LETTER

On the relationship between mass and diameter distributions in tree communities

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Abstract

It has been suggested that frequency distributions of individual tree masses in natural stands are characterized by power-law distributions with exponents near $-3/4$, and that therefore tree communities exhibit energetic equivalence among size classes. Because the mass of trees is not measured directly, but estimated from diameter, this supposition is based on the fact that the observed distribution of tree diameters is approximately characterized by a power-law with an exponent ≈ -2. Here we show that diameter distributions of this form are not equivalent to mass distributions with exponents of $-3/4$, but actually to mass distributions with exponents of $-11/8$. We discuss the implications of this result for the metabolic theory of ecology and for understanding energetic equivalence and the processes structuring tree communities.

INTRODUCTION

The idea of energetic equivalence was first suggested by Damuth (1981). Damuth noted that, because the average population density of a species, N, was related its mass, M, raised to the $-3/4$ power and the metabolic rate of an individual, B, was related to its mass raised to the $+3/4$ power, the population energy use of a species was invariant with respect to mass (i.e. $Q = BN \propto M^{3/4}M^{-3/4} \propto M^0$). This pattern has been dubbed the Energetic Equivalence Rule and is commonly observed at broad spatial scales for mammals, invertebrates, fish and trees (Damuth 1987; Cyr *et al.* 1997; Enquist *et al.* 1998; Ernest *et al.* 2003; White *et al.* 2007).

It has recently been suggested that a related pattern occurs for individual-size distributions (ISDs) within forest communities. By assuming that the scaling of the distribution of plant masses within communities behaves in the same manner as the scaling of plant mass and density across communities, Enquist & Niklas (2001) suggested that the number of individuals in a mass class, n, should be proportional to the mass of that class raised to the $-3/4$ power. If this assumption is valid, then energetic equivalence occurs among mass classes within tree communities.

Because diameter, D, not mass, is typically measured in forest communities, Enquist & Niklas (2001) provided indirect support for energetic equivalence across mass classes by deriving a prediction for the form of the size distribution in terms of diameter, $n \propto M^{-3/4} \propto D^{-2}$. In support of this model, Enquist & Niklas (2001) showed that, for many of Alwyn Gentry's forest plots (Phillips & Miller 2002), abundance among size classes declines approximately to the -2 power of diameter (but see White *et al.* 2008). While the precise form of the empirical diameter distribution and the value of the exponent have recently been questioned, it does appear that diameter distributions of many forests can be approximately characterized by this pattern over some range of body sizes (Coomes *et al.* 2003; Muller-Landau *et al.* 2006b; White *et al.* 2008; see also Fig. 2).

This result suggests a roughly equal partitioning of resources, energy flux and net primary production among mass and diameter classes within forests and may provide insights into the processes structuring forest communities (Enquist & Niklas 2001; Enquist 2002). This pattern has subsequently been used to provide linkages from individual-level energetic constraints to community structure to whole ecosystem processes, and in turn, advance the metabolic theory of ecology as a powerful and predictive

tool capable of integrating across levels of biological organization (Enquist *et al.* 2003; Brown *et al.* 2004; Kerkhoff & Enquist 2006, 2007). However, here we show that the derived form of the diameter distribution is incorrect and discuss the implications of this result for metabolic theory, energetic equivalence and the processes structuring tree communities.

RELATING MASS AND DIAMETER DISTRIBUTIONS

Enquist & Niklas (2001) established the predicted form of the diameter distribution by first assuming that N and n scale with body size in the same manner (i.e. $n \propto M^{-3/4}$) and then substituting the relationship between individual mass and tree diameter, $M \propto D^{8/3}$ (Niklas 1994; West *et al.* 1997, 1999), into the predicted form of the mass distribution. This yields $n \propto M^{-3/4} \propto (D^{8/3})^{-3/4} \propto D^{-2}$ (see also Coomes *et al.* 2003; West & Brown 2004, 2005; Marquet *et al.* 2005; Muller-Landau *et al.* 2006b; Woodhouse 2006). However, this substitution is not a valid approach for transforming between variables when dealing with size distributions, which, unlike other allometric relationships, are characterized by probability density functions. The problem occurs because changing from mass to diameter not only changes the position of individual points, but also changes the position of those points relative to one another and hence the density of those points along the size axis.

