

Preface

Editorial Commentary: Body Size and the (Re)unification of Ecology

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THE NEED FOR A MORE INTEGRATIVE APPROACH TO ECOLOGY AND A RETURN TO THE ROOTS OF THE SCIENCE

Despite having its roots among the polymath pioneers of the late nineteenth and early twentieth centuries, ecological research has, for many decades, been increasingly divided and compartmentalised into seemingly discrete subdisciplines, often with each developing its own unique approaches and parlance. This trend has recently started to reverse somewhat, as new (and old) bridges are formed (or reformed) between previously disparate fields, largely as a result of increased collaborative efforts from groups of researchers attempting to achieve a more synthetic understanding. In some ways this represents a renaissance of the early days of ecology, before the often arbitrary distinctions between behavioural, community, and ecosystems ecology became firmly entrenched (Ings *et al.*, 2009; Riede *et al.*, 2010). The stimulus behind much of this more integrated approach, and credit for the undoubted dividends it has started to pay, can be attributed at least in part to financial support structures that have been put in place specifically for the express

purpose of enabling such unifying ventures to develop, via, for instance, the LTER research networks in the United States, the European Union Framework Programmes and European Science Foundation (ESF), among others. The ESF, in particular, has supported a wide range of international collaborations in ecological science, from funding primary research grants to more discursive research networks. The latter have been designed primarily as think-tanks to bring scientists together to work on existing datasets and to develop new ecological theories, by integrating their respective fields of expertise and facilitating access to information that would otherwise be difficult (or impossible) to obtain. There have been many notable success stories emerging from this approach, including the production of a series of highly influential papers arising from the InterACT Network over the past decade (e.g. Berlow *et al.*, 2004). The current thematic volume of *Advances in Ecological Research* continues in this tradition, by presenting a selection of papers that have arisen from the recent ESF research network, *SIZEMIC* (<http://www.sizemic.org>), which was initiated and led by Richard Law and Julia Blanchard between 2006 and 2011 (Blanchard, 2011). The primary objective of the network was to integrate pure and applied approaches from aquatic and terrestrial ecology to support and develop an ecosystem approach, with the principal focus being on assessing the role of body size in multispecies systems (communities, food webs, ecosystems).

The seven papers in this volume are the product of collaborations resulting from the activities of *SIZEMIC*, and the evolution of the ideas presented here can be linked to recent publications that have appeared in other thematic volumes of *Advances in Ecological Research* and elsewhere within the past few years, several of which (e.g. Woodward *et al.*, 2010a,b) were also wholly or partly supported by this ESF network. Although funded by the ESF, the *SIZEMIC* network is by no means exclusively European in its membership nor in its outlook, as highlighted by the fact that many of the authors contributing to this volume are from further afield, with contributors from North and South America, Europe and Asia, and study systems ranging from the Arctic to the Temperate and Tropical Zones, and to the Antarctic. As such, the network of researchers and the range of available data sources that have emerged are truly global in scope, and this in itself is an impressive and notable achievement of the ESF programme, even beyond the scientific discoveries that have been made. This has facilitated important new insights into both the generalities (e.g. Gilljam *et al.*, 2011) and the apparent uniqueness of the role of body size or other drivers (e.g. Henri *et al.*, 2011; Jacob *et al.*, 2011) within ecosystems across the world.

A CHANGING WORLD VIEW?

In the earliest days of ecology, little distinction was made between the different branches of the science, as most of these fields were still aggregated within the broad field of natural history or its precursor, natural theology, and many of its first practitioners were able to turn their hands to a wide range of scientific disciplines, from geology to evolution and, more broadly, from science to philosophy. Since then the nascent science has inevitably branched into a diverse range of specialist areas as it has grown, largely due to the particular knowledge and sets of skills required by practitioners working in different environments (e.g. as marine, terrestrial and freshwater cleaved off into their own distinctive fields) and using different approaches (e.g. as empiricism and mathematical modelling approaches became increasingly disengaged, particularly from the 1970s until the turn of the twenty-first century). Further schisms opened up over the course of the twentieth century as, for example, pure and applied ecology became more distinct from one another, with parts of the latter becoming more of a technology than a scientific discipline *per se*, as evidenced, for instance, by the increasing dominance of the field of biomonitoring since the 1960s (Friberg *et al.*, 2011).

