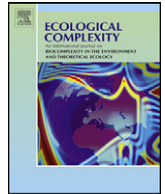




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The scale-dependence of population density–body mass allometry: Statistical artefact or biological mechanism?

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ABSTRACT

The relation between population density and body mass has vexed ecologists for nearly 30 years as a consequence of high variability in the observed slope of the relation: No single generalisation of the relation has been accepted as universally representative. Here, we use a simple computational approach to examine how observational scale (the body mass range considered) determines variation in the density–mass pattern. Our model relies on two assumptions: (1) resources are partitioned in an unbiased manner among species with different masses; (2) the number of individuals that can be supported by a given quantity of resources is related to their metabolic rate (which is a function of their mass raised to the power of a scaling coefficient, b). We show that density (1) scales as a function of body mass raised to the power of $-b$ on average, but (2) the slope of the relation varies considerably at smaller scales of observation (over narrow ranges of body mass) as a consequence of details of species' ecology associated with resource procurement. Historically, the effect of body mass range on the slope of the density–mass relation has been unfailingly attributed to a statistical effect. Here we show that the effect of body mass range on the slope of the density–mass relation may equally result from a biological mechanism, though we find it impossible to distinguish between the two. We observe that many of the explanations that have been offered to account for the variability in the slope of the relation invoke mechanisms associated with differences in body mass and we therefore suggest that body mass range itself might be the most important explanatory factor. Notably, our results imply that the energetic equivalence rule should not be expected to hold at smaller scales of observation, which suggests that it may not be possible to scale the mass- and temperature-dependence of organism metabolism to predict patterns at higher levels of biological organisation at smaller scales of observation.

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1. Introduction

The relation between organism density (D) and body mass (M) has been a consistent source of discussion in the ecological literature for more than 25 years (Damuth, 1981; Lawton, 1989; Currie, 1993; Blackburn and Gaston, 1997; Arneberg et al., 1998; Griffiths, 1998; Cyr, 2000; Makarieva et al., 2004; White et al., 2007). While the origin and consequences of density–body mass allometry have stimulated theorists (Damuth, 1981; Peters and Raelson, 1984; Brown and Maurer, 1987; Enquist et al., 1998; Lawton, 1990; Enquist et al., 2003; Brown et al., 2004; Makarieva et al., 2004; Long et al., 2006), the true form of the relation has pre-occupied empiricists and remains a subject of considerable

analysis and debate (White et al., 2007). The empirically driven debate concerning the form of the relation has cast serious doubt on its general utility and had dire consequences for developing theories (Peters and Wassenberg, 1983; Lawton, 1989, 1990; Cotgreave, 1993; Currie and Fritz, 1993; Blackburn and Lawton, 1994; Marquet et al., 1995; Cyr, 2000; Loeuille and Loreau, 2006). There is, however, some general agreement that the revelation of the true nature of D – M allometry has been confused by the use of a variety of system definitions (White et al., 2007), data collection methodologies (Lawton, 1989; Damuth, 1991; Cotgreave, 1993; Blackburn and Gaston, 1997; Cyr et al., 1997), analytical techniques (LaBarbera, 1989; Griffiths, 1998; deBuryn et al., 2002), and differences in observational scale (Lawton, 1989; Nee et al., 1991; Currie, 1993; Blackburn and Gaston, 1997; Arneberg et al., 1998; Griffiths, 1998; Silva et al., 2001; Ackerman and Bellwood, 2003; White et al., 2007).

Despite the ongoing debate regarding the general form of the relation, body mass remains the best single predictor of population density, explaining 75–85% of the variation on average, and up to

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90% in some cases (Damuth, 1981, 1987; Arneberg et al., 1998). This strong link between population density and body mass is thought to follow from the mass-dependence of metabolic rate: The number of individuals of a species that can be supported in a given region (i.e. D), must be a function of the quantity of resources available to individuals of a given size (R) divided by the quantity of resources individuals of that size use, their total metabolic rate (B), such that $D = (R/B)$ (Enquist et al., 1998; but see Li et al., 2004). Since metabolic rate is mass-dependent, we can substitute M for B . The mass-dependence of B is best described as a power function, $B \propto M^b$, where b is the slope of the regression on log–log axes. Thus, D is expected to be proportional to R , assuming that R is mass-independent, and M raised to the negative power of b : $D = (R/B) \propto (R/M^b) \propto (R \cdot M^{-b})$. Although the value of b is debated (McNab, 1988; Dodds et al., 2001; White and Seymour, 2003; Bokma, 2004; Kozłowski and Konarzewski, 2004), it is generally accepted that $B \propto M^{3/4}$ (Dobson et al., 2003; Agutter and Wheatley, 2004; Savage et al., 2004). Thus, assuming that R is mass-independent, D is generally expected to scale as a function of $M^{-3/4}$, which is exactly the relation that Damuth (1981, 1987) originally found for terrestrial mammals.