The appropriate univariate transformation between two probability density functions $f_X(x)$ and $f_Y(y)$, where x is related to y by $x = h(y)$ is

$$f_Y(y) = h'(y)f_X(h(y)), \tag{1}$$

where $h'(y)$ is the derivative of $h(y)$ with respect to y (e.g. Freund 1971; Mood *et al.* 1974; Ross 2006). This is the standard method from calculus for a change of variables in a definite integral (Thomas & Finney 1996). The derivative accounts for the change in the position of the points relative to one another. Therefore, the predicted diameter distribution for a model where the mass distribution is characterized by $f_M(M) \propto M^{-3/4}$, and where M and D are related by $M \propto D^{8/3}$, is given by

$$f_D(D) \propto D^{5/3} f_M(D^{8/3}) \propto D^{5/3}(D^{8/3})^{-3/4} \propto D^{-1/3}$$

demonstrating that the predicted relationship between abundance and diameter is actually $D^{-1/3}$, not D^{-2}. Equivalently, we can determine the form of the mass distribution that corresponds to a diameter distribution with an exponent of -2:

$$f_M(M) \propto M^{-5/8} f_D(M^{3/8}) \propto M^{-5/8}(M^{3/8})^{-2} \propto M^{-11/8}$$

suggesting that observed ISDs of diameter actually support distributions of mass with exponents near $-11/8$, not $-3/4$. These results were confirmed by both simulations (Fig. 1) and analyses of empirical data (Fig. 2).

This variable transformation error has also occurred in other areas of ecology. Notably, May (1986), Peters (1983) and Southwood *et al.* (2006) did not properly transform between size variables when evaluating the form of species body size distributions. The error is likely a result of thinking about frequency distributions from the perspective
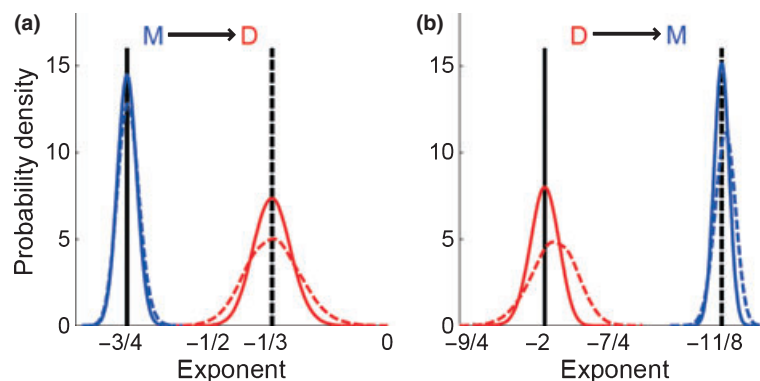
Figure 1 Simulation results confirming the analytical solutions for transformations between different measures of body size. Random datasets of 500 individuals each were generated from power-law distributions with the appropriate exponents, a minimum value of 1 and a maximum value of 10 000. These datasets were treated as either mass data (exponent = $-3/4$) or diameter data (exponent = -2). The exponent of each dataset was determined using both maximum likelihood estimation (solid lines) and normalized logarithmic binning (dashed lines), the values were converted to the alternate measure of size (diameter or mass) using $M \propto D^{8/3}$, and finally the exponent for the alternate size measure was determined. Distributions of the results of 10 000 of these simulations are presented for (a) Converting from mass (exponent = $-3/4$; blue lines) to diameter (red lines; analytical solution for exponent = $-1/3$) and (b) converting from diameter (exponent = -2; red lines) to mass (blue lines; analytical solution for exponent = $-11/8$). The simulated data clearly replicate the analytical result.
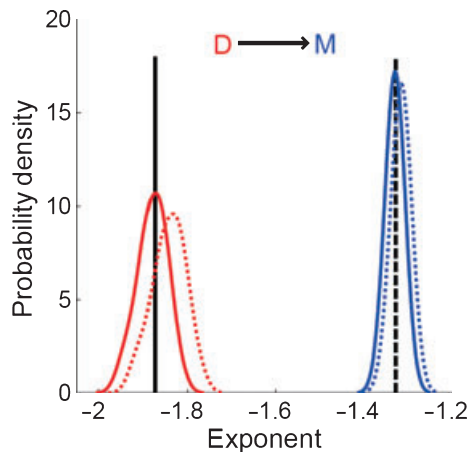
Figure 2 Empirical results confirming the analytical solutions for transformations between different measures of body size and rejecting the previously assumed distribution: $f_M(M) \propto M^{-3/4}$. Data from the 50-ha plot at Barro Colorado Island (Condit 1998; Hubbell *et al.* 1999, 2005) were subdivided into 50 1-ha subplots. Diameters (red lines) where converted to masses (blue lines) using $M \propto D^{8/3}$. Power-laws were fit to the data using maximum likelihood estimation based on the Pareto distribution (solid lines) and the Truncated Pareto distribution (dotted lines; using the maximum value of diameter or mass for the entire 50-ha plot as the maximum attainable value). The mode of the Pareto diameter distribution exponents is indicated by the solid black line and the predicted value for the mass exponent based on this observed diameter exponent is indicated by the dashed black line.

