, provide the basis for a rigorous comparison of ecosystem structure and can be used to compare the slope, elevation, and r^2 of log-log allometric relationships between different ecosystem types (provided the data are collected in a systematic way; Box 1) using the statistical framework described above. As we have described for the body mass–metabolism relationship, there may be marked differences in the nature of these local allometric relationships among different ecosystem types.

Populations and assemblages

Populations and assemblages are comprised of individuals that can be assigned to species, functional groups, or size-classes (Box 1). There are many possible allometric relationships at the population or assemblage level. For instance, the abundance, stability, or extinction probability of a population, the taxonomic diversity within a size range and the home-range size of a species are all potentially related to average body size (Cardillo 2003, Hendriks 2007, Reuman et al. 2008, Davidson et al. 2009). Here we focus on two: body mass–abundance and body mass–diversity relationships.

The scaling of abundance with body mass is one of the most pervasive and well-studied of all ecological phenomena, particularly because it provides information on how resources and energy are partitioned in ecosystems (White et al. 2007). Within a local community this relationship is typically negative (i.e. small organisms are typically very abundant while the largest organisms tend to be the rarest). Body mass–abundance relationships are therefore a fundamental axis of size-structure, and the form of this bivariate relationship can reveal important similarities and differences among ecosystem types.

This relationship, when expressed as the distribution of the body sizes of all individuals within the spatial boundaries of an ecosystem, irrespective of species identity, has been called the individual size distribution (ISD) (White et al. 2007, Reuman et al. 2008). The ISD is often a power law, and this representation is related mathematically to the abundance spectrum: the abundance spectrum slope is equivalent to the ISD exponent plus 1 (White et al. 2008). Blanchard and colleagues (2009) analysed abundance spectra for pelagic and benthic detritivore communities in a marine ecosystem. They found that assemblages within the same ecosystem had different abundance spectrum slopes, being generally shallower for benthic assemblages (−0.56 to −0.87) than for pelagic assemblages (−1.2 to −2.25, the shallower end of this range corresponding to unexploited systems).

Do the same sorts of relationships hold in terrestrial systems? Interestingly, a recent study of terrestrial soil detritivore systems (Meehan 2006), which may be comparable to the benthic food webs studied by Blanchard et al. (2009), revealed remarkably similar abundance spectrum slopes (−0.72). Furthermore, in another recent study, Reuman et al. (2008) analysed the ISDs for 147 soil food webs. The mean value of their ISD exponents plus 1 was 0.71 (95% CI −0.68 to −0.74), again remarkably similar to that reported by Meehan (2006) and Blanchard et al. (2009). The three aquatic systems analysed by Reuman et al. (2008) had significantly more negative values for the ISD exponent plus 1 (−0.94, −0.9 and −1.11); these values were comparable to abundance spectrum slopes of about −1 that are typical of unexploited pelagic marine systems (Sheldon et al. 1972, Jennings and Mackinson 2003). To make a rigorous across-ecosystem comparison by comparing the slope (and also the elevation) of the ISD would ideally involve analysis of a single dataset containing data from several ecosystem types. Cyr et al. (1997) and Reuman et al. (2009a, b) have carried out similar studies using the ‘local size–density relationship’ in place of the ISD. They did not assess systematic variability in this relationship between different ecosystem types, although Reuman et al. (2009a) did assess the nature of variability among sub-types of the soil ecosystem type.

Body mass and abundance allometries in local communities have also been analysed from a different perspective, where species’ average body masses and population abundances are recorded (Cyr et al. 1997, Cohen et al. 2003, Jonsson et al. 2005) and these have been termed local size density relationships (LSDRs). LSDRs are typically highly variable (but see Layer et al. 2010) and rather than following consistent linear relationships (like abundance spectra) they may often be better-defined as a ‘constraint space’ (Gaston and Lawton 1988, Lawton 1990, Leaper and Raffaelli 1999). In

terrestrial ecosystems LSDRs are frequently non-linear, indicating that the most abundant species within the community occur at intermediate body size (Gaston and Lawton 1988, Blackburn et al. 1990, Lawton 1990, Siemann et al. 1996), but it is still unclear whether these patterns reflect important biological processes or are simply artefacts of the difficulty of sampling rare or small organisms with transient populations (Lawton 1990). Importantly, LSDRs are distinct from abundance spectra because the entity of analysis (species rather than size class) is not the same (Box 1). Direct comparisons of abundance spectra and LSDRs should generally be avoided because although their form may be superficially similar, the relationships are generated by ecological mechanisms operating at fundamentally different levels of organisation (e.g. the species level and the individual level, White et al. 2007).