The apparent simplicity of the pattern revealed by Damuth (1981, 1987; $D \propto M^{-3/4}$) initiated a widespread search for similar patterns in other systems. The results of this search are somewhat inconclusive, with a variety of patterns reported (White et al., 2007). Three general forms of the D – M relation have been identified: (1) negative linear; (2) positive linear; (3) polygonal (“constraint envelope”; Marquet et al., 1995). The three general patterns exhibit a degree of scale-dependence (Lawton, 1990; Cotgreave, 1993; Currie, 1993; Blackburn and Gaston, 1997; Griffiths, 1998; White et al., 2007). At large scales (e.g., across broad taxa, wide ranges of body mass, and large geographic areas), the relation tends to be negative and linear with a fairly consistent slope of approximately $-3/4$ (Damuth, 1981, 1987; Blackburn and Gaston, 1997; Enquist et al., 1998; Schmid et al., 2000; Belgrano et al., 2002; Meehan et al., 2004; but see Silva et al., 2001). At small scales (e.g., within lower taxa, narrow ranges of body mass, and small geographic areas) there is much less consistency in the pattern: some studies report strong negative linear relations (Marquet et al., 1990; Schmid et al., 2000; Ackerman and Bellwood, 2003); others report positive linear slopes (Patterson, 1992; Cotgreave and Harvey, 1994; Arneberg et al., 1998); and still others report a polygonal distribution of data points, with no or only a weakly detectable negative linear trend (Griffiths, 1986; Brown and Maurer, 1987; Morse et al., 1988; Nee et al., 1991; Cyr and Pace, 1993; Marquet et al., 1995; Navarrete and Menge, 1997; deBuryn et al., 2002).

Much of the debate about the form of the D – M relation has been attributed, in various ways, to the effect of scale (Damuth, 1991; Cotgreave, 1993; Currie, 1993; Blackburn and Gaston, 1997; Arneberg et al., 1998; Griffiths, 1998; Cyr, 2000). Many authors have recognised that the body-size range considered and the observed slope (and shape) of the D – M relation are intertwined (Peters and Wassenberg, 1983; Lawton, 1989; Currie, 1993; Cyr and Pace, 1993; Blackburn and Lawton, 1994; Blackburn and Gaston, 1997; Arneberg et al., 1998; Griffiths, 1998; Cyr, 2000; Ackerman and Bellwood, 2003). Arneberg et al. (1998), for example, undertook a meta-analysis of empirical values obtained for the scaling exponent and variance explained for D – M relations from the literature and found that much of the variation in the D – M pattern (b and r^2) was associated with the range of body mass included in any particular study. Other overviews of the literature have reached similar conclusions (Lawton, 1989; Currie, 1993; Blackburn and Gaston, 1997; Griffiths, 1998), with the notable exception of Damuth (1993), who found no correlation between body mass range and observed slope. Here we use a simple

computational approach to examine how observational scale (defined as the range of body mass considered) determines variability in the D – M pattern observed and compare the simulated results against observations collected from the literature. Specifically, we examine the effect of observational scale on variability in the D – M pattern using four kinds of simulation models. The first two models were designed to address whether the way in which resources are partitioned among members of a community of co-existing species affects variability in the D – M pattern observed. Thus, we created two kinds of “real-type” communities in which the species present must split the total amount of resources available using (1) the broken stick and (2) the niche preemption model of resource partitioning. Our third model, “compendia-type” communities, was created to address the fact that many of the studies that have examined the D – M relationship in the past involve the use of data collected from many literature sources. As such, our third model was designed to mimic literature-based examinations of D – M scaling by drawing species randomly from the many different communities created in the broken stick “real-type” communities simulation, in order to examine the possibility that some of the variability in the D – M relation might result from differences in sampling methodology or system definition. Our fourth model, “statistical artefact” communities, was designed to investigate the idea that the variability in the D – M relation observed at smaller scales of observation is a statistical artefact resulting from the examination of small sections of global regressions: We investigate the statistical artefact hypothesis by randomly selecting species from small sections of the global density–body size distribution generated in the broken stick “real-type” communities simulations. Finally, we compare the results of each of the four models to observations from the literature.

2. Method

We adopt simple models based on two assumptions: (1) resources are partitioned in an unbiased manner (i.e. evenly partitioned on average) among species with different body masses; (2) the number of individuals that can be supported by a given quantity of resources is related to their metabolic rate (which may be described as an allometric function of their mass).

2.1. “Real-type” communities

“Real-type” communities were generated using (a) broken stick and (b) niche preemption models of resource partitioning—the dominant models describing how resources are divided among members of a community (He and Tang, 2008). For each of the two resource partitioning models, density–mass relations were determined for 10,000 communities comprising n species that were randomly generated in Mathematica 5.1. The number of species in each community (n) was drawn from a log-normal distribution with mean 1.563169 and variance 0.365628, which were chosen based on the shape of the sample size distribution of observations collected from the literature (see “observations from the literature,” below). For each community, each of the n species was assigned two random real numbers between 0 and 1. The first random number was assigned as the average mass of that species (M_i , where i is an integer between 1 and n and represents the identity of a species in a community). The value of M_i was drawn from a log-normal distribution with mean -15 (i.e. $\log 10^{-15}$) and variance equal to a whole number between 1 and 8 drawn from a uniform distribution (in order to ensure that a sufficient range of body masses were obtained among communities). The second random real number between 0 and 1 assigned to each of the n species in each community (A_i) was drawn from a uniform distribution and was used to calculate the share of available

