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Multiplicity in Unity: Plant Subindividual Variation and Interactions with Animals

Author: Wardle, David A.

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SUBINDIVIDUAL PLANT TRAIT VARIATION MATTERS

Multiplicity in Unity: Plant Subindividual Variation and Interactions with Animals. Carlos M. Herrera. University of Chicago, 2009. 437 pp., illus. $40.00. (ISBN: 9780226327945).

Any ecologist working with plant communities will soon encounter the variability of plant organ traits at the within-individual level. Sun and shade leaves produced by the same tree often differ conspicuously in size, shape, and toughness. Foliage produced by juveniles and adults of the same plant species can differ greatly in their palatability to herbivores, as well as in the traits that cause palatability. Individual plants may produce flowers of contrasting characteristics to attract a wider spectrum of pollinating organisms. In these and numerous other cases, the occurrence and adaptive significance of within-species organ-trait variability is immediately apparent, yet many ecophysiologists and community and ecosystem ecologists largely ignore this variation, regarding it simply as unwelcome noise. For example, much work on plant-trait variation over the past 40 years, including its latest incarnation as the "leaf economics spectrum," has been preoccupied with characterizing differences among species (see Whitfield 2006). This work has often represented key functional traits of a whole species by single values, with variability of leaf trait values within species or individuals often ignored. As such, recent and rapidly growing global plant-trait databases all but ignore subindividual variability. Serious recognition in the functional plant-traits literature that even within-species (let alone within-individual) variability of traits might be important has come about only very recently (e.g., Albert et al. 2010, Hulshof and Swenson 2010).

Multiplicity in Unity: Plant Subindividual Variation and Interactions with Animals, by Carlos N. Herrera, is the only substantial book in existence whose primary focus is the within-individual trait variability of plant organs. Herrera, a professor at Estación Biológica de Doñana in Seville, Spain, has published extensively on plant reproductive and evolutionary biology, notably in relation to pollination and frugivory. Perhaps unsurprisingly, this book draws heavily on that literature, although the scope of *Multiplicity in Unity* is considerably wider than this, and is of great relevance for a much broader range of ecologists than just those who work on plant reproduction. The message of the book is simple: Within-individual trait variability of plant organs—leaves, inflorescences, or fruits—can be considerable and of high ecological and evolutionary significance. As the author asks in the prologue, "Could there be…some interesting biology hidden behind the familiar nuisance of within-plant variance, routinely brushed under the rug of the mean?" (p. viii).

The book (excluding the introduction) consists of nine chapters that can be classified into four parts. The first part (containing chapters 2–4) characterizes the degree to which subindividual trait variation occurs in different organs with determinate growth (leaves, flowers, fruits, and seeds); other aboveground organs and all belowground structures are not considered. These three chapters collectively synthesize a vast amount of literature, alongside additional analyses, to highlight the magnitude and extent of variation across time and space (for example, across gradients within a single plant). The second part (chapters 5–7) then explores the source of this within-plant variation, including underlying ontogenic and genetic mechanisms. Here, Herrera provides compelling and recurrent evidence to show that, far from being unwanted or meaningless noise, within-plant variation is an important ecological attribute driven by plausible underlying mechanisms. At this point, any reader who has focused on the extensive array of examples presented by the author should have little doubt that within-plant variation is real, widespread, and ecologically meaningful.

The third part (chapters 8 and 9) considers the ecological consequences of within-species trait variation, both for herbivores and for the fitness of the plant itself. The chapter on herbivores synthesizes the literature linking animal behavioral responses and selectivity to within-individual variability of plant reproductive structures and leaves, as well as associated costs and benefits for herbivores. This chapter in particular is an important overview that should be of great interest to anyone who has worked in the vast field of plant-herbivore interactions. The chapter on fitness consequences makes the case that subindividual variation in plant organs may have important consequences for both plant growth and fecundity, further reinforcing Herrera's message that within-species variation is ecologically meaningful. This leads logically into the fourth section (chapter 10), which reassures us that this ecologically meaningful variation even has an evolutionary basis that can be driven and maintained by selection as well as plant-animal interactions.

Herrera's focus on plant reproductive and evolutionary biology is apparent throughout the book. There are, of course, a range of other branches of ecology in which the issue of subindividual trait variation is also highly relevant but that receive either fleeting or no attention from the author; for example, ecosystem processes, plant defenses, and the many plant community processes that drive vegetation composition.

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It would be easy to criticize the book for this but unfair to do so; the author has provided a unique synthesis of an important issue that many ecologists ignore or overlook, and draws on a body of literature from a field that he clearly knows very well. It is then up to those readers working in other fields to consider how the ideas and issues raised in the book might be relevant to their own areas of interest. *Multiplicity in Unity* deserves to be read by a wide cross section of ecologists, and herein lies my only real niggle about the book. It is written in a style that would no doubt appeal to other plant evolutionary and reproductive biologists, but nonspecialists who would also benefit from reading it might find parts of the book densely written and heavy going; some paragraphs are more than 1.5 pages long. Further, chapter summaries appear at the ends of some chapters but not others, making it difficult to derive a take-home message from some chapters without giving them a thorough reading.

Although *Multiplicity in Unity* was not written explicitly for the growing number of ecologists who study plant functional traits, this subset of the ecological community would particularly benefit from the information in this book. This field has seen some truly pioneering work in the 1970s and 1980s (e.g., Grime 1979), but in the last few years it has become particularly crowded (as in any field for which a few earlier publications have enjoyed a high profile), and fewer truly major conceptual advances are now emerging. As work in this field has taken almost entirely an across-species focus, one significant way forward would be to explicitly recognize that there can be huge plasticity in functional traits both among and across individuals within the same species, and that this variability may itself have considerable functional significance in driving community and ecosystem processes. As such, *Multiplicity in Unity* should be required reading for anyone involved in studying plant functional traits, and particularly those who develop and use plant-trait databases. At a broader level, this book would be a most useful bookshelf addition for anyone interested in the study of variability in plant ecology, including those who work on very different systems and questions to those explored by the author.

DAVID A. WARDLE
David A. Wardle (david.wardle@svek.slu.se) is professor of plant and soil ecology at the Department of Forest Ecology and Management at the Swedish University of Agricultural Sciences.

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