Another important axis of size structure at this level of organisation is that defined by the strength of the relationship between body size and taxonomic diversity. Size–diversity relationships have typically been studied within broad taxonomic clades, often on intercontinental scales (Hutchinson and MacArthur 1959, Marquet et al. 2005), although some recent research has analysed these patterns within local communities (Reuman et al. 2008). Hutchinson and MacArthur (1959) were the first to hypothesise that there should be fewer large species within taxonomic groups, by suggesting that available niche space limits the number of large species that an environment can support. Later, Marquet et al. (2005) showed that the number of species of South American mammals of a given size decreased with increasing size, following a power law with an exponent of $\sim -3/4$ (Marquet et al. 2005).

Reuman et al. (2008) have taken a new perspective in their study of size–diversity relationships at local scales, which are generated by fundamentally different ecological processes, namely rules of community assembly and competition, and which provide information on how energy is apportioned among the species in a local community. They found remarkably consistent negative exponents across 147 soil food webs, hinting at the existence of general rules that determine the assembly of local communities. A mechanistic basis for this recently characterised relationship, however, has yet to be formulated.

These examples illustrate how abundance and diversity are related to individual size and how these relationships may vary among and within ecosystem types. In addition to those we have highlighted, there are many other population level axes of size–structure that are similarly fundamental to the structure of communities. For instance, we might expect to observe strong relationships between population stability or extinction probability and body mass. This is because large species at the top of food chains are typically rare, with low mass specific production and slow life histories (Cardillo 2003, Lyons et al. 2004, Cardillo et al. 2005, Davidson et al. 2009). These traits dramatically increase their susceptibility to population fluctuations and local extinction.

Pair-wise interactions

Ecological networks provide a road map of the interactions among individuals, populations and assemblages in a

community (*sensu* Paine 1988). These interactions can be predatory, mutualistic, parasitic, or competitive. The characteristics of some interactions scale allometrically with the body sizes of the protagonists (Yodzis and Innes 1992b, Cohen et al. 1993, Jonsson and Ebenman 1998, Woodward and Hildrew 2002a, Emmerson and Raffaelli 2004, Woodward and Warren 2007). Body size is an important determinant of predation (Warren and Lawton 1987, Cohen et al. 1993, Woodward and Hildrew 2002a, Woodward et al. 2005a, b, Brose et al. 2006a), host–parasitoid interactions (Cohen et al. 2005) and parasitism (Leaper and Huxham 2002). In aquatic systems, body size can be especially important in determining the presence or absence of trophic interactions (Cohen et al. 1993, 2003, Scharf et al. 2000, Woodward and Hildrew 2002a, Berlow 2004, Woodward et al. 2005b, Brose et al. 2006a, Woodward and Warren 2007, Barnes 2008, Berlow et al. 2009, Barnes et al. 2010). For instance, in pelagic ecosystems large fish predators are typically constrained to consume only individuals sufficiently smaller than themselves, the boundaries of which are set by the dimensions of their gape (Brooks and Dodson 1965, Persson et al. 1996). Similarly, herbivorous zooplankton can consume only phytoplankton and bacterioplankton that fall within the size constraints set by their feeding apparatus (Brooks and Dodson 1965, Sommer and Stibor 2002).

Key components of predation, such as handling time, encounter rate and attack rate, also often scale with the body sizes of the interacting organisms (Woodward et al. 2010). This scaling imposes restrictions on predation in both aquatic and terrestrial ecosystems in ways that can be described using optimal foraging theories (Costa et al. 2008, Costa 2009). For example, the time taken to handle prey by the dragonfly *Cordulegaster boltonii* decreased as it increased in body size, leading to higher ingestion rates at large consumer body sizes (Woodward and Hildrew 2002b).

Body mass may therefore also be important for determining the strength of interactions between predators and their prey (the effect of the predator population on the prey population; Wootton and Emmerson 2005). For example, Emmerson and Raffaelli (2004) demonstrated a positive relationship between the ratio of predator–prey body mass (PPMR) and interaction strength in experimental estuarine communities. Similar patterns have also been documented in kelp forests (Sala and Graham 2002), and bird communities (Wootton 1997, Sala and Graham 2002, Wootton and Emmerson 2005). Furthermore, Reuman and Cohen (2005) proposed several potential models of the strength of biomass flux (another measure of interaction strength) from each resource to each consumer in the Tuesday lake food web, which they tested against real data. Each model used body size information to make predictions of prey to predator biomass flux. Body size appears to be a fundamental determinant of the strength of trophic interactions in food webs (Wootton 1997, Sala and Graham 2002, Emmerson and Raffaelli 2004, Emmerson et al. 2005, Reuman and Cohen 2005, Wootton and Emmerson 2005), which in turn are important for the dynamic stability of the community (McCann 2000, Neutel et al. 2002, 2007, Berlow et al. 2009).