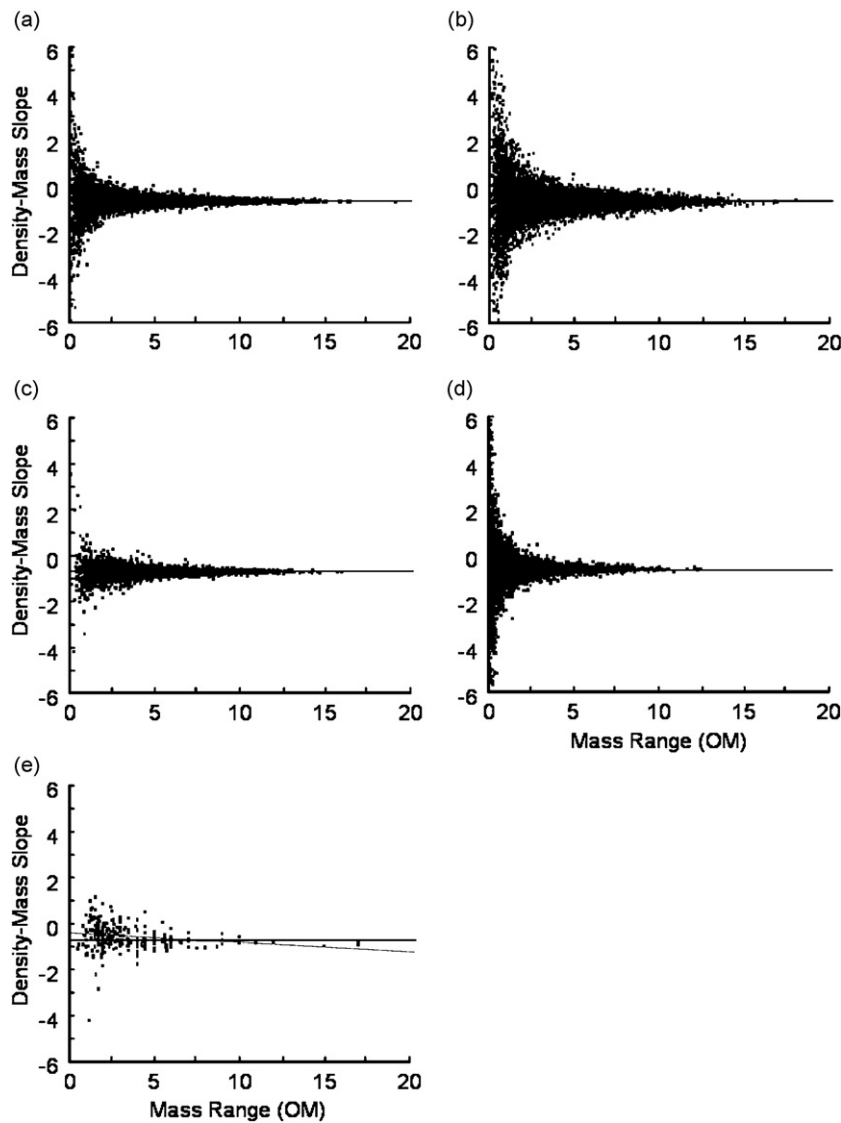


Fig. 1. Observed slope of the D – M relation vs. the range of body mass in a community. Each point represents the slope of the density–mass relation in a) a “real-type” community of n species generated in a simulation based on a broken stick model of resource partitioning; b) a “real-type” community of n species generated in a simulation based on a niche preemption model of resource partitioning; c) a “compendia-type,” composite community generated by randomly selecting n species from all the species created in the “real-type” communities simulation; d) a “statistical artefact” community generated by regressing smaller segments of the global D – M relation created using all of the species generated in the “real-type” communities simulation; e) an observation of the slope of the D – M relation for real species, as found through an extensive literature search (see Appendix A for sources). For a)–d) the average slope of the relation is -0.75 at all scales, but the variability in the slope observed is drastically higher at small scales. When the range of body sizes included in the community is less than 5 OM, the probability that a slope of -0.75 will be found in any given study is low. For the sake of presentation, slopes with an absolute value greater than 6 were omitted from Fig. 1 (9, 25, 1, and 114 cases in Fig. 1 a)–d) respectively).

resources obtained by species i (R_i). R_i was calculated differently for (a) the broken stick and (b) the niche preemption “real-type” communities. (a) For the broken stick “real-type” communities, R_i was calculated as $R_i = A_i / (A_1 + A_2 + A_3 + \dots + A_n)$. This method of calculating R_i ensures that all species have an equal share of the resources, on average, across all communities. (b) For the niche preemption “real-type” communities, A_i served two independent purposes. First, the total amount of resources available to all of the species in a given community (R_c) was calculated as $R_c = A_1 + A_2 + A_3 + \dots + A_n$. R_i was then calculated for each species as $R_i = [(A_i) \cdot (R_c - (R_1 + \dots + R_{i-1}))] / [R_1 + \dots + R_n]$. As such, every species subsequently added to a community obtained a fraction (A_i) of the resources that remained after all of the previously added species had taken their share of resources from the total resource pool (R_c). Note that the standardization of each R_i by $\sum R_i$ equalizes the total amount of resources available across all 10,000 communities, allowing for a meaningful comparison of the results

of the niche preemption “real-type” communities against the broken stick “real-type” communities. Failing to standardize each R_i would have increased the magnitude of the scatter of the D – M slopes across all body mass ranges without changing the overall shape of the curves presented in Figs. 1 and 2.