In the complex world of ecological research, it has become evermore difficult to keep pace with the cutting edge of any scientific (sub)discipline, especially because highly specialist skills and knowledge are now required within every field of scientific endeavour. Unfortunately, there is an inevitable cost to offset against the benefits of this expansion and diversification: the ability to synthesis and unite different traditions and perspectives has become increasingly limited as the discipline as a whole has grown. This has resulted in the apparent paradox that ecology has become both more diverse *and* more specialised over time.

There has, however, been something of a sea change in the past decade, which may be ascribed to both the new funding mechanisms that have become available and a greater willingness among the new generation of scientists who have grown up within this more collaborative environment to engage with one another (Petchey and Belgrano, 2010). This stands in stark contrast to the long-standing tendency for different camps to set up entrenched and often opposing positions, which had previously hindered the development and closer integration of different fields within ecology, as was the case, for instance, during the decades of disagreements between empiricists and theoreticians in the now largely resolved complexity–stability debate (McCann, 2000). There is also the additional urgency, recognised across all the branches of ecology, that, if we are to tackle the pressing real-world threats to the functioning of the planet's ecosystems then, we must collaborate more effectively in order to

understand and predict the likely responses to future global change (de Visser *et al.*, 2011; Woodward *et al.*, 2010a). This trend for previously disconnected subdisciplines to reconnect into a more synthetic approach goes further still, as ecology is becoming increasingly interconnected with other disciplines within the life sciences (e.g. functional genomics of microbial assemblages), the physical sciences (e.g. the use of stable isotopes to track global biogeochemical cycles) and the social sciences (e.g. the socioeconomics of ecosystem goods and services). As such, our science is now an extremely broad church, which makes it both an exciting and challenging field in which to work.

SEARCHING FOR SIMPLIFYING RULES WITHIN A COMPLEX SCIENCE

Given that modern ecology must operate within such a complex interdisciplinary arena, a necessary first step to developing a more united perspective is to identify some simplifying "rules" or common ground that can be used to form links across different systems, fields of research, and levels of organisation. One of the most obvious contenders in this context is the role of body size, which is perhaps the most fundamental (yet relatively easily measured) of all ecological traits (de Ruiter *et al.*, 1995; Reuman *et al.*, 2009; Woodward *et al.*, 2010a,b). It is also, importantly, a trait that can be applied to characterise species and other aggregated entities (e.g. feeding guilds) within complex systems, as well as individuals. These key points recur throughout this volume and also in several related papers in Volumes 42, 43 and 44 (Gilljam *et al.*, 2011; Hladyz *et al.*, 2011; Layer *et al.*, 2010, 2011; McLaughlin *et al.*, 2010; Mulder *et al.*, 2011; O'Gorman and Emmerson, 2010; Perkins *et al.*, 2010): in particular, using individuals as a prism through which to view other levels of organisation is emphasised here, as the realisation that this approach can provide a unifying perspective has become increasingly apparent.

The focus on the role of body size at the higher (multispecies) levels of organisation has intensified exponentially in recent years, although its role as a structuring force in ecology was recognised by some of the first forefathers of the modern discipline, including, perhaps most notably, Elton (1927), Haldane (1927) and Hutchinson (1959). In the intervening period, a range of seminal papers have paved the way for much of the work presented here, enabling today's ecologists to stand on the shoulders of these earlier giants: in particular, the clear connection between the energetic currency of ecology and individual body size has underpinned many of the most recent leaps forward (e.g. Brown *et al.*, 2004; Cohen *et al.*, 2003; Emmerson and Raffaelli, 2004; Peters, 1983; Sheldon *et al.*, 1972; Yodzis and Innes, 1992). It was not, however, just the pioneers of classical community ecology that have long recognised the significance of body size: some of the earliest fisheries

scientists, such as Hardy (1924), also identified it as the key driver in their study systems. Fisheries science has developed subsequently into a discipline in its own right, often in striking parallel to mainstream ecology, yet this insight was not incorporated until the latter part of the twentieth century.

