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On the Importance of First Principles in Ecological Theory Development

Houlahan and colleagues claim that we have ignored the fact that a good theory should accurately and precisely describe the way the world works. This is not correct; we value accuracy and precision if it is based on understanding. Our point of departure is precisely the discussion of theories that aim to improve our understanding of the natural world. We agree that it is critical to confront predictions of theory with data; there must be a basis for replacing or complementing existing theory with new. For example, we say, "Advances in data stimulate theory, and new theory refines, expands, and replaces old theory, thereby correcting flaws and explaining and predicting phenomena in the domain in which they apply" (Marquet et al. 2014, p. 701). However, accurate description does not necessarily imply understanding. We want to be emphatic on this point: Although specific, calibrated parameters may indeed improve the accuracy and precision of predictions, the basis of understanding and the fundamental logic of underlying causes do not depend on these features. Therefore, accurate description, although it is necessary, is not sufficient, because theories should explain and predict with as few assumptions and free parameters as possible in order to "yield a compressed description of the system or phenomenon under study, thereby reducing its complexity" (Marquet et al. 2015, p. 703). Furthermore, we claim that, for this compressed description to provide understanding, it should be based on first principles.

First principles increase understanding because they lead to a transparent, logical, and rigorous development of theory structure and to *a priori* predictions. Houlahan and colleagues claim that to base the development of theory on first principles is an unnecessary and potentially confusing criterion. We agree with Houlahan and colleagues in that the identification of first principles may not be easy in some situations. But difficulty should not deter theory development. We defined first principles as "quantitative law-like postulates about processes underlying a given class of phenomena in the natural world with well-established validity, both theoretical and empirical (i.e., core knowledge)" (Marquet et al. 2015, p. 703). Pauli's exclusion principle and the Arrhenius equation for the temperature dependency of reaction rates are examples of first principles in chemistry that satisfy this definition, the same as natural selection in biology. Indeed, the metabolic theory of ecology is based on evolutionary optimization of the physics of resource transport and the Arrhenius equation to yield predictions and understanding of several ecological phenomena. Furthermore, birth–death processes and stochasticity in neutral theories; the principle of maximum entropy as used in the maximum entropy theory of ecology; and mass–energy conservation and chemical stoichiometry, as used in optimal foraging and ecological stoichiometry theory, are all first principles that provide a foundation for theory. It is worth noting that most of the first principles above are not "ecological" per se but were discovered in chemistry, physics, and mathematics. The lack of appreciation of the role of first principles in ecological theory is probably due to the academic isolation fostered by disciplinary science. We claim that we need more a transdisciplinary science, one that embraces phenomena instead of disciplines and synthesis instead of reduction.

Kearney and colleagues make the point that the number of free parameters used to judge the efficiency of a theory in relation to an alternative one should be evaluated relative to the number of processes explained. We agree with this statement to the extent that the theory is based on first principles (as dynamic energy budget [DEB] is) and is prediction rich. We cannot engage here in a detailed accounting of how well DEB performs in terms of explaining and predicting in relation to its 14 parameters, nor of its relationship and comparison with the metabolic theory of ecology (MTE), although this could be a useful exercise to do and welcome the possibility that DEB might be more efficient than we previously thought.

We strongly believe that ecology would benefit by embracing the development of efficient theories based on logical articulations of first principles directed toward increasing our understanding of the natural world and fostering scientific unification. Articulating first principles is particularly important: Without them, there is only pure phenomenology, limited understanding, and isolation. With them comes deeper understanding, greater synthesis, the stimulus for bigger questions, and an appreciation for the value of transdisciplinarity and the unity of science.

We would like to end our letter by saying that, to a large extent, our article was motivated by the mounting dismissal of the value of theory in the biological sciences. This is particularly acute in systems biology and ecology, disciplines that are currently awash in data. The complexity of the ecological challenges that we face as a species requires our best effort to find efficient solutions based in understanding how nature works. And we think this can ultimately be achieved only by developing efficient theories based on underlying first principles.

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