For both the broken stick and niche preemption “real-type” communities, the density of individuals of species i (D_i) was calculated as $D_i = (R_i / M_i^b)$. We chose $3/4$ to approximate b because it is accepted generally (Kleiber, 1932; Peters, 1983; Dobson et al., 2003; Agutter and Wheatley, 2004; Brown et al., 2004; Savage et al., 2004) but note that the implications of our results are transferable to any scaling exponent ($2/3$ or otherwise). We then examined the relationship between population density, body mass, and resource procurement by regressing D_i against (1) M_i and (2) R_i (Type III OLS) for all n species in the community and recorded the slope, r^2 , and p -value of the community-wide D – M and R – M relations. The slope, r^2 , and p -value for the D – M and the r^2 and p -value for the D – R relations

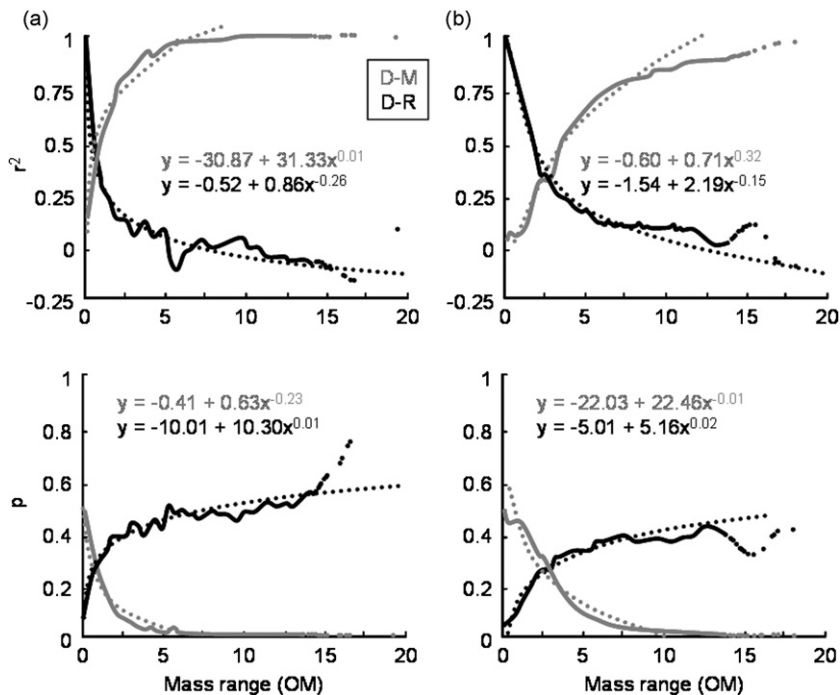


Fig. 2. Explained variance (r^2) and significance (p -value) of the D – M relation (red) and the D – R relation (blue) for the 10 000 a) broken stick and b) niche preemption “real-type” communities following LOWESS (at 55%). Dashed lines are the curves fit to LOWESS data (equations provided). For both a) and b), as the M range increases the explanatory power of M increases while the explanatory power of R diminishes: D is best predicted by R at small scales and by M at large scales.

were plotted against the range of M_i in the corresponding community. Locally weighted sequential smoothing (LOWESS) and subsequent curve fitting were performed using Table Curve 2.0. LOWESS is a non-parametric, local least-squares regression procedure (a form of density estimation) used to estimate the value of y at each value of x based on the (weighted) values of y over a designated window of neighbouring x values (Cleveland, 1979; Kaufman et al., 1997; Silva et al., 2001). LOWESS can be thought of as a more statistically robust means of calculating a moving average to discern patterns in and fit curves to refractory data. In this study, LOWESS was used to demonstrate how variation in the D – M exponent changes systematically with observational scale (while the average value of the exponent remains constant).

2.2. “Compendia-type” communities

5000 communities of n species (with n determined as described in the “real-type” communities simulations, above) were generated by randomly selecting n species (with replacement) from all of the species that were created during the broken stick “real-type” communities simulation. Analyses were carried out as for the “real-type” communities simulation(s).

2.3. “Statistical artefact” communities

5000 communities of n species (with n determined as described in the “real-type” communities simulations, above) were generated by (1) sorting all of the species created in the broken stick “real-type” communities simulations in ascending order by mass, (2) randomly selecting two whole numbers, a and z (where $a < z$), between 1 and the total number of species created in the broken stick “real-type” communities simulations, and (3) selecting n species evenly across the a th and z th species in the list, beginning with a (but not necessarily ending with z since $[(z - a)/n]$ must be a whole number). Analyses were carried out as for the “real-type” communities simulation(s).

2.4. Observations from the literature

306 observations of D – M slopes and body mass ranges were collected from the literature (see Appendix A for sources). The observations included here represent an extensive but not exhaustive compilation from the literature. Multiple slopes from the same source were used when possible, including isolated subsets of global regressions already included (e.g., following separation by trophic guild). Observed slope was regressed against observed body mass range using an orthogonal OLS regression in Statistica 6.0.

3. Results

The slope of the density–mass relations obtained through computer simulation averaged $-b$ at all scales of observation, but variability in the slope was much greater at smaller scales (Fig. 1). This was true whether the D – M relations were generated using data from individual “real-type” communities based on either the broken stick or niche preemption models of resource partitioning (Fig. 1a and b), by selecting species randomly from all of the communities that were generated in the broken stick “real-type” communities simulation (“compendia-type” communities; Fig. 1c), or when randomly sampling smaller segments of the global D – M regression (“statistical artefact” communities, Fig. 1d). When the range of body mass included was less than five orders-of-magnitude (OM), the probability that a slope of $-b$ would be found in any individual study was extremely low. Deviations from $-b$ were much greater at small scales of observation: It was not until the range of body size was >7 OM that slopes of $-b$ were consistently found in individual broken stick “real-type” communities. Slopes as steep as -1.5 and as shallow as zero arose even when the range of body mass considered was as large as 3 OM; when the mass range included was less than 1 OM, slopes as steep as -2 and 1 were commonly observed. Using a niche preemption, rather than a broken stick type model of resource partitioning,

introduced more variation into “real-type” communities, with slopes as steep as -4 and 3 commonly arising when the mass range included was less than 1 OM, and with slopes as steep as -1.5 and as shallow as zero arising when the range of body mass considered was as large as 9 OM. For the sake of presentation, slopes with an absolute value greater than 6 were omitted from Fig. 1 (9 , 25 , 1 , and 114 cases in Fig. 1a–d respectively).