It is intriguing to consider now, with the benefit of hindsight, why the study of the role of body size developed in fits and starts over the twentieth century and why it has only recently attained the substantial head of pressure that has led to the current mushrooming of size-related papers. This renaissance has been particularly evident in the spheres of food web ecology and biodiversity–ecosystem functioning research, which have driven many of the advances in both community and ecosystems ecology within the past decade, where body size has emerged repeatedly as a critical organismal trait (Reiss *et al.*, 2009; Rudolf and Lafferty, 2011). Body size has also long been firmly embedded within behavioural ecology as a core component of foraging theory, another branch of ecology that is starting to be reconnected to the study of multispecies systems (e.g. Costa *et al.*, 2008; Petchey *et al.*, 2008). The strong emphasis in fisheries science has also helped in the reintegration of this highly applied field into more general ecology, which has undoubtedly been accelerated further by the growing general awareness of the current parlous state of global fisheries and the devastating consequences of decades of intensive size-selective harvesting in marine ecosystems.

THE DIVISION AND RECONNECTION OF FISHERIES SCIENCE AND ECOLOGY

The divorce of fisheries science from general ecology offers an interesting example of how scientific fields diverge and develop fundamentally different worldviews and approaches. Fisheries science emerged in the early part of the twentieth century as its own discipline, with the aim of understanding and managing fisheries. It developed into an interdisciplinary field comprising biology, oceanography, economics and statistics, and large research institutes were set up to address its aims. Fisheries science developed its own conferences, its own journals, and many of the important developments were published in the grey literature. During the course of its evolution, there have been ebbs and flows in the degree of cross-fertilisation with other disciplines. A significant step change in both fisheries science and ecology was the development of the theoretical framework for describing exploited fish stocks by Beverton and Holt (1957). The emergence of this framework influenced mainstream ecology (e.g. population dynamics, life-history theory) profoundly, but it also marked a turning point in fisheries science as a purely applied field, in which the emphasis thereafter was on developing methods to

assess the sizes of stocks and determine how they could be exploited optimally from a resource productivity perspective.

Almost since its inception, fisheries science recognised the need to describe the structure of fish populations, as fish have very different egg and adult sizes, as well as indeterminate growth. However, for purely technical reasons, age was chosen as the structuring variable, not size. Subsequently, food web and species interactions were also acknowledged as important drivers. Extensive dietary data collection programmes, which involved dissecting vast numbers of stomach contents, were carried out in the 1980s and 1990s, where measurements of interactions between species were recorded at the individual level. Ironically, once the measured size was transformed into age, the information of size was in many cases discarded in the surviving databases. From a food web perspective, the information in these databases are still underutilised, as fisheries scientists have been less focussed on understanding the fundamental structures of food webs than on the consequences for conservation and management. These data have been applied widely to parameterise multispecies and ecosystem models, ranging from simple to complex, used to address wider concerns about the effects of fishing on marine ecosystems (Pinnegar *et al.*, 2008). Due to the sheer complexity of many of these systems, data requirements and lack of consensus among modelling approaches, some of the earlier proponents of multispecies fisheries models went “back to basics” by considering the role of body size in exploited fish communities (Pope *et al.*, 1988).

Marine ecology, like its sister fisheries science, was one of the first branches of ecology to realise the importance of individual body size, as evidenced by seminal papers relating the size of individuals (or groups of similar-sized individuals) to abundance (Sheldon *et al.*, 1972), population growth rate (Fenchel, 1974) and predator–prey mass ratios (Ursin, 1973). Within fisheries science, the idea of size distributions (size spectra) was taken up and developed both empirically (Boudreau and Dickie, 1989; Daan *et al.*, 2005) and theoretically (Borgmann, 1987; Dickie, 1976; Kerr, 1974). More recently, these ideas are being condensed into “size-spectrum models” for assessment of fish stocks and for making ecosystem-oriented assessments of the impacts of fishing (Andersen and Rice, 2010; Hall *et al.*, 2006; Pope *et al.*, 2006; Rochet *et al.*, 2011). The new generation of fisheries scientists are not constrained by the narrow circle of the field’s specialist literature, and these researchers are looking to the developments in ecology to integrate these advances in order to develop practical methods for applied fisheries science. *SIZEMIC* has been an important venue for this initial stage of cross-fertilisation to occur, and its inception may be seen in hindsight as one of the decisive moments when fisheries science and other branches of ecology became engaged anew.

