**Title:** Metabolic Partitioning Across Individuals in Ecological Communities

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**STRUCTURED ABSTRACT (250 words max)**

**Issue**

The mechanistic origin and shape of body-size distributions within communities are of considerable interest in ecology. A light-limitation model by Farrior, Bohlman, Hubbell *et al*. (2016) and the Maximum Entropy Theory of Ecology (METE) predict remarkably similar and relatively accurate distributions of tree sizes in a tropical forest plot. However, the latter makes no explicit mechanistic assumptions, leaving open the question as to whether light limitation is an essential mechanism.

**Evidence**

We test METE’s predictions of the size distribution in three disparate communities: trees in a tropical forest plot, herbaceous plants in a treeless subalpine meadow, and arthropods on an island.

**Conclusion**

The METE predictions appear to match data widely, including in ecosystems where light is not limiting. The distribution of metabolic rates across individuals that is predicted by METE has approximate power-law behavior in the size range where Farrior, Bohlman, Hubbell *et al*. predict a power law, and exponential behavior in the size range where their light limitation model predicts an exponential tail; the success of METE’s predicted form across systems, including those that are clearly not light limited, casts doubt on the mechanistic explanation even in potentially light-limited systems.

**INTRODUCTION**

Among the many patterns in nature that macroecologists seek to predict are the shape and spatial-scale-dependence of the distribution of body sizes or metabolic rates across individuals within a broad taxonomic group (Brown and Maurer, 1986; Gaston and Blackburn, 2000). Attempts to do so have used resource allocation models (Hutchinson and MacArthur, 1959; Ritchie, 2010), evolutionary models (Clauset and Erwin, 2008; Clauset and Redner, 2009), models incorporating random diversification (Maurer, 1988), and birth-death processes (Maurer, Brown and Rusler, 1992). Although nearly all such efforts make the very general prediction that small individuals should outnumber large individuals, there is no consensus as to the underlying mechanisms that shape body size distributions, nor if any common distribution function, such as the lognormal, provides the best description (Gaston and Blackburn, 2000).

To describe the distribution of tree sizes in the Barro Colorado Island (BCI) forest plot in Panama (Hubbell et al., 2005), Farrior, Bohlman, Hubbell *et al*. (2016) recently proposed a light-competition model. With suitably chosen parameters it describes adequately the distribution of stem diameters in that 50-hectare (ha) plot. In particular, the model predicts power-law behavior for the size distribution of the smaller trees and exponential behavior for the size distribution of the larger trees.

We show here that the Maximum Entropy Theory of Ecology (METE; Harte *et al*., 2008; Harte and Newman, 2014) predicts a very similar behavior to that of Farrior, Bohlman, Hubbell *et al*. (2016) for the body size distribution. METE’s predictions derive from the maximum entropy inference procedure (Jaynes, 1957; 1982; Harte, 2011; Harte and Newman, 2014) and do not assume a light-limitation mechanism. Indeed, we show here that this predicted size distribution describes communities regardless of whether they are light limited. METE makes no explicit assumptions about governing mechanisms, contains no fitted parameters, and successfully predicts many other macroecological metrics, such as the species-abundance distribution and the species-area relationship (Harte et al., 2008; 2009; 2011; 2015), in addition to the size distribution across individuals (Harte 2011, Newman et al. 2014, Xiao et al. 2015).

**METHODS**

METE predicts the distribution of metabolic rates, rather than of sizes or masses, across individuals in the community. To extend the prediction from metabolic rate to tree basal area, we use results from tree allometry and metabolic scaling theory and thus assume metabolic rate scales as the square of stem diameter (Enquist and Niklas, 2001; Xiao et al., 2015). We recognize that this substitution of basal area for metabolic rate introduces some amount of error because there is evidence for size dependent deviations from the ¾-power metabolic scaling rule and the tree allometry that link basal area to metabolism (Muller-Landau et al., 2006). However, using an alternate estimate of metabolic scaling for plants (cite) does not substantially change the fit of METE to BCI trees across size classes.

The METE prediction for the distribution of metabolic rates *ε*, across all individual organisms of a focal group in a well-defined area is (Harte et al., 2008):

 (1)

Here, *β* = *λ*1 + *λ*2, *γ*(*ε*)= *λ*1 + *λ*2*ε*,and *λ*1 and *λ*2 are Lagrange multipliers that are uniquely determined from the values of the state variables, *S*0, *N*0, *E*0, which correspond, respectively, to the total number of species in the plot, the total number of individuals in the plot, and their total combined metabolic rate. For details of the calculations, see Harte (2011). Analyses were carried out using the meteR package (Rominger and Merow, 2016) in R (R Core Team 2016).