Observations collected from the literature show similar trends in variability of the D – M relation as the simulated communities, but the average slope is significantly shallower at smaller scales of observation (Fig. 1e). The average slope of the D – M relation is -0.46 (-0.56 – -0.35) at a body mass range of 1 OM and decreases toward a slope of -0.75 as the body mass range considered increases ($b = -0.04$ (-0.06 – -0.02), $r^2 = 0.03$, $p < 0.01$). The variance in the slope of the observed D – M relation explained by body mass range is notably low.

The capacities of resource acquisition and body mass to predict population density were scale-dependent (Fig. 2). When the range of body mass included in the simulation was small, resource acquisition was the primary determinant of the slope of the D – M relation; as the body mass range included increased, body mass emerged as the primary determinant of population density. Results for broken stick and niche preemption “real-type” communities were similar, but the quantity of resources obtained by a species remained a more important determinant of population density over a greater range of body masses under a niche preemption resource partitioning regime.

4. Discussion

Both our two “real-type” communities and our “compendia-type” communities models suggest that the value of the slope of the D – M relation will average $-b$ (i.e. the negative value of the B – M scaling exponent) at all observational scales, but that the value observed will vary greatly at smaller scales, with positive and steep negative slopes commonly observed (Fig. 1a–c). Thus, whether a slope of $-b$ is found in any particular study will depend largely on the size range of organisms considered: The larger the range in body mass included, the more likely that a slope of $-b$ will result. Note, then, that variability in the slope of the D – M relation at smaller scales of observation is expected, despite the fact that M is an explicit determinant of D .

In addition, we find that control over community-level patterns in population density switches from the amount of resources each species is able to procure to species mass as the range of mass in the community increases (Fig. 2). Thus, when differences in mass among species in a community are small, the effects of species ecology (each species’ competitive ability in reference to the biotic and abiotic conditions in the community where they must compete for resources) mask the limitations imposed by the mass-dependence of organism metabolism on the population density each species can potentially obtain. As differences in species mass become larger, the effects of metabolic constraints on potential population densities overcome the effects of variation in species-specific traits and community-level patterns in population density are primarily determined by metabolic constraints.

That the mechanisms controlling community-level patterns in population density are scale-dependent translates into scale-dependence in the variability of the slope of the density–mass relation (Fig. 1). This secondary observation neatly explains discrepancies among empirical patterns reported in the literature, discrepancies that have caused nearly 30 years of debate regarding whether organism metabolism influences population density in any meaningful way. Although the average slope of the D – M relation approximates $-b$ (i.e. the negative value of the B – M scaling

exponent) at all observational scales, variation in the density–mass pattern observed, including frequent observations of both positive and steep negative slopes, should be expected when only narrow ranges of body mass are considered (Fig. 1). The seemingly scale-dependent nature of the slope of the allometric equation relating D and M based on evidence accumulated in the literature (Lawton, 1989; Damuth, 1991; Cotgreave, 1993; Currie, 1993; Brown, 1995; Blackburn and Gaston, 1997; Arneberg et al., 1998; Griffiths, 1998) may, therefore, actually result from the *scale-dependence of variation* in the slope, rather than variation in the average slope *per se* (Peters and Raelson, 1984).

Our models suggest, therefore, that an examination of the literature should reveal wide variation in the slopes obtained at smaller scales of observation, but a convergence of the values on $-b$ across all scales of observation, unless large species garner competitive advantages (in which case the average value for the slope should be shallower than $-b$, see below) or energy is not generally a limiting factor (Wright, 1983; Marquet et al., 1990, 1995; Cotgreave, 1993; Navarrete and Menge, 1997). In fact, our review of the literature shows that there is a convergence toward a slope of $-b$ at all scales of observation, but that there is a bias toward shallower slopes at smaller scales of observation (Fig. 1e). This bias toward shallower slopes at smaller scales of observation points to the importance of size-structured competition at these scales, a matter which we will return to below.

4.1. The effect of observational scale: biological or statistical mechanism?

The effect of body mass range on variability in the density–mass pattern observed is usually attributed to a purely statistical effect: ‘Local’ segments of a ‘global’ regression are expected to have lower explained variance than the global regression (Draper and Smith, 1981; Currie, 1993; Blackburn and Gaston, 1997). However, while explanatory power is expected to decrease as smaller segments are drawn from a global regression, the observed slope is expected to remain unaffected (Draper and Smith, 1981; Currie, 1993; Blackburn and Gaston, 1997). As such, traditional, statistical explanations of the variation in the D – M relation involving body mass range seem incomplete since they do not explain the observed variation in the slope of the relation. We tested whether a statistical explanation might suffice to explain the observed variation in the slope of the D – M relation by regressing smaller segments of the global D – M regression that was produced using all of the species created in the “real-type” communities simulation (“statistical artefact” communities; Fig. 1d): The slope of the D – M relation shows variability similar to that observed in the “real-type” and “compendia-type” communities when smaller segments of the global regression are regressed as independent units (Fig. 1). Thus, it is not possible to distinguish between a statistical and a biological cause for the variation in the slope at smaller scales of observation.

