

## Resource Strategies of Wild Plants

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studies carried out by very experienced scientists dedicated to advancing urban ecological studies in a rigorous manner. The book accurately reflects the multiple personalities inherent in an extraordinarily multidisciplinary field of study that is experiencing a rapid upsurge in public interest. At the same time it offers perspectives for implementing frameworks that would enable a comparative approach for tying together the range of work considered.

*Ecology of Cities and Towns* cogently defines many of the philosophical issues confronting scientists in structuring urban ecology studies and breaks the inertia created by entrenched perspectives, making it an excellent addition to any library. The work presented will surely influence future directions in the field.

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### WANTED: A GENERAL AND PREDICTIVE THEORY FOR TRAIT-BASED PLANT ECOLOGY

**Resource Strategies of Wild Plants.** Joseph M. Craine. Princeton University Press, 2009. 352 pp., illus. \$45.00 (ISBN 9780691139128 paper).

We are currently in the midst of an exciting new synthesis between plant physiology, evolutionary biology, and community and ecosystem ecology. In plant ecology, many older ideas and debates that seem to have left the field scattered and mired in controversy have been recast and focused around a trait-based plant science. There is hope that new analytical tools, phylogenies, large data sets, and recent insights in linking traits with ecosystems will enable plant ecology to

become a more synthetic and predictive science. Arguably, a central aspect of this synthesis is a renewed interest in measuring traits and understanding plant strategies in different environments—a foundation that has long been part of plant ecology and is now heralded as its central paradigm (Westoby and Wright 2006).

Joseph M. Craine is a research professor at Kansas State University. In his book *Resource Strategies of Wild Plants*, he presents a scholarly overview of the building of a trait-based plant ecology. The book is a hybrid academic saga and scholarly text explaining how, since the 1970s, plant ecologists have tried to make sense of the enormous diversity of seed plants. The book is well written and fascinating. Craine focuses on the concept of plant strategies as central to the problem of understanding diversity and for linking pattern and process in ecology and evolution. The antagonist of the story is natural selection. Specifically, how has selection shaped functional diversity in different environments? According to Craine, a plant strategy is a reflection of functional convergence, and the goal of plant ecology is to identify the main strategies that characterize different environ-



ments. Specifically, strategies “are sets of traits that lead to successful growth and reproduction in a particular environment.” The fundamental assumption is that because of trade-offs, “traits that lead to success in one environment do not lead to success in another environment.” Thus, understanding how

traits vary with the environment and with each other is the basis of a search for plant resource strategies as well as a potential means of addressing how climate change will influence ecosystem function.

In the first part of *Resource Strategies*, Craine introduces the concept of plant strategies by following its historical development. The protagonists of this academic story are ecologists Philip Grime, Terry Chapin, and David Tilman. Craine compares and contrasts the similarities and differences of their work as well as the debates and insights that emerged from it. Rather than saying who was more wrong or right, his goal is to set straight the historical record that underlies our modern understanding of plant strategies. Along the way he points out how our understanding of plant competition has changed and how differing types of resource limitation influence selection of plant traits.

Although I found the first half of the book interesting, most of the second half follows a more laborious bearing. Here, Craine leads us on a long slog through past and current literature. The approach is detailed and at times overly narrow, but in the end, Craine provides some new empirical patterns and summarizes the key traits that characterize plants in different environments (low nutrient, high nutrient, low light, low water, etc.). Along the way, he also notes which ideas of Chapin, Tilman, and Grime have survived.

Clearly, any attempt to synthesize a rapidly growing field will not cover all bases or appease everyone. And although I thoroughly enjoyed this book, I found many of its central goals and arguments to be not entirely realized, and the book's logic at times was not clear. First, despite giving the impression that he intended to provide an unbiased overview, by the end Craine does significantly inject his own opinions. This is certainly reasonable, but it leads to a somewhat colored and sectarian perspective on trait-based ecology. For example, a significant fraction of the book is focused on nitrogen limitation as the primary constraint shaping

plant strategies. Most of the featured research is from grasslands (which is understandable in the light of Craine's research focus). Studies on trees, tropical forests, and any broad comparative life history study across life forms, however, are barely mentioned. Despite the fact that minimum temperatures and water limitation (water balance) are arguably the central constraints that have shaped the evolution of land plants, the role of temperature, water, and hydraulic architecture is given relatively little attention.