The value of *λ*1 is on the order of (*S*0/*N*0)/ln(*N*0/*S*0) << 1 and the value of *λ*2 is on the order of *S*0/*E*0 << *λ*1. For relatively small values of *ε*, such that *λ*2*ε* << 1, the term  in the numerator in Eq. 1 is ≈ 1, and the denominator is (to leading order) ≈ *γ*2(*ε*). If *ε* is sufficiently small, this expression in the denominator is ≈ (*λ*1)2, while for values of *ε* such that 1 >> *λ*2*ε* > *λ*1,it is ≈ (*λ*2*ε*)2. Thus for very small values of *ε, Ψ*(*ε*) is predicted to be constant and for intermediate values of *ε* it is approximately power-law. For still larger values of *ε*, such that *λ*2*ε* > 1, the exponential term in the numerator becomes influential and the denominator is ≈ 1, resulting in:

 (2)

Fig. 1 shows METE’s predicted distribution of metabolic rates (Eq 1) using the numerical values of the state variables for the BCI plot (1995 census; Hubbell et al. 2005). The domain in *ε* over which approximate power-law behavior is predicted is 10 < *ε* < 10000, in normalized units such that the smallest tree (with stem diameter = 1 cm) is defined as having *ε* = 1. This range of metabolic rates over which power-law behavior is predicted corresponds to stem diameters between approximately 30 and 1000 mm. This range of diameters corresponds well with the range over which Farrior et al. (1) predict power-law behavior. The exponential term in the numerator should begin to exert influence over the shape of the metabolic rate distribution for values of *ε* > 10000, corresponding to stem diameters > 1000 mm, which matches well the transition threshold between exponential and the power-law dominance in Farrior, Bohlman, Hubbell *et al*. Because there are no adjustable parameters in METE, the transition between power-law behavior and exponential behavior, as well as the power law exponent and the coefficient in the exponential term are all uniquely predicted from the theory.

A comparison of the prediction in Eq. 1 with metabolic rates estimated from basal area at BCI is shown in Fig. 2a. We use rank plots to display the data and the prediction in order to avoid the arbitrary choices involved in binning data into size classes, which also results in a loss of information. Systematic differences between the METE prediction and observation are revealed in Fig. 2a, just as was the case for the model in Farrior et al. We do not know how much of the discrepancy is simply due to inaccuracies in the tree allometry and the metabolic scaling rule that were used here to replace metabolic rate with basal area, particularly for the ~30 largest individual trees in the plot (out of ~230,000) for which the deviation between theory and observation is greatest.

Xiao, McGlinn, and White (2015) show that the MaxEnt prediction accurately describes the distribution of tree metabolic rates in the 60 globally distributed forests they analyzed. Their data sets included a total of ≈ 2000 species and ≈ 300,000 individuals. Newman et al. (2014) show it equally well describes meadow vegetation (Fig. 2b). Rominger et al. (2016) and Harte (2011) show it applies to arthropods (Fig. 2c). It is noteworthy that the open-canopy meadow vegetation and the arthropod communities in Figs 2b-c would not be considered light-limited.

**DISCUSSION**

We are not claiming that the METE prediction is, statistically, better than the model prediction in Farrior Bohlman, Hubbell *et al*. (2016). Comparing the merits of METE and a light-limitation model at this stage is not straightforward because METE predicts many other macroecological metrics besides the metabolic rate distribution, such as species-area relationships, abundance distributions, size-abundance relationships, and distributions of species richness over higher taxonomic classifications (Harte et al., 2008; 2009, 2015; Harte, 2011; Harte and Newman, 2014). Instead, we are pointing out that a null theory that makes no explicit assumptions about light competition or power-law behavior results in a comparably accurate predicted distribution of metabolic rates (Eq. 1).

The combination of an approximate power law domain and an exponential domain in the metabolic rate distribution, as predicted by Eq. 1, is observed in many systems that are not light limited, suggesting that light limitation is not the driver of the size distribution of trees at BCI. On the one hand, it may be that light limitation is indeed the driver at BCI, while other mechanisms result in similar size distributions for subalpine meadow flora and arthropod communities. If that is the case, auxiliary tests (cite) of the light limitation model must be developed that differ from the null statistical theory represented by METE; and the question remains as to how different dominant mechanisms operating in different systems can all be captured by the maximum entropy theory of ecology. On the other hand, it is possible a null statistical theory such as METE is successful precisely because a multiplicity of mechanisms operate at every site to structure size distributions.

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**DATA ACCESSIBILITY**

All data used in this study has been previously published as cited in the main text. Analyses were carried out in the R package “meteR” (Rominger and Merow 2016).

**BIOSKETCH**

**John Harte** is a professor in the Energy and Resources Group and the Department of Environmental Science, Policy and Management at the University of California, Berkeley. His research broadly spans topics of biodiversity, climate-ecosystem feedbacks, and applications of the Maximum Entropy Principle to ecology.