The form (i.e. the slope, strength or elevation) of the allometric relationship between predator body mass and the

body mass of their prey within food webs may be expected to vary between ecosystem types and metabolic groups (e.g. between endotherms and ectotherms) (Brose et al. 2006a). In general, the relationship between prey and predator body mass is positive (Cohen et al. 1993, Brose et al. 2006a). This relationship, when drawn for all the interactions in a given ecosystem, can be used to estimate the average predator–prey mass ratio (PPMR) and might be important for the stability of the food web because it is an important determinant of interaction strength (Brose et al. 2006b). Average PPMRs often differ between freshwater, marine and terrestrial ecosystems (Brose et al. 2006a). For instance, PPMRs involving vertebrate predators are typically larger than those involving invertebrate predators (Brose et al. 2006a). The PPMRs of vertebrate predators tend to be highest in freshwater ecosystems, intermediate in marine systems and lowest in terrestrial systems (Cohen et al. 1993, Brose et al. 2006a). Such patterns might reveal profound differences in the underlying size-structure among ecosystem types because the average PPMR in a food web is determined by an intricate balance between maximising energy transfer across trophic links and maintaining the overall stability of the food web (discussed in ‘Correlations between dimensions’).

Although the broad patterns described above may illuminate differences between ecosystem types, it is also necessary to consider other interpretations, which may arise from the method by which individuals are aggregated. Most often this is by taxonomic identity, to derive, for instance, the relationship between the average size of individuals of a prey species and those of a predator species (Brose et al. 2006a) (Box 1). This might create a ‘fallacy of averaging’ and could potentially mask a considerable amount of intraspecific variability. Species with large intraspecific variability in body size can exhibit strong ontogenetic diet shifts that may even outweigh interspecific differences (Jennings et al. 2001, Woodward and Hildrew 2002a). The effect of species averaging has been documented recently for the food web of the Broadstone Stream in which species-averaged PPMRs were compared with ratios calculated from data from the individual-based web (Fig. 2). Essentially, species-averaging resulted in the PPMR being underestimated by close to one order of magnitude across the food web as a whole (Woodward and Warren 2007): i.e. individual predators typically fed on prey that were far smaller than themselves than suggested by the species-averaged data, and only subsets of the respective populations were in fact interacting within a feeding link (Fig. 2). See also Cohen et al. (2005) for a related early example and Barnes et al. (2010) for an individual-based analysis of PPMRs in marine systems.

Network topology

Ecological networks often show characteristic topological properties, such as nested interactions, characteristic degree distributions, and non-random patterns of consumer generality (the number of resource nodes a consumer has in a food web) and resource vulnerability (the number of consumer nodes a resource has) (Dunne et al. 2002, Montoya and Sole 2002, Stouffer et al. 2005, Montoya et al. 2006, Olesen et al. 2010). Recent research has focused on the ability of body

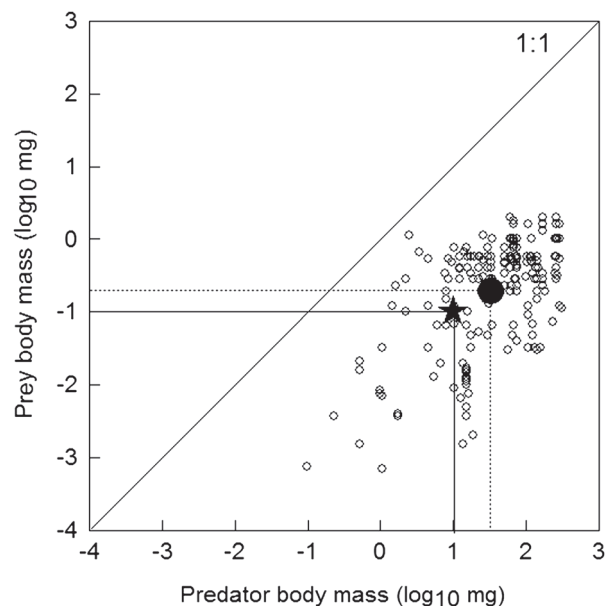


Figure 2. Prey body mass as a function of predator body mass for the top predator in the Broadstone Stream food web (the dragonfly *Cordulegaster boltonii*) and one of its dominant prey items, the stonefly nymph *Nemurella pictetii*. Data show the values obtained for the species-averaged web based on size distributions in the benthos (large solid star); individual predation events (small open circles) derived from direct observation of gut contents; and the mean body mass of predators and prey involved in observed predation events (large solid circle). Note the species-averaged data, which is commonly used to infer predator–prey mass ratios in food webs, underestimates the extent of the size disparity by a factor >2 . The diagonal represents the 1:1 line.

size to explain network properties, particularly in predator–prey food webs. Although it has been little explored to date, we propose that the size structure of network topology can be compared across different ecosystem types, by extending the approach described above, which we illustrate here with several examples.

