

## Community ecology made easy

**Mark Vellend: *The theory of ecological communities*. Princeton: Princeton University Press, 2016, xix+229pp, US\$50HB**

**Max W. Dresow<sup>1</sup> · Jake J. Grossman<sup>2</sup>**

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Reflecting on the state of community ecology, John Lawton rendered a famously uncharitable verdict. Community ecology “is a mess,” riddled with “so much contingency that useful generalisations are hard to find” (Lawton 1999, 178). Nearly two decades later, the field presents a similar aspect. Community ecology is “widely perceived as...a theoretical and conceptual bucket case,” Mark Vellend observes (42). Over the past century, its practitioners have devised literally hundreds of conceptual and theoretical models intended to explain patterns of diversity, abundance, and composition in ecological communities. However, because nearly all these models are “relevant to at least one type of community somewhere on earth, the list of explanations ... only ever gets longer, never shorter” (2). Vellend’s new book, *The Theory of Ecological Communities*, sets out to reframe this tangle of models in a way that highlights linkages between various extant theoretical ideas. In it, he brings together diverse empirical and theoretical traditions in an unprecedented, engaging, and productive manner.

Vellend’s book consists of four sections: a primer of ideas in community ecology, a formal elaboration of the theory of ecological communities (ToEC), an application of the theory to key empirical questions, and a meditation on future directions. In the first section, Vellend sets the ambit for his consideration of community ecology and deftly explores how ecologists go about studying ecological communities. He begins by articulating the concept of a *horizontal ecological community*: “a set of species sharing common needs in terms of resources or space” (11). In the ToEC, communities are sets of locally occurring

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✉ Max W. Dresow  
dreso004@umn.edu  
Jake J. Grossman  
gross679@umn.edu

<sup>1</sup> Department of Philosophy, University of Minnesota, Minneapolis, MN, USA

<sup>2</sup> Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, USA

species belonging to the same taxon or sharing the same trophic level. Hence, all the plants in a meadow belong to a community, but their pollinators, predators, fungal symbionts, and avian seed dispersers do not. Vellend's proposed synthesis of preexisting theory in community ecology hinges on this restricted definition. The ToEC applies only weakly to communities spanning multiple trophic levels. Yet some readers may be unsatisfied with a view of the field that downplays investigations spanning trophic levels, for instance, relationships between hosts and symbionts, or predators and prey.

In the remainder of the section, Vellend unpacks some important concepts like abundance, diversity, and scale, and attempts an explanation of the field's theoretical predicament. He observes that community ecology was washed, during the twentieth century, by three "overlapping waves of enthusiasm for a particular phenomenon, process, or approach" (32). First came models based on interspecific competition, which were met with a pair of criticisms: that many communities are more strongly structured by predation than by competition, and "that the real world should not be expected to look like the equilibrium solution to a simple model" (34). This led to the initiation of three lines of research: the use of null models to assess whether patterns can arise in the absence of competition, "patch dynamics," which concerns the causes and consequences of spatial heterogeneity, and a renewed emphasis on field experiments to test for particular mechanisms. Eventually, the second wave broke and a reaction set in whose watchword was "spatial ecology." But the third wave, which called for a renewed emphasis on processes occurring at regional scales, did not clear away what came before. Instead, it muddied the waters further, frustrating those still hoping for a unified theory of community dynamics.

In the second section, Vellend presents the ToEC and sketches its connections to existing ecological theory and practice. The gist of the theory is that all dynamics in horizontal ecological communities owe to four "high-level processes," which comprise a logically complete set of processes capable of influencing dynamics. These high-level processes are analogs of the "big four" processes in population genetics, mutation, migration, drift, and selection, namely: speciation, dispersal, drift, and selection. It is a tribute to Vellend's adaptation that readers with an introductory biological background will have no trouble grasping the basics of this framework. In community ecology, species play the role of alleles in population genetics. Speciation increases diversity à la mutation and indeed integrates mutation over larger temporal and genomic scales. Dispersal operates like migration and leads to increased diversity in sink communities. Drift adds a random component to community dynamics and menaces populations at low abundance. Finally, selection is represented by any process that deterministically alters the contribution of a species to the community's demographics, whether positively or negatively.