INDIVIDUAL-BASED DATA AND THE "CURSE OF THE
LATIN BINOMIAL"

The reason for the surprising scarcity of detailed data on both body size and taxonomy within a single study can be ascribed largely to the fact that the different strands of each subdiscipline have tended, at least until recently, to follow their own trajectory, building on the historical and inherited traditions of preceding work, often with little crossover between them (Brown and Gillooly, 2003). Thus, the vast majority of community or ecosystem studies have recorded data on taxonomy or body size, yet surprisingly few have recorded information on both—and fewer still have collected information at the individual level. This has therefore been something of a rate-limiting step to the pace of change within the field: gathering such information allows multispecies systems to be seen from truly multivariate perspectives, as data can be aggregated in a range of different ways to view the same system through numerous different prisms simultaneously (Gilljam *et al.*, 2011).

Much of ecology to date has fixated on the importance of taxonomic identity, which undoubtedly reflects our concerns with declining biodiversity in the ongoing sixth Great Extinction as well as ecology's deep historical roots in natural history. Whilst the species concept has clearly been extremely useful to ecologists, it is not the only prism through which to view the world, and it now clear that it is not enough to know what an organism *is*, but also to know what it *does*, and much of the latter is dependent on both taxonomic identity and size.

Despite this traditionally strong emphasis on taxonomy, there are several branches of ecology that have not been so bound to the so-called *curse of the Latin binomial* (Raffaelli, 2007): in these fields, body size has been the primary focus, often to the exclusion of taxonomic identity *per se*. This situation applies to much of fisheries science, where species identity is often not a useful context for describing the key attributes of an organism, especially from a trophic ecology or food web perspective, since the functional role of an individual (e.g. its position in a food chain) is determined primarily by its size. As many fishes span several orders of magnitude from the larval to adult forms, with accompanying dramatic changes in their ecology and feeding behaviour, a useful simplifying approach has been to use size spectra or individual size distributions to map the broad patterns of energy flux through an assemblage (or commercial fishery): in fact, this size-based approach is typically far more revealing than those that are taxonomically based (Jennings *et al.*, 2002, 2007).

At the other extreme of what we might term the "species-versus-size" continuum, terrestrial animal ecologists have often ignored the role of body size and focused almost exclusively on species identity: this reflects the widely held view that these systems are less size-structured and hence more

idiosyncratic than their aquatic counterparts, as well as the strong historical influence of classical entomology in this field (Ings *et al.*, 2009; Yvon-Durocher *et al.*, 2011). Similarly, terrestrial plant ecologists have concentrated on characterising a diverse range of functional traits for far longer than has been the case for animal ecologists, probably because here body size is often difficult to determine in an ecologically meaningful way: for instance, how can it be applied to modular organisms, and what is the unit of interaction (e.g. the leaf or the plant)? In reality, neither of these extreme positions is entirely able to capture the true determinants of higher-level organisation, as both species and body size are likely to be important, but to differing degrees (Ings *et al.*, 2009; Yvon-Durocher *et al.*, 2011; Zook *et al.*, 2011): the “curse of the Latin binomial” might therefore be more accurately described as a “mixed blessing”.

This realisation that both size and species matter has stimulated recent research interest in attempting to partition the relative contributions of each in multispecies systems, and one way in which this can be done is to take an individual-based perspective, since every individual has, at any given time, both a taxonomic identity and a measurable body size: by recording both, it is possible to view food webs, communities and ecosystems from several different perspectives simultaneously (Ings *et al.*, 2009; Yvon-Durocher *et al.*, 2011).

