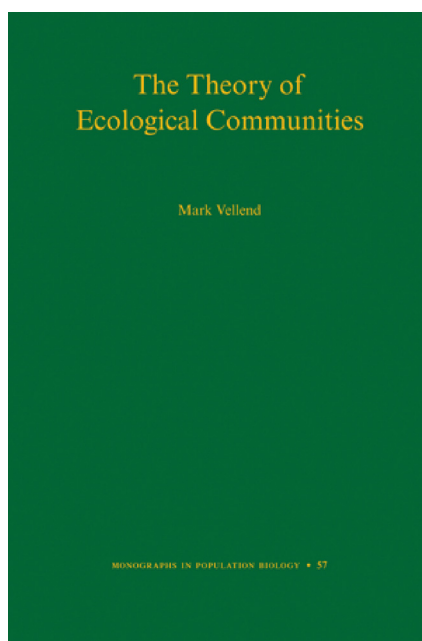


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## Book Review

# Putting Community Ecology in a Better Order

Madhav P. Thakur<sup>1,2,\*</sup>



In 1986, Thomas W. Schoener wrote a thought-provoking book chapter describing ecological communities along five organismal and five environmental axes [1]. It was thought-provoking in the sense that Schoener attempted to unify community ecology using a minimal set of variables at a time when ecologists were doubtful of any unifying principle in community ecology [2]. After three decades of Schoener's chapter, community ecologists are still divided about whether there could be a general theory of community ecology [2,3]. Mark Vellend elegantly attempts to bridge this divide by introducing the theory of high-level processes in ecological communities in his Princeton Population Monograph entitled *The Theory of Ecological Communities*. His theory of ecological communities is largely drawn from the four fundamental principles of population genetics: selection, drift, mutation, and gene flow. He replaces mutation and gene flow by speciation and dispersal respectively, and advocates that the four high-level processes (selection, drift, speciation, and dispersal) are universally present across ecological communities in any environment.

Vellend's book can broadly be divided into two parts: the first part (chapters 1–5) lays a conceptual foundation of high-level and low-level processes and the underlying relations between them. The second part

(chapters 7–10) consists of empirical evidence for each of the four high-level processes across a wide variety of ecological communities. One chapter in the book (chapter 6) is dedicated to simulating ecological communities using R programming software. Vellend concludes his book (chapters 11 and 12) with recommendations on how his theory could unify community ecology.

Vellend argues that the patterns observed in ecological communities (e.g., species–area relations, diversity–productivity relations, disturbance–diversity relations, etc.) are a consequence of a plethora of low-level and high-level processes. Low-level processes in ecological communities may range from competition between species in the same trophic group, to predator–prey or host–pathogen interactions, to trait–environment relationships. The structure and function of a given ecological community are likely to be driven by a given set of low-level processes, which often differ among ecological communities (Figure 1). By contrast, Vellend highlights that the four high-level processes are always present in any ecological community, and are fundamental drivers of community structure and function. For instance, speciation and dispersal are the high-level processes which will always play a crucial role in determining the number of species in a community. It is, however, possible that the relative importance



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Figure 1. A Conceptual Figure To Depict Vellend's Theory of Ecological Communities. The blue part of the circle represents the four high-level processes and the orange part represents the low-level processes. All three communities in the figure are subject to the four high-level processes; however, the relative roles of these processes can differ among communities. Numerous low-level processes are present in every community, but a given set of low-level processes in one community may not be present in another community.

of the four high-level processes may vary across ecological communities (Figure 1). Vellend advocates that modern community ecology should delve into investigating the relative contributions of these four high-level processes across ecological communities.

Is Vellend's theory new? Vellend acknowledges that most of his ideas are already part of past and present community ecology research. He provides an exhaustive list of how most extant ecological theories/models incorporate the four high-level processes (Table 5 in the book). Take 'selection', for example. Vellend outlines 22 of 24 commonly used ecological theories that are partly or entirely based on variation in selection pressure on species owing to differences in their reproductive ability, ability to escape predation, ability to thrive in a low-resource environment, or ability to acquire greater number of mutualists. Vellend maintains that, despite of obviousness of the four high-level processes, greater awareness of their presence may enhance the ability of ecologists to explain the observed ecological patterns.

Will Vellend's theory unify community ecology? This is a difficult question, and the success of Vellend's theory may only be assessed in the years to come. Unifying community ecology is a daunting task [2]. This is mainly because most ecologists measure low-level processes, whereas high-level processes are often difficult to directly measure. Further, ecology has been advocated more as a puzzle-solving discipline than as a system-building discipline (in contrast to physics) [4]. Every ecological puzzle is unique, and thus special rather than general rules have been more successful in ecological research [2]. Perhaps the omnipresent context-dependent results in community ecology could be better understood if examined through a combination of low- and high-level processes. Vellend's book is certainly a push in this direction.

### Acknowledgments

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<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

<sup>2</sup>Institute of Biology, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany

\*Correspondence: [madhav.thakur@idiv.de](mailto:madhav.thakur@idiv.de) (M.P. Thakur). <http://dx.doi.org/10.1016/j.tree.2016.10.015>

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## Letter

### How Species Boundaries Are Determined: A Response to Alexander *et al.*

Mark Westoby,<sup>1,\*</sup>  
Georges Kunstler,<sup>2</sup>  
Michelle L. Leishman,<sup>1</sup> and  
John Morgan<sup>3</sup>

Alexander *et al.* [1] made two really important points about species range boundaries. First, we still know very little about which boundaries are set by competition rather than by direct effects of temperature or other environmental variables. Second, reliable knowledge about this can come only from field experiments, transplanting species beyond the boundary, with and without exclusion of competitors. When competition is confounded with climate, correlative analyses are not able to resolve the causation.

Among the thousands of field experiments on competition since the 1960s, rather few have been beyond a boundary [2]. This is quite surprising. Connell's seminal barnacle experiment was a transplant beyond the boundary [3]. Krebs's widely-adopted textbook *Ecology* [4] was subtitled 'the experimental analysis of distribution and abundance'. Chapters 2 to 8 proceed through a logical sequence (indeed there is a logic diagram on page 16). Introductions beyond the boundary alone, without manipulating other factors, test whether the species has been unable to disperse there up to the present. Then there follow introductions with different factors manipulated, notably with and without exclusion of competitors or predators. So the importance of field transplants beyond boundaries has been very clearly understood for 50 years. It is true that such experiments can be difficult and labour-intensive and prone to field accidents. Nevertheless, they are surely the essential reality-test for species distribution models, and ecology as a discipline over the past 50 years has somehow failed to accumulate enough of them to make strong generalisations.

How can the global research community now acquire reliable knowledge about boundaries as briskly as possible? If we rely on chance decisions by individual research groups to undertake experiments, it might take several more decades before we have a well-founded overview. Can we collaborate to target experiments in such a way as to arrive at generalizations across species-types and boundary-types as efficiently as possible?

Ideally experiments would yield an assessment of the most important working hypotheses. We can suggest three to begin with. (We are thinking mainly about land plant species, as also were Alexander *et al.*)

- (i) Species boundaries are likely to be determined by competition when travelling in the direction of higher leaf area index or taller vegetation canopy (e.g.,