of the binning-based approaches often used to analyse the data. These approaches typically treat frequency distribution data as bivariate functional relationships, making it appear that the substitution discussed above is valid. Avoiding binning-based approaches when modelling and analysing frequency distribution data may help alleviate confusion regarding the type of size–abundance relationship being studied, and thus clarify the appropriate approach to transforming between variables.

We have focused on the transformation originally laid out in Enquist & Niklas (2001). However, the form of both the ISD and the relationship between diameter and mass are subjects of debate (Niklas 1994; West *et al.* 1997, 1999; Enquist & Niklas 2001; Coomes *et al.* 2003; Chave *et al.* 2005; Muller-Landau *et al.* 2006b; Price *et al.* 2007). The general approach we take is valid for any proposed form of the ISD and functional relationship between diameter and mass. The transformation can generally be expressed as,

$$f_M(M) = \int P(M \mid D) f_D(D) \mathrm{d}D. \qquad (2)$$

In concept, this general solution makes it possible to incorporate alternative and/or more complex forms of the component relationships including the incorporation of: (1)

error around the allometric relationships; (2) species level variation in the normalization (e.g. through variation in wood density; Chave *et al.* 2005) and exponent of the allometric function relating M to D (Price *et al.* 2007); and (3) the use of different distributions and functional relationships (e.g. those in Chave *et al.* 2005 and Muller-Landau *et al.* 2006b). In practice, analytical solutions to the transformation described in eqn 2 may prove more difficult in the presence of these additional sources of complexity. Preliminary simulation results suggest that variability in the exponent does not affect the transformation (Appendix S1), but that error around the allometric relationships may have some influence on the results (Appendix S1). Further research will be necessary to fully understand the implications of these and other complexities for transforming between different forms of the size distribution.

IMPLICATIONS FOR THE METABOLIC THEORY OF ECOLOGY

Because the observed form of the diameter distribution in tree communities is not consistent with an ISD of the form $f_M(M) \propto M^{-3/4}$, the published metabolic theory explanation for the form of the ISD (Enquist & Niklas 2001) is not supported by empirical data. Therefore, metabolic theory has yet to provide a mechanistic explanation for ISDs within forests (see also Torres *et al.* 2001; Coomes 2006; Muller-Landau *et al.* 2006b). In addition, the two studies in animal communities that have offered support for the predicted −3/4 form of the individual mass distribution (Ackerman *et al.* 2004; Meehan 2006) did so using incorrect statistical methods (see White *et al.* 2008 for a detailed explanation). Specifically, a value of 1 must be subtracted from the exponent when using logarithmically binned size classes (see Bonnet *et al.* 2001; Andersen & Beyer 2006; Sims *et al.* 2007; White *et al.* 2008). As a result, these studies support an exponent near −7/4, not −3/4. It has been suggested that these studies should be interpreted as deriving $f_{\log(M)}(\log(M))$, and thus actually predict $f_M(M) \propto M^{-7/4}$ (Reuman *et al.* in press). Regardless, we are aware of no data that support an ISD with the $f_M(M) \propto M^{-3/4}$ form.

