assessment of theory that does not use the ability of the theory to predict independent observations as its foundation is fundamentally flawed. The most important criterion by which to judge a theory is how well its predictions match observations.

Some of the criteria proposed by Marquet and colleagues may have value, but two of the criteria—parsimony and that the theory be from first principles—would, we believe, be a deterrent to progress in ecology.

It is a mistake to suggest that simplicity has inherent value when, in fact, the entire value of simplicity and parsimony is practicality. Simplicity and parsimony have value because when using finite data to construct and test theory, parsimony, used systematically and rigorously, will often increase the probability of identifying the true underlying process, and when making predictions in an applied context, it may be useful to simplify the description of natural processes to lower the costs of acquiring the inputs necessary to make predictions. Both of these benefits arise from practical constraints—one imposed by limited data and the other by limited resources. There is no inherent value in choosing a simple theory that is far from the truth over a complex one that is close to it.

Theory from first principles is problematic because it restricts theory development by requiring an unnecessary and potentially confusing criterion: How should we define *first principles*? One formal definition is "a basic, foundational proposition or assumption that cannot be deduced from any other proposition or assumption" (Wikipedia contributors 2014). What are those propositions or assumptions in ecology that cannot be deduced from any other proposition? Marquet and colleagues imply in their discussion of optimal foraging theory that conservation of mass and energy is one first principle and that natural selection is another, and in their discussion of resource ratio theory, that resource supply and consumption are first principles, but it is not clear from these examples what the criteria are that qualify these processes as first principles. For almost all the examples provided by Marquet and colleagues, we were left attempting to identify the first principles of the theories that were designated as efficient and how the inefficient theories demonstrably did not include first principles. In fact, it appeared that most decisions about whether theories used or ignored first principles were relatively ad hoc. One valuable contribution that could be made in this regard is to define and identify ecological first principles. Before we can demand of ecologists that they develop theory from first principles, we must identify what those ecological first principles are.

Marquet and colleagues have suggested that ecologists need to do a better job of developing ecological theory and have provided a blueprint for constructing "efficient" theory. We agree with the identification of the problem and, in particular, that a proper balance between theory and data is needed—data without theory is description, and theory without data is storytelling. Understanding, the objective of all science, results from theory confronted by data. It is important to assess the current state of theory in ecology but not based on the six criteria provided by Marquet and colleagues. Rather, we must focus on *the* critical characteristic of a theory—how accurately and precisely it describes how the natural world works.

JEFF E. HOULAHAN
SHAWN T. MCKINNEY
RÉMY ROCHETTE

Jeff E. Houlahan (jeffhoul@unb.ca) and Rémy Rochette are affiliated with the Department of Biology at the University of New Brunswick, in Saint John, New Brunswick, Canada. Shawn T. McKinney is affiliated with the US Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, and with the Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine, in Orono.

References cited

Marquet PA, et al. 2014. On theory in ecology. BioScience 64: 701–710.

Scheiner SM. 2013. The ecological literature, an idea-free distribution. Ecology Letters 16: 1421–1423.

Wikipedia contributors. 2014. First principle. Wikipedia: The Free Encyclopedia. Wikimedia Foundation. (10 October 2014; *http://en.wikipedia.org/wiki/First_principle*)

doi:10.1093/biosci/biv014

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.

PABLO A. MARQUET, ANDREW P. ALLEN, JAMES H. BROWN, JENNIFER A. DUNNE, BRIAN J. ENQUIST, JAMES F. GILLOOLY, PATRICIA A. GOWATY, JOHN HARTE, STEVE P. HUBBELL, JORDAN G. OKIE, ANNETTE OSTLING, MARK RITCHIE, DAVID STORCH, AND GEOFFREY B. WEST

Pablo A. Marquet (pmarquet@bio.puc.cl) is affiliated with the Department of Ecology in the School of Biological Sciences, at the Pontifical Catholic University of Chile, in Santiago; the Institute of Ecology and Biodiversity, also in Santiago; the Santa Fe Institute, in Santa Fe, New Mexico; and the Instituto de Sistemas Complejos de Valparaíso, Chile. Andrew P. Allen is affiliated with the Department of Biological Sciences at Macquarie University, in Sydney, Australia. James H. Brown is affiliated with the Department of Biology at the University of New Mexico, in Albuquerque. Jennifer A. Dunne, Brian J. Enquist, and Geoffrey B. West are affiliated with the Santa Fe Institute; JAD is also affiliated with the Pacific Ecoinformatics and Computational Ecology Lab, in Berkeley, California; and BJE is also affiliated with the Department of Ecology and Evolutionary Biology at the University of Arizona, in Tucson. James F. Gillooly is affiliated with the Department of Biology at the University of Florida, in Gainesville. Patricia A. Gowaty and Steve P. Hubbell are affiliated with the Department of Ecology and Evolutionary Biology and the Institute of the Environment and Sustainability, at the University of California, Los Angeles, and with the Smithsonian Tropical Research Institute, in Panama City, Panama. John Harte is affiliated with the University of California, Berkeley. Jordan G. Okie is affiliated with the School of Earth and Space Exploration at Arizona State University, in Tempe. Annette Ostling is affiliated with the Department of Ecology and Evolutionary Biology at the University of Michigan, in Ann Arbor. Mark Ritchie is affiliated with the Department of Biology at Syracuse University, in Syracuse, New York. David Storch is affiliated with the Center for Theoretical Study and with the Department of Ecology, in the Faculty of Science, at Charles University, in Prague, Czech Republic.

Reference cited

Marquet PA, et al. On theory in ecology. BioScience 64: 701–710.

doi:10.1093/biosci/biv015

Copyright of BioScience is the property of Oxford University Press / USA and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.