Body size exerts strong constraints on the range of prey sizes that a predator consumes (Cohen et al. 1993), with large predators often consuming prey that are also high (in terms of their trophic level) in the food web. Positive relationships between body size and trophic position are probably the most well documented topological allometry within food webs, particularly those from aquatic ecosystems, as seen, for instance in Tuesday Lake (Jonsson et al. 2005). Similarly, Jennings and colleagues (Jennings et al. 2001, 2002) found that individual body size was a remarkably good predictor of trophic height in the North Sea, although Layman et al. (2005) found no relationship between size and trophic level in a Venezuelan river. In these examples trophic height is measured as the $\delta^{15}\text{N}$ of a consumer, which is assumed to increase by $\sim 3.4\text{‰}$ per trophic level (Vander Zanden and Rasmussen 1999). Trophic level can also be measured as mean food chain length in binary food webs (Jonsson et al. 2005). The slope and strength of the trophic-height-versus-body-size relationship is a quantitative measurement of the size structuring of food web networks that may differ among ecosystem types, and could be used to characterize and categorize food webs more broadly.

The relationship between body size and species degree (i.e. the number of links a species has to other species in a community) represents another topological axis of size structure in ecological networks. A species' degree is comprised of two types of connections: links to the species' consumers (this is known as its "out degree" or vulnerability), and links to the species' resources (its 'in degree' or generalism). In several aquatic food webs generalism increases while vulnerability decreases with body mass (Otto et al. 2007). This is supported by our novel analysis of 15 highly-resolved food webs, in which we find that body mass–generality relationships are typically strongly positive, while body mass–vulnerability relationships tend to be negative (Box 2, Fig. 3). Therefore, large species in the food web typically consume many other species, but tend to be consumed by only a few species, while small species are generally preyed upon by many, but prey on a few. These general patterns suggest that size-structure is important in determining the topology of these food webs because species' diet breadth is often constrained by their size – i.e. large species have broader diets because there are many smaller species that fall within the range of potential prey. If generalism increases with body size this can often result in "nested" food web interactions, as commonly seen in aquatic food webs (Woodward and Hildrew 2002a, Yvon-Durocher et al. 2008), in which the diet of the smallest species forms a subset of that of the next largest species, and so on.

In terrestrial systems, mutualistic networks of plant–pollinator and frugivore interactions are also highly nested (Bascompte et al. 2003, Joppa et al. 2009). At present we have limited knowledge as to what biological constraints operate in these systems and whether size is important in ordering these feeding hierarchies (but see Stang et al. 2009). However, Vasquez (2005) found that a simple model using information on the frequency of interaction of the nodes was sufficient to predict the degree of the node. This metric does not, however, reveal the underlying mechanism responsible for the interaction, as it could be affected by the abundance of both pollinators and plants, flower and fruit attractiveness,

and pollinator mobility, as well as morphological constraints (Vazquez 2005, Stang et al. 2006).

We can, however, find examples of size structure in mutualistic networks. Chamberlain and Holland (Chamberlain and Holland 2009) provide strong evidence for an allometric degree distribution in ant–plant networks and found that body size was an important determinant of the number of extra-floral nectar-bearing plants visited. In other studies the length of a pollinator's proboscis (which is correlated to its body size) appears to determine whether or not it can interact with particular plants within a mutualistic network, such that plants with wide, shallow nectar holders are generally visited by a wider selection of pollinators (Stang et al. 2006). Investigations of this kind are still scarce, and more subtle consequences are sure to appear. For example, it has been suggested that understanding the energy requirements of differently sized pollinators will further help explain visitation patterns (Stang et al. 2009).

Correlations between dimensions of size-structure

We have discussed the axes of size-structure within four levels of organisation: individuals, populations/assemblages, pair-wise interactions and network topology. The identification of potential mechanistic linkages between levels would therefore assist greatly in elucidating if, and how, size structuring operates in a unified way across multiple levels of ecological complexity. For instance, many explanations of the allometries at one level of organisation are based upon, or lead to, allometric relationships at others (Fig. 4). By linking particular dimensions of size-structure across levels of organisation, we can develop new multi-dimensional perspectives for comparing across ecosystems (Fig. 1e).