It should be noted, however, that Enquist & Niklas (2001) do provide a simulation model from which a size distribution characterized by $f_D(D) \propto D^{-2}$ emerges. Their model follows the succession of spatially explicit forest communities from an initial 'seeding' of propagules to an equilibrium forest structure. Metabolic theory provides the basis for growth such that partitioning of new biomass into stems, leaves and reproductive biomass is assumed to scale with mass as predicted by metabolic theory (West *et al.* 1999; Enquist *et al.* 2000; Enquist & Niklas 2002; Niklas *et al.* 2003). In addition to purely metabolic constraints, mortality and growth in this model are also affected by light

competition due to light attenuation caused by overhead canopies (see also Coomes 2006; Muller-Landau *et al.* 2006a; Coomes & Allen 2007). The simulated ISDs are well characterized by $f_D(D) \propto D^{-2}$ (Enquist & Niklas 2001). Similar results are also seen in more complex simulation models with allometric foundations (Chave 1999). The rough concordance between observed and simulated distributions suggests that the rules governing biomass partitioning, as predicted by metabolic theory, may have important influences on the form of the size distribution.

In addition to predicting the form of the ISD, a small branch of metabolic theory has utilized the presumed form of the mass distribution to make predictions for the scaling of ecosystem properties such as carbon storage and flux, and whole community nutrient stocks (Kerkhoff & Enquist 2006). Determining the specific implications of our central result for this study will require re-derivation of the model and re-analysis of the affected predictions. While detailed redevelopment is beyond the scope of this study, it is clear that within-size-class predictions for any community or ecosystem attribute will be sensitive to the assumed ISD. In addition, any model for ecosystem processes where the size distribution plays a meaningful role will be influenced by the use of the incorrect form of the ISD (e.g. Kerkhoff & Enquist 2006). The form of the ISD is thus important for understanding how organismal processes 'scale-up' to populations, communities and ecosystems. In general, our results impact the metabolic theory predictions for the form of the ISD and for community and ecosystem-level properties based on the ISD, but our results have no implications for the network model itself (West *et al.* 1997, 1999) or for any predictions of individual- and species-level properties (e.g. metabolic rate, mortality rate, etc.).

IMPLICATIONS FOR ENERGETIC EQUIVALENCE

Different processes are responsible for generating the ISD and the species-level size–density relationship (SDR; *sensu* White *et al.* 2007), the pattern Damuth (1981) originally proposed to exhibit energetic equivalence (Jennings *et al.* 2007; White *et al.* 2007). These two patterns also take different mathematical forms. The ISD is a frequency distribution and is thus characterized by a probability density function, while the SDR is a bivariate functional relationship. Our results have no implications for the traditional SDR-based energetic equivalence rule because if population-level metabolic rate, Q, is invariant with respect to body size for one size measure, by definition it is invariant with respect to the other size measures (since direct substitution is the appropriate way to change variables for the SDR). For example, given the size dependence of metabolic rate ($B \propto M^{3/4} \propto D^2$), popu-

lation size must decline with body size such that $Q \propto BN \propto M^{3/4}M^{-3/4} \propto M^0$ and $Q \propto BN \propto D^2D^{-2} \propto D^0$ (Enquist *et al.* 1998).

In contrast, for the ISD, only a single measure of size (or a set of size measures that are related isometrically) can exhibit energetic equivalence. For example, observed diameter distributions in tree communities are fairly close in many cases to exhibiting energetic equivalence while mass distributions exhibit a steep decline in energy use with increasing size class: $q \propto Bn \propto D^2D^{-2} \propto D^0$ and $q \propto Bn \propto M^{3/4}M^{-11/8} \propto M^{-5/8}$, where q is the energy flux within a size class. More generally, it is a mathematical certainty that, within any community, energy will not be partitioned among size classes in the same manner for different characterizations of body size when those characterizations are related allometrically (e.g. fish mass $\propto$ fish length^3 or tree mass $\propto$ tree diameter$^{8/3}$).

