The paradox of energy equivalence

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ABSTRACT

Energy equivalence, the notion that population energy flux is independent of body mass, has become a key concept in ecology. We argue that energy equivalence is not an ecological ‘rule’, as claimed, but a flawed concept beset by circular reasoning. In fact, the independence of mass and energy flux is a null hypothesis. We show that our mechanistic understanding of size–density relationships (SDRs) follows directly from this null model and the assumption that energy limits abundance. Paradoxically, without this assumption energy equivalence has no meaning and we lack a mechanistic understanding for SDRs. We derive an expression for the strength ($r^2$) of SDRs under the null model, which provides a framework within which to compare published SDRs. This confirms that tight correlations between mass and abundance are a trivial consequence of the span of body masses considered. Our model implies that energy flux varies by five to six orders of magnitude among similarly sized mammals and to a far greater extent in birds. We conclude that the energetic paradigm can be strengthened by considering alternative, non-energetic, hypotheses.

Keywords

Abundance, Damuth’s rule, ecology, energetics, invariance, macroecology, metabolic scaling, null models, size–density relationship.

INTRODUCTION

The relationship between body size and abundance is a key focus of research in ecology (White et al., 2007). Damuth reported a size–density relationship (SDR) following a power law with a scaling exponent close to $-3/4$ (equation 1a), first among mammals (Damuth, 1981) and later across a wide range of vertebrate taxa (Damuth, 1987). He realized that this value was the inverse of Kleiber’s metabolic scaling exponent $3/4$ (equation 1b), which implies that the population energy flux per unit area, estimated as the product of metabolic rate and abundance, will be independent of body mass (equation 1c). In the scaling jargon, energy flux is said to be ‘invariant’ with respect to mass, $M$. Nee et al. (1991) reported the same pattern among British birds, and coined the phrase ‘energetic equivalence rule’ for situations where the allometric scaling exponents for whole-organism metabolic rate, $I$, and population density, $N$, sum to zero. This was formalized as part of the metabolic theory of ecology (Brown et al., 2004) in the context of the availability (supply rate) of resources, $R$:

$$N \propto M^{-3/4}$$  \hspace{1cm} \text{(1a)}

$$I \propto M^3$$  \hspace{1cm} \text{(1b)}

$$R \propto IN \propto M^0.$$  \hspace{1cm} \text{(1c)}

This set of relationships constitutes the general concept of energy equivalence (EE), which has become a cornerstone of macroecology and forms the basis of theories about population dynamics (Savage et al., 2004) and biodiversity patterns (Allen et al., 2002). EE is underpinned by the assertion that abundance is directly dependent on energy available to the population: an increase in energy input leads to an increase in abundance, mediated by the energy requirements of each individual (Brown et al., 2004; Ernest et al., 2008, 2009). We refer to this paradigm as the ‘energetic view of abundance’ (see also Taper & Marquet, 1996; Morlon et al., 2009).

Some authors considered the independence of body mass and energy flux to be a fundamental rule. For example, it has been stated that EE ‘reflects mechanistic connections . . . and the partitioning of available energy among species in a community’ (Allen et al., 2002), and ‘suggests that some combination of physiological and ecological processes results in energetic trade-offs, such that resources are divided equally across species’ (White et al., 2007). However, there is no strong theoretical basis...
for EE across species (Damuth, 1981; Brown, 1995; Brown et al., 2004; Carbone et al., 2007; White et al., 2007), although there have been several attempts to fill this gap. Charnov et al. (2001) suggested that EE in mammals is a consequence of life-history trade-offs (between fecundity and longevity) and population dynamics (including density-dependent juvenile survival). Damuth (2007) developed a simulation model that produced EE through competitive interactions between pairs of species. Harte et al. (2008) have argued that EE may be a consequence of the maximum entropy principle, i.e. that it results from the most probable statistical distributions of body sizes, species and individuals in space within particular constraints given by total number of individuals, total number of species and total energy available within given area.