Further, Craine seems to take a more postmodern view of science. Despite the author's claims in the introduction, model testing is not a part of this book. I found this frustrating, as it leaves the reader with an "all views are equally valid" approach to science (e.g., "In the end, no combination of theoretical or empirical research is enough [as there is no] way to reject [Tilman's] hypothesis" [p. 116]). This approach does not clarify and clearly point a way forward.

At the end of the book, in summarizing the literature, Craine concludes that all seed-plant diversity can be collapsed onto four central resource strategy axes: strategies for (1) low nutrients, (2) low light, (3) low water, and (4) low CO<sub>2</sub>—with modifications for increases in resource supply. I was looking forward to something more insightful, as these proposed strategies seem rather obvious. Further, it is unclear how Craine's synthesis advances us beyond Phillip Grime's original scheme (1977) or Mark Westoby's (1998) more recent classification (not cited by Craine). Each approach is also based on plant life histories and traits.

*Resource Strategies of Wild Plants* also focuses and relies almost entirely on empirical correlations and experiments. Theory and quantitative arguments do not drive Craine's synthesis and he does not give even one equation. The units of the traits mentioned throughout the book are surprisingly hard to find. All of this points to the fact that trait-based plant ecology has been largely driven by observations, verbal arguments,

and correlations, and is not based on testing, refining, and proposing novel predictive theories. Craine's synthesis, while mentioning the role of theory in driving the work of Tilman, is more inclined to count published empirical and experimental studies as if they were votes. I find this unfortunate, as there is a critical need for theory to help guide the explosion of trait-based data collection and to organize the rapidly developing ideas underlying trait-based plant ecology.

Several research areas are also conspicuously missing from the book—areas that will undoubtedly assist in defining and synthesizing plant resource strategies. For example, the central role of plant size (allometry) in understanding plant performance and trait variation is absent. Although variation in relative growth rate (RGR) and patterns of allocation to roots, stems, and leaves are central to Craine's identification of resource strategies, the well-attested primary role of plant size in driving these differences is not mentioned. Many of the differences in strategy listed by Craine may well be caused by simple differences in plant size. Indeed, many of the key traits listed by Craine as influencing ecology and ecosystems (RGR, organ allocation, surface-to-mass ratios, tissue density, specific leaf area, rates of gas exchange, etc., as well as plant size) are ones that I and others have shown to be mechanistically linked through metabolic scaling theory (Enquist et al. 2007, McCarthy and Enquist 2007). Further, despite the obvious link between plant strategies and life history, there is little reference to life-history theory.

Lastly, I find it interesting that the concept of a "resource strategy" (defined by trait convergence) seems to be in conflict with a niche-based view of diversity. Craine does not really cover in much detail species coexistence, species interactions (other than competition), or the fact that, in contrast to the resource strategy concept, classical niche-based theory emphasizes trait divergence. Indeed, many of the functional traits covered in this book have been shown to express as much variation within a

given environment as there is among environments—suggesting that biotic interactions may be more important in driving functional diversity than resource strategies are in limiting trait diversity. These differing views present a paradox for trait-based ecology and need to be reconciled.

Despite my hesitation about aspects of Craine's arguments, *Resource Strategies of Wild Plants* is a significant contribution. Because the ideas are broad, they will appeal to anyone interested in the historical development of ecology and plant functional biology. Further, because of Craine's easy writing style and clear, scholarly approach, as well as the treasure trove of ideas and references presented, I enthusiastically recommend this book to new graduate students interested in plant ecology. *Resource Strategies of Wild Plants* is a must read for any plant ecologist or physiologist interested in synthesis in the plant sciences. It will provoke spirited discussion and spur new ideas that will undoubtedly help propel the current trait-based renaissance in plant ecology.

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