4.2. Broader implications

4.2.1. The energetic equivalence rule

First, our results suggest that a slope of $-b$ should be found on average regardless of whether the species considered in any study co-exist in community or not (Fig. 1a–d). Since our results apply equally well to literature compendia (Fig. 1c), where species do not share a common resource base, we suggest that our explanation of the observed variation in the density–mass relation puts to rest at least one critique of the theory underlying the energetic equivalence rule (EER). Marquet et al. (1995; p. 326) suggested that “...like other coevolutionary models...Damuth’s EER model requires that organisms make use of, and therefore interact

through the use of, a common energy (resource) base within a common uniform ecosystem type through evolutionary time.” Given our results, this assumption may be unnecessary: A slope of $-b$ is found on average for the D – M relation even when species are pulled randomly from all of our simulated communities (Fig. 1c). Our results therefore suggest that D – M scaling is the result of metabolic constraints operating at the level of individual organisms (as suggested by Enquist et al., 1998) rather than a consequence of inter-specific interactions through evolutionary time. Thus, population energy use might be expected to be mass-invariant on average at all scales (as originally suggested by Damuth, 1981) regardless of whether or not organisms share a common resource base.

On the other hand, our simple modelling exercise shows that even if body mass is inherently assumed to directly control population density, the relation between population density and body mass will be masked by other factors at smaller scales of observation. While this is not sufficient cause for the rejection of the idea that the mass-dependence of organism metabolism is an important determinant of population density, the expected variability at smaller scales of observation does imply that the energetic equivalence rule should not be expected to consistently hold at smaller scales. This, in turn, has important implications for the utility of the “metabolic theory of ecology” at these scales: The extension of metabolic theory to derive predictions regarding structural and functional patterns at higher levels of biological organisation invokes the energetic equivalence rule (Enquist et al., 1998, 2003; Enquist and Niklas, 2001; Allen et al., 2005; Kerkhoff and Enquist, 2006; Hayward et al., 2009) and the predictive ability of the theory at these levels of organisation is contingent on the energetic equivalence rule holding true (despite the fact that the EER pre-dates the development of metabolic theory by nearly two decades). As such, our results suggest that it may not be possible to use the metabolic theory of ecology to accurately predict patterns in higher level structure and function at smaller scales of observation.

4.2.2. Deviations from expectations

Perhaps of greatest practical interest here is the fact that both species- and community-level deviations from D – M scaling expectations reveal important information about the ecology of a community and its constituent species. Deviations of individual species densities from the D – M regression line and deviations from a slope $-b$ in a community as a whole reflect each species’ ability to obtain resources relative to the other species present in the community and, thus, provide insights into both species’ and community ecology (Peters and Wassenberg, 1983; Peters and Raelson, 1984; Sprules and Munawar, 1986; McNab, 1988; Riska, 1991; Griffiths, 1992; Cotgreave, 1993; Brown, 1995; Marquet et al., 1995; Carbone and Gittleman, 2002; Jennings and Blanchard, 2004). Consequently, much information can be garnered from the D – M relation observed in a given community. We have shown here that slopes approximating $-b$ suggest unbiased partitioning of resources among species of varying body size. Slopes more negative than $-b$ suggest that smaller species obtain a relatively greater share of resource pools (Griffiths, 1992; Blackburn and Lawton, 1994; Marquet et al., 1995; Makarieva et al., 2004). Smaller species might be expected to control resource pools in conditions where faster rates of growth and reproduction and early sexual maturity are favoured (Makarieva et al., 2004, 2005; Tilman et al., 2004). Flat or positive relations, on the other hand, suggest that large species obtain a relatively greater proportion of resource pools (Damuth, 1991; Nee et al., 1991; Griffiths, 1992, 1998; Marquet et al., 1995; Makarieva et al., 2004). Larger species may be more likely to have an advantage over smaller species when long-term persistence through periodically

Box 1. Eight mechanisms suggested to explain observed differences in the D – M relation (Blackburn and Gaston, 1997).

- 1) type of data used (literature compendia vs. samples of real, local communities),
- 2) spatial scale (geographic vs. local),
- 3) measure of density used (ecological vs. crude),
- 4) range of body size included in the study,
- 5) statistical artefacts (polygonal relationships are random samples from a global body-size abundance distribution),
- 6) difference among species in the use space (existence is fundamentally in two or three spatial dimensions),
- 7) taxonomic composition/phylogenetic relatedness,
- 8) effects of migrant species on local relations.

unfavourable conditions is favoured (Enquist, 2003; Makarieva et al., 2004; Tilman et al., 2004). Thus, slopes shallower than $-b$ point to the importance of size-structured competition (Damuth, 1991; Nee et al., 1991; Enquist, 2003), a point that we will revisit below.

4.2.3. Species richness–resource availability–population density

Our “real-type” communities models hint that increasing species richness should result in more clearly defined D – M patterns at smaller scales of observation: If total available resources are held constant while species are added to a community, resources necessarily become more finely partitioned among the species present and the potential density of each species decreases as a consequence of increasingly limited relative resource availability. Since species are forced to share resources more evenly as species richness increases (on average, in our broken stick “real-type” communities model), the relative importance of the mass-dependence of organism metabolism as a determinant of population density would be accentuated at smaller scales of community-level observation as species richness increases. This may or may not be reflected in natural communities, depending upon how species richness is related to resource availability.