EE has been challenged on both empirical and conceptual grounds. Marquet et al. (1995) described problems with both the assumptions of EE and the statistical approaches to testing EE. A growing number of studies have reported patterns inconsistent with EE at a variety of spatial scales (Blackburn & Gaston, 1997; Russo et al., 2003; Hayward et al., 2009; Morlon et al., 2009; Isaac et al., 2011b), although Carbone et al. (2007) showed that geometric considerations could lead to a range of SDR exponents even when mass and energy flux are uncorrelated.

Others have proposed non-energetic explanations for the SDR (Blackburn et al., 1993; Cotgreave, 1993).

Here we argue that EE is not a useful concept in ecology. We highlight logical flaws in the concept of EE itself, and of the evidence used to test it. We discuss what insights might be possible from the SDR, and suggest new directions for research in this field.

THE PARADOX

We contend that the concept of EE is at best misunderstood and at worst fundamentally flawed. Equation 1c does not imply that all species use equal amounts of energy, merely that energy flux is independent of mass. The absence of a correlation between mass and energy should not be surprising: it is, after all, a null hypothesis which does not require any specific mechanism. Accepting EE as the null has two important implications: (1) that neither resource partitioning nor inter-specific competition need to be invoked; (2) that authors claiming to find support for EE have fallen into that most basic statistical trap, namely of accepting the null hypothesis rather than failing to reject it.

Such shortcomings of logic might be explained by the fact that energy flux is never measured, but is inferred as the sum of individual metabolic rates (equation 1c). The ‘evidence’ (or lack thereof) for EE is usually based on a simple comparison of the SDR exponent with some nominal value of the metabolic scaling exponent (usually 3/4). This too is flawed: the coincidence of scaling exponents becomes a trivial consequence of the fact that population energy flux is unbiased with respect to body size. From this it follows, paradoxically, that energy equivalence is a trivial and uninformative pattern under the energetic view of abundance, but is a meaningless concept if we take the opposing (non-energetic) view.

TIGHT-FITTING SIZE–DENSITY RELATIONSHIPS ARE NOT SURPRISING

Inferences about energy partitioning are usually based on the tightness (or lack thereof) of the SDR. The tightness of SDRs is strongly related to the range of body sizes considered (Tilman et al., 2004; Hayward et al., 2010): we extend this observation to emphasize that EE is trivial, and that it has no real predictive power.

We derived an analytical expression (see Appendix S1 in Supporting Information) for the predictive power of body mass in SDRs under the strict version of the energetic paradigm and the null expectation of no correlation between species body mass, $M$, and energy flux, $R$. In our model, $M$ and $R$ are independent random variables, but species abundance, $N$, is wholly determined by $R/M^{\alpha}$. We refer to this as the ‘energetic null model’. Our model reveals that tight relationships occur when the variance in mass is high relative to the variance in energy flux (or resource availability). Indeed, high $r^2$ is inevitable with a large enough span in body mass (more than 10 orders of magnitude; Fig. 1), regardless of the distribution of energy flux (cf. Hayward et al., 2010).

Our energetic null model provides a framework within which to compare the fit of published SDRs whilst controlling for the span in body mass. Not surprisingly, the best-fitting SDRs (relative to the mass range) are found among studies that controlled for key factors influencing underlying variation in organism abundance, such as access to resources. For example, Carbone & Gittleman (2002) showed that prey biomass is a key determinant of abundance among mammalian carnivores: controlling for prey availability provides a dramatic improvement in the predictive power of body mass. Likewise, a study based on carrying capacity in single-species stands of plants (i.e. without interspecific competition) showed a similarly tight-fitting SDR (Enquist et al., 1998).

