Conservation Biology

Book Review

The time is ripe for general theory in community ecology

The Theory of Ecological Communities. Vellend, M. 2016. Princeton University Press, Princeton, NY, U.S.A. 229 pp. €50.00 (hardcover). ISBN 978-0- 691-16484-7.

Theory-Based Ecology: a Darwinian Approach. Pásztor, L., Z. Botta-Dukát, G. Magyar, T. Czárán, and G. Meszéna. 2016. Oxford University Press, Oxford, U.K. 301 pp. €45.99 (paperback). ISBN 978-0-19-957786-6.

The state in which the science of community ecology finds itself has been proclaimed a mess more than once. That such assertions might be hard to face for many of us working in that field is one thing; but to be fair, it is undeniable that the pure amount and disparity of different frameworks, concepts, and theories in community ecology, and underlying fields such as population ecology, are overwhelming and perplexing and do not seem to do justice to the scientific goal of providing a general theory of how populations, and consequently ecological communities, evolve and behave. Such a "real" theory should provide a system of axioms from which one can deduce consequences and should be both explicative (i.e., explaining observed patterns) and predictive (i.e., predicting results of situations not yet observed). In this sense, the theory should generate testable hypotheses. *The Theory of Ecological Communities* (Vellend) and *Theory-Based Ecology: a Darwinian Approach* (Pásztor et al.) attempt such a generalization, although in quite different ways.

Vellend does a tremendous job, and accomplishes for the field of community ecology what few have attempted, and even fewer, if any, have achieved. The volume puts together most (because all is impossible) of the separately treated community ecological theories and concepts and boils down the myriad of suggested and formalized processes connected to community ecology into 4 main underlying pillars, which Vellend calls "high-level processes": speciation, dispersal, drift, and selection. As he lays out in the introductory chapter, this idea is strongly based on similar concepts in population genetics and inspired by other authors who have perceived these conceptual parallels.

Although many ecologists will very probably disagree on the relevance and importance of the devised high-level processes, to synthesize community ecological theory as proposed in the book is a great and worthwhile achievement. Moreover, it is up to all community ecologists to prove whether any of the 4 high-level processes can be omitted and which ones are most important. However, this is not going to be an easy task. And, the book could be criticized for taking a big broom and sweeping all the separated, system-contiguous, and scale-dependent theories of community ecology under 4 big rugs, so that in the end the effort could have no effect on one's daily scientific work with one's pet system under one's pet theories. This would be a justified criticism but for the 3 chapters toward the end of the book in which Vellend presents existing empirical evidence on how high-level processes are shaping communities. This evidence is summarized in tables for each of the processes that contain potential caveats and challenges. Together with the last 2 chapters, in which the author provides his view on the what and why of future research in community ecology, approximately half the book is packed with ideas for testable hypotheses and predictions.

Given the density and complexity of the matter, it is astonishing that Vellend manages to communicate his ideas with an absolute minimum of mathematical formulizations (i.e., almost none). Instead, he provides computer code (in R language) to demonstrate the application of his 4 principles. With its overall plain language and clear prose, his book is excellent material for pre- and postgraduate students. For the first time, Vellend offers this target group a fair chance of grasping the complexity that is community ecology because he connects and synthesizes a mountain of seemingly unrelated concepts and theories. In this regard, the table in chapter 5 is an invaluable overview of theories in community ecology, new and old, and how they connect to the proposed high-level processes.

After so much praise, a few critical points also seem legitimate, although we emphasize these points do not take away from the overall positive impression this book made on us. Because it is concise and focuses on the necessary, the book cannot serve as a comprehensive introduction to all the reviewed theories. Although it is a great starting point, a reader not familiar with a particular theory will need to go to the original references (which are available in the reference list of the book and cited appropriately throughout the text). The review of the literature in chapters 8–10 is a subjective, narrative review, not a systematic one. Thus, probably every experienced reader will find some points to disagree with the author's statements and conclusions or will be unsatisfied by the effort made to review the literature concerning a specific point. Although we think the presented simulation

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models serve an excellent pedagogical purpose, their benefit comes with the cost that they are overly simplistic and their usefulness for supporting the proposed high-level processes is questionable. As a last point, and if just to show we are all mortals and mistakes happen, on page 149 the pairwise beta diversity is surely meant to increase with distance instead of "decline."

The second book, a collaborative effort by a group of Hungarian scholars, although bearing a similar title, couldn't be more different from Vellend's book in volume, content, and approach.

Pásztor et al. attempt to follow a deductive approach that is strictly based on Darwinian principles. It starts with 7 such principles and builds a mathematically formulated theory around them. These 7 general principles are exponential growth; growth regulation; inherited individual differences; finiteness; survival of the fittest and competitive exclusion; robust coexistence; and constraints and trade-offs. There are some obvious similarities between these principles and Vellend's high-level processes. For example, inherited individual differences correspond well to Vellend's speciation and finiteness to ecological drift. Because the basic ideas of Vellend's theory were published in an earlier review (Vellend 2010), Pásztor et al. were able to show this equivalence in their book.