4.3. Body mass range as a blanket explanation for the variance in D – M slope

In a comprehensive analytical review of the literature, Blackburn and Gaston (1997) acknowledged the importance of body-size range but also suggested eight alternate mechanisms which might cause the observed variation in the D – M pattern found (Box 1). Most (i.e. six) of these suggested mechanisms can be reduced, in all probability, to the range of body mass considered in the study (the exceptions being differences resulting from (6), species that use habitats in two vs. three spatial dimensions, and (8), the effects of migrant species on local D – M relations). For example, a number of authors have suggested that taxonomic affiliation (phylogeny) might cause variation in the slope of the D – M relation and phylogenetic data correction is becoming an increasingly common practice (Cotgreave and Harvey, 1991, 1994; Nee et al., 1991; Riska, 1991; Cotgreave, 1993; Blackburn and Gaston, 1997; Harvey, 2000; Schmid et al., 2000). Our results lead us to suggest that the variance in the slopes observed over closely related species may result from the fact that comparisons across lower taxonomic groups (e.g., Rodentia) will likely involve a much smaller range of body sizes than comparisons across higher taxa (e.g., Mammalia) rather than artefacts of a common evolutionary history *per se*. Damuth (1991, pp. 268) has alluded to the possible tie between phylogenetic relatedness and body mass range in studies on birds: “What is going on in the relatively narrow region of body size

encompassed by birds (Fig. 1) has been subject to debate” (note that the figure to which he refers does not even cover 1 OM of body size). Notably, Nee et al. (1991), who introduced the idea that phylogenetic relatedness might be an important determinant of the exponent found in any given study, fail to recognise that more closely related species (i.e. lower taxa) are inevitably a subset of body sizes observed in a higher taxon, despite the fact that they note that the range of body mass included in any study is likely to be a key determinant of whether a slope of $-b$ will be found: Unfortunately, they do not provide any information on the body-size range covered by any of the taxonomic levels they compare in drawing their conclusions. The tie between phylogeny and body-size range is, however, demonstrated by a study on Nigerian snakes: Luiselli et al. (2005) find slightly (and weakly) positive relationships for snake abundance–body mass relations in southern Nigeria, but the range of snake size covers less than 2 OM.

4.4. Limitations of the model

4.4.1. Trophic complexity

It has been suggested that increasing trophic complexity will generally decrease the slope of the density–mass relation (i.e. it will become more steeply negative) (Carbone and Gittleman, 2002; Brown et al., 2004; Marquet et al., 2005; Long et al., 2006). This idea is based on two assumptions: (1) Inefficiencies in the transfer of energy up the trophic web will constrain higher trophic level species to relatively lower population densities; (2) Higher trophic-level species tend to be larger. Whether or not higher trophic-level species tend to be larger is debateable. First, the largest species tend not to occupy higher trophic positions (e.g., the largest whales feed on plankton; the largest terrestrial animals are herbivores). Second, there are many examples of predators that are much smaller than their prey (e.g., parasites, lions, humans, piranhas, etc.). Therefore, there is good reason to believe that the effects of trophic position might be distributed across the range of body sizes (causing a change in elevation of the relation) rather than biasing the large end of the body-size distribution to relatively lower population densities (drawing down the slope). Increasing trophic complexity may increase variability in the slope of the relation, decrease correlation coefficients, and inflate significance values, but it may not consistently bias the slope in one particular direction. In addition, increases in body-size range do not always equate with increased trophic complexity. The best example comes from plants, which can range in size by ≈ 20 OM yet compete for similar resources. Herbivores also compete for similar resources but can range in size by several orders of magnitude (e.g., mice to elephants).

Furthermore, although our “real-type” communities might reasonably be considered mono-trophic systems on account of the fact that the constituent species partition a shared resource base (but note that the same critique does not apply to our “compendia-type” or “statistical artefact” communities), the population density–body mass literature is ripe with definitions of what constitutes a community of species worthy of density–mass analysis: studies limited to specific taxa or feeding groups, for example, are common or perhaps even the norm. Although the ecological relevance of our model might be questioned on account of the fact that we do not explicitly incorporate multiple trophic levels into our “real-type” communities model (but see the previous paragraph) there are many cases, particularly in reference to previously published empirical studies, for which our results offer an important framework for interpretation.

4.4.2. Unbiased partitioning of resources

We should note that a key assumption of our “real-type” communities model – that resources are partitioned in an unbiased

manner among species of various size – is likely to be violated in natural systems (Sprules and Munawar, 1986; Nee et al., 1991; Cotgreave, 1993; Enquist, 2003; Cyr and Walker, 2004; Li et al., 2004; Makarieva et al., 2004; Coomes, 2006). Indeed, it has been argued that larger individuals may have a competitive advantage over smaller individuals and may, therefore, be able to procure a relatively greater portion of available resources than can smaller species (Nee et al., 1991; Damuth, 1993; Enquist, 2003; Dibattista et al., 2006; but see Loeuille and Loreau, 2006). Consequently, we might reasonably expect resource procurement to scale positively with body size in real communities, rather than to follow the simplifying (null) assumption of mass-independence employed in our models (Li et al., 2004; Makarieva et al., 2004). How resource procurement might scale with body mass is a decidedly ecological question, which requires understanding the interface of organism physiology and intra- and inter-specific interactions in an abiotic context (Li et al., 2004). While it may at first appear that our simple physiological models have little to say in this regard, the sorts of models presented here can be used as a basis for understanding how resources are partitioned in real communities, once the underlying effect of body mass range on the variability of the slope of the density–mass relation has been accounted for. For example, we can say with certainty that a competitive advantage in favour of larger species would have two important consequences in terms of the results presented here.