Such an approach can provide much deeper insight than can be gained from using either in isolation, as highlighted in the Gilljam *et al.* (2011) chapter in this volume. They build on a recent paper by Woodward *et al.* (2010b) to view a set of seven highly resolved individual-based aquatic food webs from a range of levels of organisation (individuals to species populations) and aggregation (e.g. species-averaging by nodes versus species-averaging by links). Nakazawa *et al.* (2011) also pick up on these emerging ideas and consider how predator–prey mass ratios, which are key parameters in many structural and dynamical food web models, are particularly sensitive to the level of organisation and aggregation used. They too explore several of the sides of the prism investigated by Gilljam *et al.*, using a dataset from four marine systems, and also emphasise the importance of considering both size and taxonomy together when using size-based community-spectrum models that describe individual-level interactions. These themes associated with the effects of data aggregation, and the potential mirages it can create due to methodological artefacts, are also addressed by Arim *et al.* (2011) in this volume. They examine different approaches to studying (global and local) mass–abundance scaling relationships and assess the relative strengths and weaknesses of different statistical models for describing different forms of the same data. They compare model fits from a set of temporary ponds as a case study and propose a new method for dealing with this problem in a more logical and consistent manner than has been the case previously.

Melián *et al.* (2011) also have an individual-based focus to their chapter, but here they extend these ideas to consider the role of both ecology and evolution within a food web context, forging a connection between another two often (artificially) disconnected realms of biology. Castle *et al.* (2011) form a connection between fisheries science and the advances currently being made in more general ecology, by again employing an individual-based approach, but in this case from a mathematical modelling perspective. They propose a spatially explicit, continuous, time-dependent model of size spectra to predict how the active movement and passive transport of individuals can influence individual growth and size spectra. They also examined the effects of aggregating data (here, in a spatiotemporal context) and found that the degree to which stability is evident in size spectra depends on the scale of aggregation, which implies that sampling at relatively large scales is necessary to compare emergent higher-level properties, such as size spectra, among regions or ecosystems.

The recognition of the importance of individual-level variation in all these papers highlights how adopting this perspective can help to link behavioural, community and ecosystems ecology to evolutionary biology, as the key processes act at (or close to) this level: for instance, individual behaviour determines foraging decisions, individual metabolic constraints determine population size and energy flux through the food web and individual variation among genotypes provides the template upon which natural selection acts (Lewis *et al.*, 2008; Melián *et al.*, 2011; Petchey *et al.*, 2008; Stouffer *et al.*, 2011; Thierry *et al.*, 2011). It is illuminating to be able, at last, to view both sides of the coin together: fisheries science and other branches of ecology have much to offer one another, as the previously perceived barriers between size-based and species-based views of the world melt away, and the *SIZEMIC* network has contributed in no small part to this rapprochement.

BEYOND TAXONOMY AND BODY SIZE?

The paper by Jacob *et al.* (2011) focuses on marine systems, but here from a slightly different perspective—they explore the distribution and role of functional traits, including, but not restricted to, body size, in terms of network stability within the complex Wedell Sea food web in Antarctica, which contains over 16,200 feeding links between 489 species. They explore the effect of different sequences of simulated species deletions on the structural architecture of the food web and the propensity for cascading secondary extinctions to be triggered under these various scenarios (e.g. loss of largest species first, random species deletions, etc.). They found that it was not simply body size that was key but that “predator type” over and above that which is determined by size *per se* was important. This highlights the

need to consider additional dimensions beyond those related to taxonomy and body size: given that we now know how important both of these are in most systems, we can start to enter a new phase of exploring what might be termed the "residuals about the line", in terms of traits that are orthogonal to size and/or identity. Plant ecologists have been doing this for decades, as have, to a lesser extent, freshwater animal ecologists, but neither have explicitly used this approach in a food web context that considers species interactions, in contrast to Jacob *et al.*'s (2011) study. This novel type of approach thus offers great potential to explore new dimensions of food web structure within a more unified theoretical framework and seems certain to initiate a new generation of research in this field.