The allometry of metabolism determines an individual's energetic requirements (Peters 1983, Brown et al. 2004). This fundamental dimension of size structure at the individual

Box 2. Generality– and vulnerability–mass relationships

The generality of a consumer species or food web entity (i.e. the number of resources it has) and the vulnerability of a resource species or entity (i.e. the number of consumers it has) are often related to body size (Otto et al. 2007), and the nature of the relationship may vary among different ecosystem types. The allometry of generality and vulnerability provides a potentially important metric for documenting variability in size structure of food webs. For illustration, we analysed 15 food webs, and calculated the mass–generality correlation and the mass–vulnerability correlation of each. The 15 food webs and size information are the same as those modelled in Petchey et al. (2008), and literature sources are given in the Supplement to that paper. There was considerable variation in how strongly size was related to generalism and vulnerability across different ecosystem types (Fig. 3). For instance, the terrestrial food webs appeared less strongly size structured in this regard than the terrestrial systems, except for the Coachella Valley system. The only food web with a positive vulnerability–mass relationship was largely composed of host–parasitoid interactions. These analyses suggest that across food webs, the size–generalism relationship might be independent of the size–vulnerability relationship: if they were both affected by the same biological constraints one would expect the webs to follow a diagonal trend on the plot (as exemplified by the cascade model in Fig. 3). Whilst fifteen food webs is too few from which to make robust generalisations, the allometric degree relationship among ecological networks may become a powerful tool for understanding the nature of variation in size structure across ecosystems. Furthermore, comparing these relationships to those produced by current structural models (e.g. the cascade and niche models, Cohen et al. 1985, Williams and Martinez 2000; Fig. 3) might help understand the mechanistic biological processes underlying the success of these phenomenological static food web models.

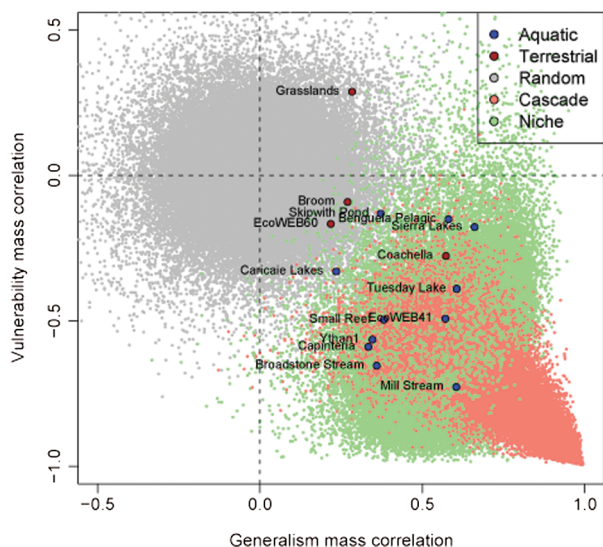


Figure 3. Variation in the topological size structure of real and model food webs. The first axis of size structure is the strength (measured by Pearson correlation) of the relationship between the log mass and generalism of species within a web. The second axis is the strength of the log mass–vulnerability relationship, again measured with Pearson correlation. Food webs from real ecosystems are shown by filled circles; food webs from three models are shown in grey, light green and salmon colour. We assumed that size was the niche axis in the cascade and niche models. There were 10 000 food webs created from each of the three models, representing values of species richness and connectance covering the range exhibited by the real food webs. Box 2 contains further details of this figure and the analyses behind it.

level pervades the organisation of all higher levels of ecological complexity (Brown et al. 2004). For example, individual size and metabolism influence the allometry of interaction strength by determining rates of resource consumption (Berlow 2004, Emmerson and Raffaelli 2004, Emmerson et al. 2005, Neutel et al. 2007, Berlow et al. 2009) (Fig. 4). Metabolic models and experiments have revealed that ‘per capita’ interactions are stronger as predator–prey body mass ratios (PPMRs) increase (Emmerson and Raffaelli 2004, Emmerson et al. 2005), whereas ‘per unit biomass’ interaction strengths decrease (Brose et al. 2005, 2006b) (Fig. 4). These patterns arise because metabolism and consumption rates scale positively with body mass when expressed per capita ($M^{-3/4}$) but negatively when expressed per unit biomass ($M^{-1/4}$). Furthermore, these patterns exemplify the importance of models that link axes of size-structure: allometries tend to be hierarchically organised, e.g. the allometry of individual metabolism underpins that of interaction strength at the subsequent level of organisation.