We found the construction of the theory quite logical: all organisms could grow exponentially, but because Earth is not covered by mountain-high stacks of organisms, there must be some limiting factors that result in negative feedbacks. Subsequently, the theory is developed to show which regulating forces will operate and which organisms will be successful. Because their theory is mathematically formulated, the authors were able to incorporate many well-known models of theoretical ecology (e.g., Lotka–Volterra models and their modifications). The book thus also serves as a reference for various models of theoretical ecology. Because of its approach, fewer theories are covered, but these are much more rigorously described than in Vellend's book. Also, Vellend concentrates mostly on "horizontal" communities (i.e., communities of organisms on the same trophic level), whereas Pásztor et al. include trophic interactions.

Regarding the use of mathematics, the difference is striking. Vellend avoids math as much as possible; Pásztor et al. formulate their theory in terms of mathematical models through (mostly) differential equations. As a consequence, the readership of Pásztor et al. probably will be constrained to (mostly graduate) students and researchers with sufficient mathematical literacy or at least to those willing to acquire such literacy while reading the book. (We sincerely hope the mathematical literacy of students entering universities will increase, but we fear this is not a realistic hope.) Nevertheless, we believe the book is more accessible than its cover might suggest, on which fragments of partial differential equations threateningly loom. We found (most of) the book reasonably accessible even with our biological knowledge of mathematics. It will help the mathematically challenged that most of the math is confined to so-called TBoxes – readers not sufficiently fit to understand all the derivations can easily skip the mathematically explicit parts. In addition to these TBoxes, the authors fence off text into other boxes called "notes" and "warnings," which keep the main text flowing and provide pertinent details. These boxes contain discussion and demonstrate some caveats and misconceptions, although sometimes in a rather rigorous and authoritative style (e.g., Note 7.1).

One of the challenges (not always sufficiently appreciated) when compiling results from published sources is to unify the use of the various types of logarithm (natural vs. decadic) and their corresponding names and to consistently follow a single convention throughout the book. The authors apparently attempted to distinguish the decadic and natural logarithm by using log and ln, respectively. In Figs. 3.6, 3.7, and 5.1, the log and ln notation seems to follow this European convention. In Fig. 10.4 (redrawn from an American journal), however, log stands for natural logarithm. Of course, the main message is not changed, but for experimenters, the values are immediately suspicious because they suggest nearly 6 orders of magnitude variation in fitness. (As a matter of fact, it took some detective work to trace the original data, and only a comparison of the very first use of these data in Europe [*Oecologia*] with their use in a review published in *American Journal of Botany* gave resolution.)

After reading about these 2 books, let's now turn back to the initial question. Is it possible (and desirable) to build a general ecological theory? Attempts to build such theory, or to at least provide some unifying principles, are not new. Both books have the word *theory* in their titles, and both accept the challenge to build a framework that can be considered a scientific theory. Although only Vellend's book title includes *community*, the realm of both books is rather similar, that is, what one would call community ecology, which, in a sense, includes population ecology (more so in Pásztor et al. than in Vellend). In both books, the basic unit of the theory is an individual, showing that communities may be understood better as systems of interacting individuals (belonging to different species) than a system of interacting populations. It seems that the development of general theory in the last half century shifted from a holistic approach (e.g., Margalef 1963) to populations (e.g., theory of island biogeography [MacArthur & Wilson 1967]) and from there to individuals (Hubbell's [2001] neutral theory and the present books). Nevertheless, we should be fair to the old theories and concepts – they are not as unrealistic as it might seem from their new presentations. Many textbooks (and even some of our own presentations) include pictures comparing Clements's (1916) superorganism with Gleason's (1926) individualistic hypothesis – similar to Vellend's Fig. 3.1. However, we believe Clements never drew such a picture and would probably think his hypothesis is misrepresented. Compare Vellend's Fig 3.1a with Clements' (1916) Fig. 4, where Clements shows a considerably wider overlap of whole communities and does not show anything for individual species. So, although we were not able to trace where such figures were used first, we believe these are later interpretations of Clements' ideas. To build a rigorous theory, the formulation of assumptions in terms of mathematical equations is instrumental. However, we should be aware that such translations do not necessarily reflect exactly the ideas of the original author. It seems this might be the case with several critical points in Pásztor et al.'s book (e.g., their treatment of the relationship between competition intensity and productivity).

Both books nicely demonstrate that a good ecological theory must be based on Darwinian principles, but they also show the usefulness of such a theory for empirical ecological research by laying down a series of ideas that field and experimental ecologists might test in their work. In particular, Vellend provides testable hypotheses (including overviews of their empirical support) – almost ready-made templates for use in one's next research proposal. We look forward to seeing the research that both of the books certainly will stimulate.

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