The remaining paper in this volume, by Henri and van Veen (2011), is from probably the most (apparently) diametrically opposite system from that of the Weddell Sea and the other aquatic systems considered in this volume: host-parasitoid networks in terrestrial ecosystems. These systems have long been suspected to be less strongly size-structured than aquatic food webs (Ings *et al.*, 2009), and indeed, the authors find compelling evidence that phylogenetic constraints on network structure are far more powerful in these systems, where the role of life history and close coupling in the phenology of host and parasitoid is paramount. Here, it seems, body size, although it plays a limited role, is now the "residual variation" rather than a major axis of determination. This chapter, when viewed alongside the others included in the volume, emphasises how ecology is not easily compartmentalised, but that natural systems more probably lie along a continuum of different dimensions of size structure, as has recently been proposed by Yvon-Durocher *et al.* (2011) (Figure 1). It is therefore important to bear this in mind and not to become dogmatic in our search for, or perception of, size structure: in the real world, it is clearly not a case of "one-size-fits-all", and we need to alter our perspective accordingly if we are to improve our understanding of, and ability to predict, how ecosystems operate. Ultimately, the work presented in this volume may aid the development of a new scientific framework for linking functional diversity, food web structure and dynamics to ecosystem services (Dobson, 2009) in the urgency to reduce the rate of biodiversity loss and provide a more holistic approach to the management of the biosphere.

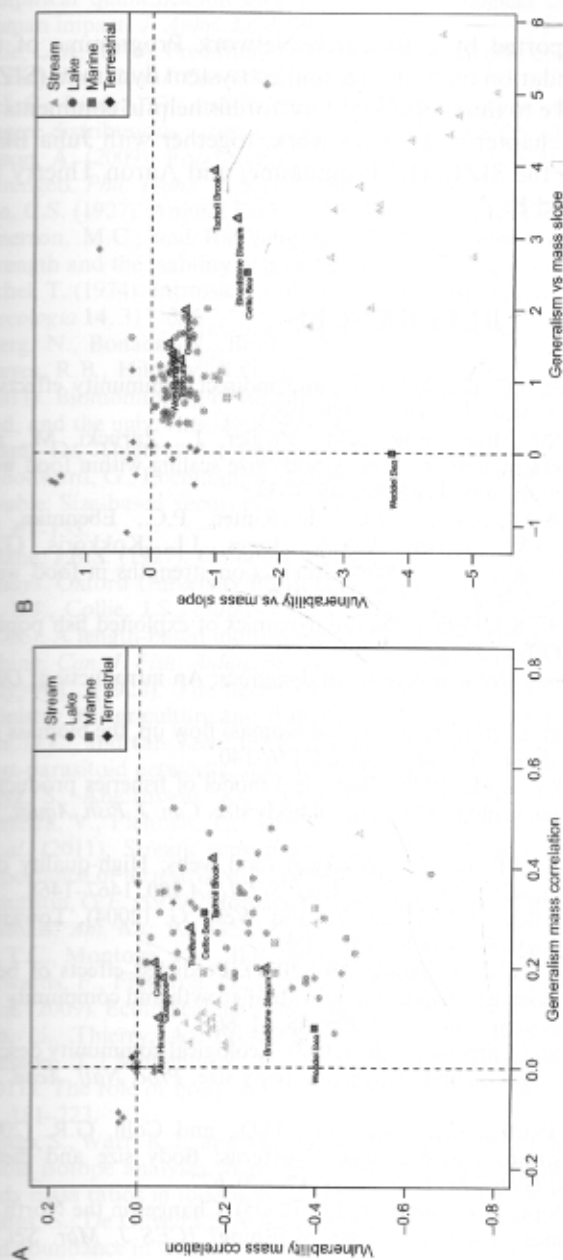


Figure 1 Variation in the topological size structure of real food webs. (A) The first axis of size structure is the strength of the relationship between the log mass and generalism of species within a web, the second is the strength of the log mass–vulnerability relationship, both quantified as Pearson correlation coefficients. (B) The strength of mass scaling with these two parameters is depicted as the slope of the relationship. Food webs from real ecosystems are shown by different symbols from a range of aquatic and terrestrial habitats, with several of the study systems presented in the current thematic volume named individually on the scatterplots (data supplied by Aaron Thierry). Data were extracted from Digel *et al.* (2011) and appended with additional information from the food webs described in this volume.

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