An allometric food web model proposed by Brose et al. (2006b) suggests a relationship between the elevation of the body mass–metabolism relationship and the mean PPMR in an ecosystem. According to their model, the mean PPMR of a food web emerges from the distribution of interaction strengths that maximises the stability of the system. We suggest that different ecosystem types may be characterised by divergent interaction strength configurations, which arise from the prevalence of different metabolic groups in these systems. Therefore, it might be possible to determine

quantitative differences in the size-structure of ecosystems by combining an individual-level axis of size-structure (the body mass–metabolism allometry) with an interaction-level relationship (PPMR–interaction strength). We may, a priori, expect to see higher elevation of the allometric metabolism relationship (i.e. higher intercept) in ecosystems dominated by ectothermic vertebrate consumers (e.g. fish in aquatic systems) compared with invertebrate consumers (e.g. phytophagous insects in terrestrial systems) because of differences in the metabolism of these different groups (Peters 1983). Consequently, consumption rates, and per unit biomass interaction strengths of ectothermic vertebrates will tend to be higher than those of similar sized invertebrates, leading Brose et al. (2006b) to suggest that invertebrate dominated food webs should persist at lower average PPMRs than those dominated by vertebrates. This is because per unit biomass interaction strengths decrease as PPMRs become larger. Because weak interactions help to stabilise food webs (McCann 2000) and invertebrate consumers interact more weakly (per unit biomass) with their resources than vertebrates, food webs with a high proportion of invertebrates tend to have lower average PPMRs. This is supported by observed patterns in the most thorough compilation of food web data in the literature (Brose et al. 2006a) and a recent study of 20 stream food webs (Layer et al. 2010).

Body mass–abundance relationships in local communities link the allometries of metabolism, interaction strength (through energy transfer across trophic levels) and abundance. Slopes of these relationships help describe how energy is partitioned among differently sized populations or assemblages within an ecosystem (White et al. 2007). Many authors have predicted the abundance spectrum slope within local or regional communities (Brown and Gillooly 2003, Jennings and Mackinson 2003, Brown et al. 2004, Andersen and Beyer 2006, Lewis et al. 2008, Reuman et al. 2008, Yvon-Durocher et al. 2008). In aquatic ecosystems this relationship has been modelled by modifying the energetic equivalence hypothesis (Damuth 1981) with a correction factor for the efficiency of energy transfer across trophic linkages (Brown and Gillooly 2003, Jennings and Mackinson 2003, Reuman et al. 2008) (Fig. 4). The energetic equivalence hypothesis (Damuth 1981), in this context, assumes that a given logarithmic size class of organisms uses approximately the same amount of energy, per unit habitat area or volume, as any other log size class of the same width. The resulting prediction is that the log abundance of a size class will be related to its log body mass by a linear relationship of slope $-3/4$. Because individual metabolism scales to the $3/4$ power of body mass, energy use by whole size classes should be approximately invariant with respect to body size when organisms share a common energy source (e.g. plants require sunlight). In food webs, organisms do not share the same energy source: rather, they are related to one another by a complex network of interactions. In this case, the form of the abundance spectrum has been well described by incorporating a correction factor which accounts for the inefficiency of energy transfer across trophic interactions and the average PPMR (Brown and Gillooly 2003, Jennings and Mackinson 2003, Reuman et al. 2008). Less efficient energy transfer or lower PPMRs result in steeper mass–abundance relationships because there is less energy available to support large organisms.