Damuth’s classic mammalian SDR (Damuth, 1981, 1987) has $r^2 = 0.65$ across nearly six orders of magnitude in body mass: random subsets with smaller mass ranges have correspondingly weaker fits (Fig. 2). These patterns are consistent with the energetic null model in which $\log_{10}(\text{energy flux})$ is a random normal deviate with a standard deviation in the range 1.25–1.65, corresponding to 95% confidence intervals of 80,000–3,000,000-fold variation in energy flux for each size class. This magnitude of variation seems at odds with the notion of EE as an ecological ‘rule’ with predictive power, even after accounting for error variance in estimating the abundance of wild mammal populations, many of which are probably below carrying capacity. The much weaker fit among bird SDRs implies still higher levels of variation (seven to eight orders of magnitude variation in energy flux being driven by energy availability, the coincidence of scaling exponents becomes a trivial consequence of the fact that population energy flux is unbiased with respect to body size. From this it follows, paradoxically, that energy equivalence is a trivial and uninformative pattern under the energetic view of abundance, but is a meaningless concept if we take the opposing (non-energetic) view.
flux). Overall, given the implied range of variation in energy flux, it seems reasonable to reject the notion that these patterns emerge from ‘resource partitioning’ or ‘energetic trade-offs’ (Allen et al., 2002).

THE WAY AHEAD

The problems associated with EE should not be interpreted as an attack on the energetic view of abundance, which has contributed much to our understanding of large-scale patterns in community structure (Brown et al., 2004; Ernest et al., 2008, 2009; McGill, 2008), and which we find to be plausible in the broadest sense. Rather we urge researchers to discard the notion of energy equivalence as an ecological ‘rule’ and to focus instead on the mechanisms underpinning abundance–energy relationships, and to consider alternative (i.e. non-energetic) determinants of species abundance.

To some degree, this is already happening, using data on abundances within communities. New applications of species abundance distributions, using currencies of energy and biomass, have provided novel insights into the partitioning of resources among species (Connolly et al., 2005; Reuman et al., 2008; Morlon et al., 2009; Henderson & Magurran, 2010). A related example is the concept of zero-sum dynamics, in which the energy flux of communities remains stable whilst the abundance (and body size) of individual species fluctuates in a way that reflects individual metabolic requirements (Ernest et al., 2008, 2009). Another prediction of the energetic paradigm is that abundance should increase with available energy: evidence supporting this prediction has been reported for a range of taxa (McNaughton et al., 1989; Meehan et al., 2004; Meehan, 2006; Barton & Zalewski, 2007; Pettorelli et al., 2009; Kaspars & Weiser, 2012), but counter-examples also exist (Currie & Fritz, 1993; Isaac et al., 2011a).

Studies taking the energetic view of abundance should be more explicit about their assumptions. A good example is how individual energy requirements are estimated: most studies use basal metabolic rates, rather than field rates (which scale more steeply; Nagy, 2005). Many studies approximate metabolic rates as $M^{3/4}$ (Ernest et al., 2008, 2009); this is reasonable for a large range in mass, but for small (less than one order of magnitude) ranges the predictive power of Kleiber’s ‘law’ is much reduced (Isaac & Carbone, 2010). In addition, correlations between mass and energy flux should be accompanied by an estimate of the power to reject the null model (with specific reference to the span of body masses under consideration).

We have alluded to the fact that the energetic view of abundance is not universally accepted. Blackburn et al. (1993) presented an explanation for the SDR based on the distribution of species body sizes and the fact that rare species tend to go unrecorded. An alternative ‘non-energetic’ view is that abundance could be conceived as a random variable between hard bounda-
ries (Marquet et al., 1995). Cotgreave (1993) has pointed out that body size imposes a physical limit on population density, and that space-filling would generate a scaling in the upper boundary of \(-2/3\) (contrast this with the \(-3/4\) upper boundary that would be expected from energy monopolization: Blackburn & Gaston, 2001). We could equally envisage a lower boundary of ecological abundance based on the fact that individuals must be able to meet each other to reproduce. Minimum density can be defined as the density at which population growth rate becomes negative due to Allee effects (Courchamp et al., 1999). We expect that minimum density would be related to daily distance traversed, which itself scales with body size (Carbone et al., 2005). Estimating extreme population densities is problematic, and probably prevents this idea from being seriously tested (but see Silva & Downing, 1994). However, similar non-energetic models might derive testable predictions. We believe that macroecology will be advanced by considering both energetic and non-energetic hypotheses in concert, and comparing the predictions of these divergent perspectives.

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statistical artefact or biological mechanism? Ecological Complexity, 7, 115–124.


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Analytical derivation for the expected explanatory power of the size–density relationship under the energetic null model.

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