The size of a tree can be defined based on various measurements including mass, trunk diameter, height (H) and crown area (i.e. leaf mass; A). Metabolic theory predicts, and/or empirical data support, allometric relationships between these measures of size such that $M \propto D^{8/3} \propto H^4 \propto A^{4/3}$ (Niklas 1994; West *et al.* 1997, 1999; Niklas & Enquist 2001; Muller-Landau *et al.* 2006a). Hence, a forest characterized by the ISDs, $f_D(D) \propto D^{-2}$ and $f_M(M) \propto M^{-11/8}$, can also be characterized by the ISDs $f_H(H) \propto H^{-5/2}$ and $f_A(A) \propto A^{-3/2}$. Combining these height and crown area ISDs with the dependence of metabolic rate on height ($B \propto H^3$) and crown area ($B \propto A$) shows that diameter is the only measure of size for which energetic equivalence is approximated within forests: $q \propto D^0$, $q \propto M^{-5/8}$, $q \propto Bf_H(H) \propto H^3H^{-5/2} \propto H^{1/2}$ and $q \propto Bf_A(A) \propto AA^{-3/2} \propto A^{-1/2}$. This occurs because the relative position of individuals along the size axis changes when transforming from one size measure to another. As a result, the number of individuals in a size class is dependent on how size is characterized, such that the amount of energy fluxed within a size class changes with the choice of size measure. This remains true regardless of taxon or community type. In contrast, the amount of energy fluxed by a population or through a whole community is not dependent on how size is characterized because the number of individuals and the fluxes of each individual remain the same by definition. Thus, energetic equivalence holds across forests (Enquist *et al.* 1998) regardless of how size is characterized.

IMPLICATIONS FOR PROCESSES STRUCTURING TREE COMMUNITIES

Approximately equal energy use across diameter classes may point to diameter as a functional attribute of tree morphology critical to resource partitioning among indi-

viduals. If diameter is directly related to resource partitioning, the observation of approximate energetic equivalence would represent an important clue to understanding how resources are divided within forests. However, diameter is unlikely to be the most relevant aspect of size given that canopy area, leaf mass and tree height are more directly related to light acquisition than is trunk diameter (see also Lawes *et al.* 2008). In fact, the observed form of the tree size distribution has been questioned due to a presumed dominance of light acquisition by larger individuals (Coomes 2006; Muller-Landau *et al.* 2006b; Coomes & Allen 2007). Dominant resource acquisition by larger individuals would suggest that tree height, the only measure of size examined here for which energy flux increases across size classes, is the aspect of size most relevant to resource partitioning in forests. However, resource acquisition should logically result from a combination of canopy area (the number of leaves) and tree height (the per leaf resource availability). Although more research is needed to determine how different aspects of tree size influence resource partitioning within forests (Schwinning & Weiner 1998), some insight is provided by the fact that realistic diameter distributions emerge from simulation models combining the ecological impacts of competition for light and stochastic mortality with allometric partitioning of biomass into growth and reproduction (Chave 1999; Enquist & Niklas 2001). In addition, Hara (1984) hypothesized that realized ISDs are sensitive to size-dependent biomass partitioning. Roughly equivalent energy flux across diameter classes may thus represent an emergent property of plant communities within which individuals are constrained to follow idealized biomass partitioning rules.

Exploring the sensitivity of the ISDs predicted by these models to the assumptions of individual biomass partitioning and light competition will provide a more rigorous evaluation of the processes leading to observed patterns of resource division among individuals. This will help determine if patterns of resource partitioning are due to a direct influence of size *per se* or if they emerge indirectly through ecological interactions and individual biomass partitioning. In addition, studying the temporal dynamics of ISDs following disturbance would allow community assembly to be examined through time from a body size perspective (Kohyama 1993). In general, understanding the relative influence of, and interactions between, individual biomass partitioning and competition should help elucidate fundamental processes structuring forested ecosystems.

CONCLUSIONS

Here we have shown that the distribution of individual tree masses predicted by Enquist & Niklas (2001), $f_M(M) \propto M^{-3/4}$, is not consistent with the observed form of tree-community diameter distributions, $f_D(D) \propto D^{-2}$, and is thus not supported by empirical data. Therefore, when properly analysed, the current metabolic theory explanation for the form of ISDs in tree communities is readily rejected. This result also demonstrates that patterns of energy use across size classes within forests are dependent upon how size is characterized. If measured in terms of diameter, all size classes flux approximately the same amount of energy whereas energy flux declines with mass and crown area and increases with height. This implies that energy is not partitioned due to size *per se*, but rather due to different functional attributes of different aspects of size. This 'context' dependence of energy partitioning occurs because of the allometric relationships between different aspects of tree size and because ISDs are frequency distributions, not bivariate functions. The nature of this dependence raises significant challenges for understanding the relative dominance of different size classes in tree communities.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1 Incorporation of additional sources of variability into the transformation between mass and diameter distributions.

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