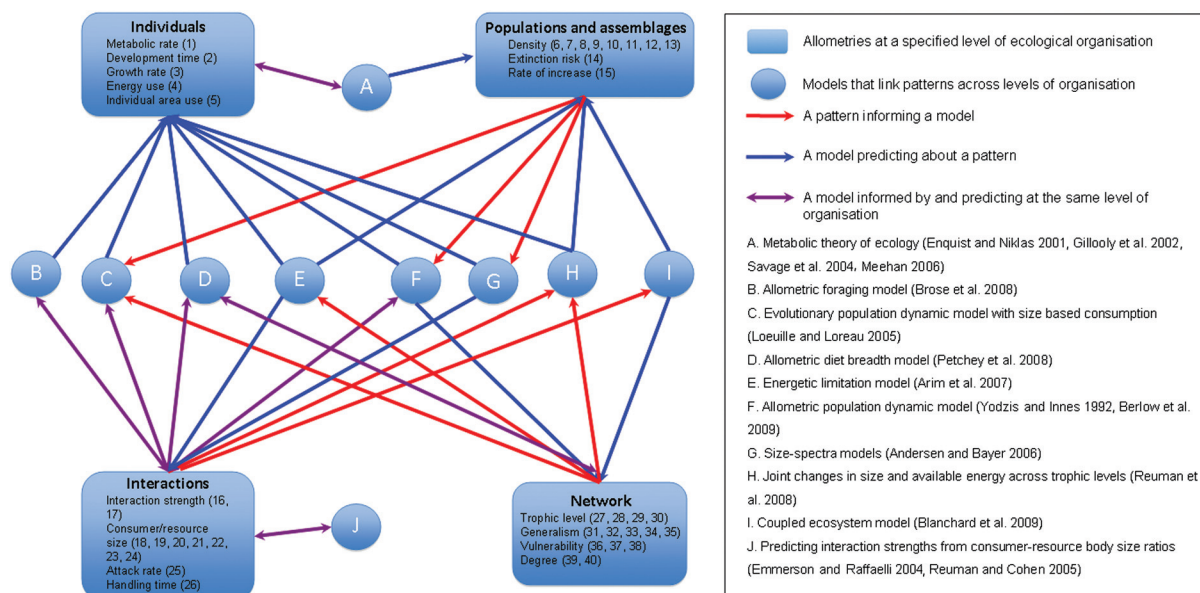


Figure 4. Allometries across four levels of ecological organisation are linked by a network of models and theories. Example allometries in each level of organisation correspond to: 1. (Peters 1983); 2. (Gillooly et al. 2002); 3. (Niklas and Enquist 2001); 4. (Enquist et al. 1998); 5. (Jetz et al. 2004); 6. (Sheldon et al. 1972); 7. (Gaedke 1993); 8. (Enquist and Niklas 2001); 9. (Cohen et al. 2003); 10. (Meehan 2006); 11. (Jennings et al. 2007); 12. (Blanchard et al. 2009); 13. (Reuman et al. 2009b); 14. (Pimm et al. 1988); 15. (Savage et al. 2004); 16. (Emmerson and Raffaelli 2004); 17. (Berlow et al. 2009); 18. (Cohen et al. 1993); 19. (Memmott et al. 2000); 20. (Leaper and Huxham 2002); 21. (Cohen et al. 2005); 22. (Brose et al. 2006a); 23. (Yvon-Durocher et al. 2008); 24. (Stang et al. 2009); 25. (Aljetlawi et al. 2004); 26. (Aljetlawi et al. 2004); 27. (Jennings et al. 2001); 28. (Jennings and Warr 2003); 29. (Layman et al. 2005); 30. (Jonsson et al. 2005); 31. (Otto et al. 2007); 32. (Woodward and Hildrew 2001); 33. (Chamberlain and Holland 2009); 34. (Cohen et al. 1993); 35. (Memmott et al. 2000); 36. (Leaper and Huxham 2002); 37. (Jennings et al. 2001); 38. (Otto et al. 2007); 39. (Woodward and Hildrew 2001); 40. (Chamberlain and Holland 2009).

The relationship between abundance and body mass within communities of locally interacting individuals is an emergent property of size structure at lower organisational levels, because body size constrains the metabolic requirements of individuals which, in turn, determines the presence and strength of their trophic interactions with other species (or size classes). Ultimately, the trophic architecture of the community determines the amount of energy available to a species (or size classes) and therefore its maximum attainable population abundance.

The mass–abundance relationship offers a potentially powerful tool for contrasting the determinants of community structure between different ecosystem types because its slope is determined in part by the efficiency of energy transfer between consumers and resources. Ecosystems with smaller PPMRs are expected to have steeper mass–abundance slopes because the abundance of larger organisms in the system are constrained by a low trophic transfer efficiency (Gaedke 1992, 1993, Kerr and Dickie 2001). It should therefore be possible to identify any systematic aggregations of different ecosystem types on plots of average PPMR against mass–abundance slopes (Fig. 1e). Distinct clusters of ecosystem types within this space could reveal important differences in their size-structure, though this relationship has yet to be explored.

The distinction between different ecosystem types, for example between aquatic and terrestrial ecosystems, might be expected to stem from fundamental differences in the body size, and therefore the stoichiometry of their primary producers. For example, we might expect to observe shallower

mass–abundance slopes in aquatic systems relative to terrestrial systems because the former tend to be dominated by smaller, more nutrient rich (low C:N:P) primary producers (Cebrian and Lartigue 2004), which facilitate efficient energy transfer to the primary consumers and subsequently to higher trophic levels. Conversely, terrestrial systems tend to be dominated by large, relatively nutrient poor autotrophs (Cebrian and Lartigue 2004) which might be expected to hinder energy transfer across the autotroph–heterotroph interface, resulting in steeper mass–abundance slopes. A recent study provides some evidence for this assertion: Mulder and Elser (2009) have shown that food webs from soil ecosystems with high soil organic matter C: nutrient ratios (i.e. greater nutrient limitation of resources) have steeper mass–abundance slopes than those with low C: nutrient ratios. They attribute this pattern to high conservation of limiting nutrients within trophic levels in the ecosystems with high C: nutrient ratios due to heterotrophic stoichiometric homeostasis (Sterner and Elser 2002), which is analogous to an inefficient transfer of energy between trophic levels, resulting in low densities of large organisms.

