Revisions to the Dimensions article: JH

Two issues arise regarding METE that need to be addressed:

1. What is METE; how and what does it predict?
2. How can deviations inform us about mechanism.

Both these issues are addressed in simple, non-mathematical language in a recent TREE article that I wrote with Erica Newman: “Maximum information entropy: A

foundation for ecological theory”, *Trends in Ecology & Evolution*, July 2014, Vol. 29, No. 7. The text I am suggesting to address the two issues is condensed from that article because it is hard to improve upon it by starting from scratch! Feel free to further condense it. I will not attempt to insert this material into the text of the article because it appears that the article will be going through some substantial revision. It should be straightforward to do that later.

One other thing: the citations at the end of this document are lifted from the full TREE article…not all are needed in this condensed excerpt.

**What is MaxEnt/METE?**

The maximum entropy method (MaxEnt) is a widely accepted statistical inference procedure [1-10] that has advanced predictive capacity in topics as diverse as thermodynamics [1,2], economics [3], forensics [4], imaging technologies [5-7], and recently ecology [8-15,ww,vv]. It is a rigorously-proven inference procedure that yields least-biased predictions consistent with prior knowledge [2]. Here the term entropy refers to information entropy, a property of a probability distribution p(n), calculated by the Shannon [20] information expression I = -∑np(n)\*log(p(n)). Information entropy is a useful measure of uncertainty about an outcome of a draw from a probability distribution because it can be shown [1,2] that the more uniform (flat and smooth) a probability distribution is, the larger will be its information entropy. A uniform probability distribution allows many outcomes with equal probability, which means that the residual uncertainty about outcomes, and therefore information entropy, is high. Consequently, maximizing information entropy is equivalent to maximizing residual uncertainty.

MaxEnt maximizes information entropy subject to the constraints imposed by prior knowledge of a system, and thus MaxEnt-based theories will differ because of differing choices about what comprises these constraints. In the Maximum Entropy Theory of Ecology (METE) [12-14,35] the constraints arise from measured values of “state variables”. In thermodynamics, pressure, volume and temperature are state variables. In the simplest version of METE, the state variables are the area (A) of the system, the total number of species (S), the total number of individuals in those species (N), and the total metabolism of those individuals (E), all within some prescribed taxonomic group such as arthropods or plants. We denote this as the ASNE version of METE. Ratios of these state variables constrain the probability distrbutions that describe patterns in macroecology, and maximization of information entropy subject to those constraints determines the forms of the probability distributions. Mathematical details are spelled out in [12-14]. From plot- to biome-scale, ASNE predicts the shapes of macroecological metrics describing patterns in the diversity, abundance, spatial distributions, and energetics of species and individuals, within ecological communities. Among the widely obeyed predictions of ASNE are the Fisher logseries species-abundance distribution, the species-area relation, and the distribution of metabolic rates over all individuals. For derivations and empirical tests of these predictions, see [12-15]. Nevertheless, in some ecosystems there is preliminary evidence that these predictions fail and one of ASNE’s predictions, the energy equivalence rule relating the average metabolic rate of the individuals in a species to a species average metabolic rate body size and abundance, often fails [31].

**How can METE allow inference of the mechanisms driving macroecological patterns?**

Failures of the predictions of a theory of macroecology can provide insight into the mechanisms that produce macroecological patterns. The ideal gas law in thermodynamics provides a useful parallel. This relationship can be derived using MaxEnt [1,2] and it is remarkably accurate in most situations. However, observations of its failure at sufficiently high pressure led to the discovery of the Van der Waals force that results from dipole-dipole interactions between molecules.

ASNE makes two implicit assumptions: i., the state variables are static, and ii. the only mechanisms that determine patterns in macroecology are the ones that determined the values of the four selected state variables (Area, Species richness S, abundance N, and metabolic rate E). Some of the occasional failures of ASNE, such as that of the species-abundance distribution, arise in stressed, highly disturbed, or rapidly changing ecosystems. The failure of ASNE’s predictions in certain ecological conditions, for example in young island ecosystems that are relatively rapidly diversifying, can lead to identification and better understanding of the dominant mechanisms that govern dynamic changes in the state variables. What distinguishes MaxEnt-based theory from more traditional theories in ecology is that the former can reveal, rather than assume in advance, dominant mechanistic drivers of ecosystem structure. Two examples follow.

In some ecosystems the ASNE-predicted Fisher logseries species-abundance distribution underpredicts the proportion of very rare species. However, if, in addition to the ASNE state variables, a new resource variable (for example, call it W for water) is included, the resulting ASNEW version of METE will produce a modified SAD, with the (1/*n*) term in the logseries function altered to (1/*n*2) [14]. In general, with a total of *r* resources (including Energy) to be allocated, the predicted abundance distribution is a product of an exponential and a term 1/*nr*. The effect of such a modification is to increase the predicted fraction of species that are rare. Intuitively this makes sense; a greater number of limiting resources provides more specialized opportunities for rare species to survive. The observation of less rarity than predicted by the logseries would suggest the absence of any resource constraints, including that of energy. METE thus provides a framework in which the degree of rarity in a community can be related to the number of resources driving macroecological patterns, demonstrating how METE, although not explicitly a mechanistic theory, can provide insight into what mechanisms might be driving macroecological patterns.

Another prediction of the ASNE version of METE is that the average metabolic rate of individuals within a species with abundance *n*0 , <*ε*|*n*0>, varies inversely with the abundance of the species. This is the energy equivalence principle, related to the Damuth rule if a scaling relationship between body size and metabolism is assumed. Empirically, there is mixed support for energy equivalence [31], with most data sets showing considerable scatter when log(metabolic rate) or log(body size) is plotted against log(abundance). Failure of ASNE’s prediction of the energy equivalence rule may, again, provide additional insight. In particular, ASNE has recently been extended from the original ASNE version to one in which knowledge of the numbers of units at coarser taxonomic category provide additional state variables and therefore additional constraints (Harte, Rominger and Zhang, in review). Most predictions of ASNE are left essentially unchanged, with the exception of the energy- equivalence prediction which is dramatically changed. Now, the species richness of the family that a species is in influences its size-abundance relationship in a predictable way. What should one conclude if the more taxonomically resolved theory, ASFNE, is more accurate than the original ASNE model? One plausible answer is that for ecosystems in which the constraints arising from higher taxonomic resolution improve the accuracy of the theory, macroecological patterns are shaped by evolutionary history as well as by extant ecological mechanisms.

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