These high-level processes are instantiated by many low-level mechanisms (the traditional focus of community ecology), but ecologists can work profitably at either level. For instance, a warming climate may alter community diversity through direct effects, with hotter temperatures favoring some species over others, or indirect effects, with heat-loving pathogens becoming increasingly abundant. But these low-level processes can all be understood as instances of selection. Indeed, selection

plays an outsized role in the ToEC because its constituent mechanisms dominate the traditional foci of community ecology; witness the theories of competitive exclusion, resource limitation ( $R^*$ ), enemy-mediated coexistence, Janzen–Connell effects, ecological niches, and multiple stable states. An early indicator of the promise of Vellend’s theory unfolds across the four pages (63–66) in which he describes these and other theories in terms of one or more high-level processes. He concludes Section 2 with an accessible chapter that guides the reader through an exploration of the ToEC in the R programming language.

The book’s third section serves to validate the ToEC by applying it to seven open hypotheses in community ecology. Examples include: “Ecological drift is an important determinant of community structure and dynamics” (drift; 138) and “Spatial variation in species diversity has been generated by spatial variation in speciation rates” (speciation; 162). For each hypothesis, Vellend presents several subsidiary predictions, describes the methods used to test these predictions, and summarizes empirical results from the last century of ecological research. The book concludes with a somewhat miscellaneous section, in which Vellend reflects on the distinction between “process-first” and “pattern-first” approaches to community ecology (177–179) and notes a few domains of horizontal community ecology that resist incorporation into the ToEC, e.g., the “maximum entropy theory of ecology” (180).

Vellend’s formulation of the ToEC has already contributed to the teaching of ecology. Since its original (Vellend 2010) publication in the *Quarterly Review of Biology* in 2010, the ToEC has been widely incorporated into syllabi for both general and community ecology courses. For instructors, including one of us (JJG), the theory provides an accessible entry into a complex literature. The four high-level processes are easy for students, most of whom have studied population genetics, to grasp. And after introducing the ToEC, instructors can refer back to these processes in teaching, for instance, the niche versus neutrality debate or island biogeography. Critically, the ToEC provides what most community ecology syllabi lack: a unifying, memorable, and relatively simple story or framework that can organize the myriad models, empirical data, and natural history knowledge that emerge in the teaching of ecology.

Vellend’s book will not just interest ecologists and educators. In addition, several parts of the ToEC will be of interest to philosophers. In the second and third sections, Vellend engages ongoing debates about the status of generalizations in ecology. But instead of getting bogged down in familiar concerns about nomotheticity, he focuses on two ways that ecologists seek generality. The “pattern-first” approach begins by characterizing patterns in nature and proceeds to infer their causation. However, since most patterns can be generated by multiple causal processes, this approach yields little general knowledge about process–pattern connections in Vellend’s view, the central intellectual challenge of community ecology. More promising is the “process-first” approach, which asks “what processes or mechanisms can cause community properties to change over space and time?” (40). This avoids asking patterns to arbitrate between causes, and therefore avoids the many-to-one problem; yet it has heretofore failed to yield a coherent body of general theory. Vellend suggests that this is because ecologists

have taken for granted that the relevant processes are low-level mechanisms like disturbance, predation, and competition. High-level processes provide the missing link “between low-level factors and the patterns we observe in nature” (178). However, Vellend goes on to observe that neither the process-first nor the pattern-first approach can be deemed “objectively better” than the other (177). Community ecologists have a variety of goals and pursue a variety of generalizations in order to achieve them. This suggests that philosophers should attend to the distinct inferential and explanatory roles generalizations play in ecology, and avoid stipulating which kinds of generalizations are “really” worth having, e.g., laws of nature.

## References

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