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**FIGURES**

Figure 1. Probability density function predicted by METE parameterized for Barro Colorado Island 1995 census. The dark gray region corresponds to power law behavior, while the light gray region represents dominance of exponential behavior.

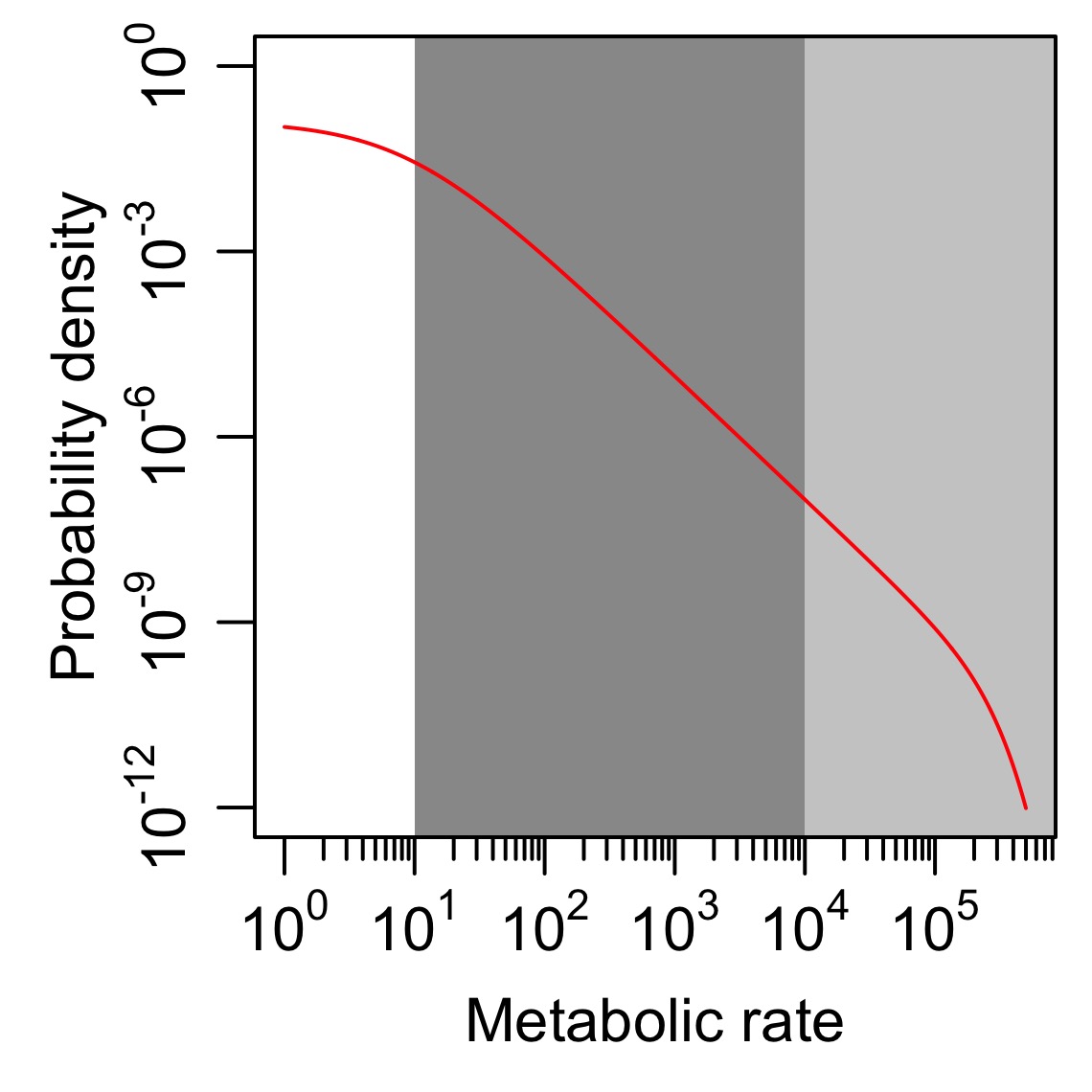


Figure 2. Comparison of the METE prediction for the distribution of metabolic rates with observed values for (A) individual trees at Barro Colorado Island (1995 census; Hubbell et al. 2005), where basal area is assumed to be a surrogate for metabolic rate, and (B) subalpine meadow plants from Rocky Mountain Biological Laboratory, Colorado, USA (Newman et al. 2014); and (C) a community of predaceous arthropods in Hawaii (data from Gruner 2007). Data and theory are presented as rank curves with log metabolic rate for each individual on the y-axis and individual rank (from largest to smallest) on the x-axis.

