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Another step towards a unifying theory for ecosystems?

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There are many ways in which methods and theories from physics can and have been applied to biology and ecology. The oldest example is the application of classical mechanics to animal movement (biomechanics), from tiny bacteria to massive whales. This application is intuitive: most people when observing an elephant lumber along would be happy to conclude that animals are machines in that they are so obviously made of moving parts designed to perform work (in its physical sense) under the constraints of elementary forces (predominantly gravity if you were an elephant!). Indeed, the potential for this link between physics and biology was foreseen by Aristotle around 2000 years before the mathematical bases of classical mechanics were founded (Nussbaum 1986).

And, if individual organisms can be thought of as fundamental units of ecosystems, then one might imagine that it should be possible to understand the emergent ‘behaviours’ and states (or descriptors) of those complex systems from the (biomechanically governed) properties of their component individuals and populations. Take ecosystem-level respiration for example: can we not infer this ecosystem-level state variable from the energy use of its myriad individuals (measured by their respiration rates)? The Metabolic Theory of Ecology (MTE) aims to do precisely this by developing equations that scale up individual metabolism to whole ecosystems (Brown *et al.* 2004). MTE has met with considerable success in predicting the properties of populations, interactions between populations, as well as whole ecosystems from individual metabolic rates (Allen *et al.* 2002; Brown *et al.* 2004; Savage *et al.* 2004; Pawar *et al.* 2012; Schramski *et al.* 2015). In its approach of building up from individual to whole ecosystem properties, MTE is essentially a ‘bottom-up’ theoretical approach.

In a recent paper, Harte *et al.* (2022) propose an alternative ‘top-down’ approach that yields a theory linking together four key and commonly measured state variables of ecosystems – species richness, energy flow, biomass, and abundance – into a single ‘equation of state’, and thus also predicts the relationships between them. The top-down nature of this theory is rooted in statistical thermodynamics, wherein micro-level properties of a system are inferred from mathematically defined constraints on the state variables at the macro-level. This is achieved by applying the MaxEnt principle, which states that the most likely probability distribution of the state variable of a system is the one with maximal entropy after applying the constraints of prior knowledge, i.e., the one that maximises the information that can be extracted from the data given some prior knowledge (Jaynes 1957). In previous, seminal work, Harte *et al.* used this principle to make this top-down link between micro- and emergent, macro-ecosystem state variables to derive a ‘Maximum Entropy Theory of Ecology’ (METE) (Harte *et al.* 2008; Harte 2011). What are these micro- and macro-ecosystem state variables or properties? In the original formulation of METE, the micro-level properties are the metabolic rates of individuals and the abundances of their populations (i.e., species), while the macro-level properties are the total number of species and individuals in the whole ecosystem and the total metabolic rate of all those individuals (in a given area). The original METE has previously been used to make predictions about a range of ecosystem and macro-ecological properties, including species richness, energy flow, biomass, and abundance. However, neither the original version of METE nor any other theory (including MTE) currently can link together these ecosystem state variables.

To address this theoretical gap, Harte *et al.* (2022) bring together METE and MTE. Specifically, they invoke MTE’s $\frac{3}{4}$ -power scaling law that links an individual’s metabolism to its mass to add another MaxEnt constraint,

and introduce a fourth ecosystem state variable (total biomass). This then allows them to derive an equation that predicts an ecosystem's total biomass from its total number of species and individuals and the total metabolic rate of all those individuals (the equation of state). More specifically, it predicts that if the total number of individuals (N) as well as species (S) across ecosystems are held constant, across each of those ecosystems, the ratio of its total metabolic rate (summed across all individuals) (E) to its total biomass (B) raised to the $\frac{3}{4}$ -power is also a constant. A corollary is that given data on total abundance N , species richness S , and total metabolic rate E across ecosystems, the new METE equation should be able to predict total biomass B . Harte *et al.* (2022) then go on to show that their theory indeed accurately predicts ecosystem biomass across 42 data sets spanning organismal groups, spatial scales, and habitats. Furthermore, they show that this concordance is not the result of a simple scaling relationship between B and E such as what MTE would predict (Brown *et al.* 2004; Enquist *et al.* 2003), but is indeed the additional effects of ecosystem-wide species abundances and richness.

So, is this new avatar of METE indeed another step towards a unifying theory for ecosystems? First, it is important to note that the micro-level properties of interest in MTE and METE are the same: metabolic rates of individuals (of each species) and abundances of those species' populations. The difference is that METE makes no assumptions about the mechanisms that lead to the emergence of ecosystem-level state variables from these micro-level properties. In contrast, MTE invokes certain mechanisms such as species interactions or energy equivalence to go from individuals to whole ecosystem properties (Allen *et al.* 2002; Pawar *et al.* 2015). Thus, METE is more parsimonious than MTE in that it makes fewer assumptions about micro-scale processes, and, arguably, more practically useful because it can predict one or more properties of ecosystems from others under those minimal assumptions, and thus requires less data.

The principle of parsimony apart, as Harte *et al.* (2022) themselves wonder in their discussion, that a mechanism-free theory should work at all in complex ecosystems is worth scratching one's head over. Their (tentative) answer is that the properties of ecosystems that the new METE's equation of state so accurately predicts are an inevitable outcome of ecosystems reaching a steady state. That is, provided the fitness-maximising processes of nature acting through biomechanical (metabolic) constraints are allowed to play out and the ecosystem reaches a steady state (its state variables remain relatively constant over time), those relationships between the state variables inevitably emerges. The authors speculate that this is analogous to physical systems where we do not need to know the specific interactions between particles, once the system reach a thermodynamic equilibrium, to predict the system's properties. The specific biological mechanisms do not matter as long as they drive the ecosystem to a steady state.

This then means that this top-down theory would fail to predict the properties of ecosystems that are not at steady state because they have been displaced from it by a disturbance (and have not yet reached a new steady state). Indeed, the four main outliers in Harte *et al.*'s data-model fits are temperate tree communities that are currently undergoing secondary succession. This is, of course, expected from the general fact that parsimony in theory often comes at a cost: while METE makes predictions by making minimal assumptions about microscale processes by ignoring mechanisms, it is not equipped to make predictions in scenarios where those mechanisms drive the system's dynamics. But it raises an important question about the future directions that the updated METE can take: can it be extended to predict the behaviours and state variables of naturally and anthropogenically disturbed ecosystems in an increasingly uncertain world? To answer this question, for starters (again, as Harte *et al.* acknowledge), it will be necessary to account for that fundamental environmental variable, temperature. Recent work has shown how temperature, by its direct and dominant effect on individual-level metabolism, can amplify the nonlinearities inherent in complex ecosystems, holding those ecosystems away from steady state (Yvon-Durocher *et al.* 2017; García *et al.* 2022; Kordas *et al.* 2022). Furthermore, microbes, which account for a major proportion of ecosystem metabolism, do not adhere to the same scaling laws and thermal physiological constraints as eukaryotes (DeLong *et al.* 2010; Smith *et al.* 2019), so how well this theory predicts the properties of microbial communities will be an interesting future direction.

Ultimately though, the goal of science, and in particular one such as ecology which aspires to explain the behaviours of complex (eco)systems, is indeed to find parsimonious explanations for observed phenomena. The path from empirical observations to models to theories to general laws needs to be traced using both bottom-up and top-down theoretical approaches. Harte *et al.* (2022)'s modification to METE is a promising step in that direction by merging a fundamental element of the mechanistic MTE with the MaxEnt principle.

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