Recent theoretical insights that predict food web topology from allometric principles may offer a first insight into how individual, interaction, population and network levels might be linked. Since mass-dependent variations in metabolic rate determine physiological rates, such as consumption and digestion, that are critical for interspecific interactions (Yodzis and Innes 1992a, Brown et al. 2004) the effects of mass on attack rates should also be predictable (Fig. 4). Encounter rates are the product of attack rates

and prey density, hence the individual-level allometries of encounter rates are predicted by the respective allometries of density (i.e. population level) and attack rates (i.e. interaction level). From the allometries of encounter rates and handling times a range of network level properties can be predicted, such as the relationships between body mass and vulnerability, generalism, and trophic level (Petchey et al. 2008). The recent allometric diet breadth model (ADBM) (Petchey et al. 2008) predicts the topological structure of food webs based on the allometries of attack rate and handling time. The success of the ADBM in correctly predicting the position of up to 65% of links within a food web can give an insight into the relative importance of size in determining the network structure within, and also among, ecosystem types. However, an important caveat that needs to be borne in mind here relates to the quality and type of data used to verify the model. For instance, food web data collected at the individual level, rather than the species-averaged data used by Petchey et al. (2008), may provide the most thorough test of the ADBM, because ultimately interactions occur between individuals (with their associated traits, e.g. size) not species (Box 1). Unfortunately, to date very few food webs have been constructed at this level of organisation (Ings et al. 2009).

Conclusions, caveats and future directions

Body size is a crucial determinant of the structure of many ecological communities, and its influence is manifested in a myriad of ways within and across multiple levels of biological organisation. Ecosystem types may even be differently size-structured at different levels. We have sought to set out a new conceptual framework to assess the extent and form of size-structuring in natural systems, from the level of individuals to the whole ecosystem. This framework moves away from the binary and traditional aquatic versus terrestrial view of size-structure versus the lack of size-structure, and instead can compare specific types of size-structure that may vary continuously among ecosystems. Some of the components of this conceptual framework are not new, but their integration in such a way that enables rigorous across-ecosystem comparisons is novel. We are hopeful that this new synthesis and proposed allometric framework can improve the quantitative and objective assessment of the role of body size in structuring communities from different ecosystem types. Ultimately, if a more fundamental understanding can be attained, it could have important implications for predicting the responses of natural systems to future environmental change.

At present, insufficient high quality data have been collected in a systematic and standardised way from multiple ecosystem types to implement and test the proposed framework fully. To understand variation in the role of body size among communities, new data need to be collected on allometries at each of the levels of organisation outlined here, for a range of ecosystems. At present, information from multiple levels of organisation (individual, population, interaction and network) is rarely collected, even from a single system. This may be in part due to the large workload this represents, but it probably also reflects existing discipline-specific boundaries

within ecology. For example, the focus on size, rather than taxonomic identity, in the study of many marine-pelagic ecosystems contrasts with the focus on species, rather than size, in terrestrial ecosystems. Nevertheless, it is becoming increasingly apparent that individual-level data, collected in the context of the entire ecological network, will help facilitate the conceptual unification of these divergent branches of ecology (Ings et al. 2009).

Ultimately, understanding how communities are structured and whether this differs among ecosystem types is a fundamental goal for ecology, especially in the context of accelerating biodiversity loss and global change. Indeed, environmental warming favours small species in aquatic ecosystems, as highlighted by the study of Daufrense et al. (2009), who state: 'reduced body size is the third universal ecological response to global warming in aquatic systems besides shifts of species ranges toward higher latitudes and the seasonal shifts in life cycle events' (p. 12788) (see also Yvon-Durocher et al. 2011 for recent experimental evidence). Such changes in size-structure have potentially profound implications for the functioning and robustness of aquatic and undoubtedly many other ecosystems. Overexploitation of commercial fisheries has also altered the size-structure of many marine ecosystems around the world, as the largest individuals have been selectively removed (Pauly et al. 1998, Shin et al. 2005, Duplisea and Castonguay 2006, Blanchard et al. 2010). These results are consistent with theoretical expectations and simulation studies of the direct and indirect effects of fishing on marine fish communities (Jennings and Blanchard 2004, Shin and Cury 2004, Andersen and Pedersen 2010) and reductions in trophic level of catches (Pauly et al. 1998). Furthermore, recent applications of size-based analyses in terrestrial below-ground soil systems have revealed that their underlying size-structure is influenced by agricultural practices (Mulder and Elser 2009, Reuman et al. 2009a). An improved understanding of the consequences of multiple drivers acting on size structure at multiple organisational levels is clearly required (Blanchard et al. 2005, Shackell et al. 2010). An important task for future research will be to apply and test the conceptual framework developed here, in conjunction with existing mechanistic theoretical frameworks (i.e. metabolic theory, stoichiometry theory, foraging theory), to investigate how ecological systems might respond to not only current, but also future, perturbations.

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