First, if being large offers a competitive advantage, causing resource procurement to scale positively with body size, we would expect to observe a tendency toward positive deviations from the expected slope of $-b$. We might, therefore, expect to find positive or polygonal D – M relations, particularly in communities with only small inter-specific differences in mass, as a consequence of real advantages garnered by being of slightly larger size relative to competitors. In other words, the polygonal (where slopes approximate zero) or positive relationships often observed at small scales may not result solely from the theoretical increased variability in the slope of the D – M relation demonstrated here, but, instead, may arise as a consequence of a real competitive advantage garnered by larger individuals (and, thus, species with larger average size) on average at these scales. In fact, this is exactly what our review of the literature shows (Fig. 1e). Considered in combination with our findings that resource partitioning is of greater importance in determining the D – M relation at smaller scales (Fig. 2), we suggest the possibility that the advantages of being of relatively larger size may have more profound consequences when the relative difference in size among organisms is small (see also Damuth, 1991). Second, a competitive advantage in favour of larger species would increase the range of body size required to consistently find a D – M slope approximating $-b$ above the roughly 7 OM shown here.

5. Conclusions

Our results suggest that the variability in the slope of the D – M relation observed in the literature may result from *scale-dependence in the variation of the slope* rather than variation in the *average slope* of the D – M relation *per se*. While the effect of body mass range on variability in the density–mass pattern observed is usually attributed to a purely statistical effect, our results suggest that such variability may equally result from a biological mechanism, where the partitioning of resources among members of a community introduces variability into the D – M relation, particularly when the difference in body mass among members of the community is small. We have shown here that slopes approximating $-b$ suggest unbiased partitioning of resources among species of varying body size and, thus, that the consistency in the average slope of the D – M relation across all ranges of body

size suggests that population energy use might be expected to be mass-invariant, on average, across all scales of observation regardless of whether or not organisms share a common resource base. However, the bias toward shallower slopes at smaller scales of observation observed in the literature points to the importance of size-structured competition in real communities and suggests that it may not be possible to use the mass- and temperature-dependence of metabolism to accurately predict patterns in higher level structure and function at smaller scales of observation.

Thus, we have shown that variability in the density–mass relation should be expected over small scales of observation on the basis of inter-specific differences in resource acquisition; consistency in pattern will arise at larger scales, where size-based differences in metabolic demands dominate the determination of population density over differences in resource partitioning. While variation at small scales may be brought about by real and biologically meaningful differences between species and among communities, the high variability in the D – M relation found at small scales should not be interpreted so as to imply that energetic limitation (via the mass-dependence of organism metabolic rate) is not a considerable determinant of population density at these scales. Both resource partitioning and the mass-dependence of organism metabolic rate control population density, each exerting dominant control over population density at different scales of observation: Dominant control switches from R to B as the range of M considered is increased, but both R and B are relevant and considerable controls at all scales. We should, therefore, hesitate to discard the idea that energetic limitation (via the mass-dependence of metabolic rate) is an important determinant of population density just because we frequently find substantial deviations from the expected slope of $-b$ in individual communities, particularly at very small scales of observation. However, since our results suggest that the energetic equivalence rule should not be expected to hold consistently at smaller scales of observation, the utility of metabolic theory in predicting higher level patterns in structure and function at these scales of observation is uncertain.

Arneberg et al. (1998) wisely pointed out that “[I]f common processes generate size-abundance relationships among all animals, then similar patterns should be observed across groups with different ecologies. . .” We submit that similar patterns do occur across groups with different ecologies on average, but that these patterns are likely to be observed in single studies at smaller scales of observation only after the effects of species-specific attributes and inter-specific interactions have been accounted for. Perhaps of greater practical importance, however, is that the mass-dependence of organism metabolic rate can be used to unmask patterns of interest in other community and ecosystem properties: Residual variation in population densities obtained following mass-correction can be examined for other ecological meaning (e.g., species-specific traits, inter-specific interactions, community history, habitat heterogeneity, resource availability) (Peters and Wassenberg, 1983; Peters and Raelson, 1984; McNab, 1988; Riska, 1991; Griffiths, 1992; Cotgreave, 1993; Brown, 1995; Marquet et al., 1995; Carbone and Gittleman, 2002; Jennings and Blanchard, 2004; Tilman et al., 2004).

Although the macroecological approach has been criticised in regard to the ecological relevance and interpretability of the patterns found (Lawton, 1989; see Currie, 1993), our simple model suggests that real and biologically relevant patterns are revealed at macroecological scales which may not have otherwise been readily discernable at smaller scales (Marquet et al., 2004; Tilman et al., 2004). Furthermore, although a relatively greater importance of other ecological and physiological factors at smaller scales is implicit whenever a pattern emerges only at larger scales, more meaningful information can be garnered (and greater under-

standing achieved) at smaller scales if the effects of the larger patterns are accounted for first.

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Appendix A. Sources for the “observations from the literature” (Fig. 1e).

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