

Ellison and Gotelli, Scaling *Sarracenia*: Ecology of a Model System

1. What are the purposes, main arguments and conclusions of the manuscript:

The purpose of the manuscript is to consider, and explore major ecological concepts through the lens of (extensive study of) a single ecosystem – the ecosystem associated with the pitcher plant *Sarracenia*. The book is not just about this amazing ecosystem and all that ecologists have learned about it. (Though that alone would interest many ecologists). This book is really about our current understanding of major ecological processes, and how they operate across scales.

The book argues that there is a place for model systems in ecological research and thinking, and that careful study of them can teach us much about nature. Additionally, the book argues that integrating observations and concepts across scales is essential to a fuller understanding of nature and how it changes.

The book concludes that *Sarracenia* does provide a scalable model for ecological systems, and that it has provided useful and important support for, examples of and challenges to ecological concepts.

2. Is it a significant contribution to the field? Why?

I consider this book to be an important contribution to the field of ecology for several reasons. It is a rare and complete synthesis of research and observations on a single study system, and through this system, major themes and theories in ecology are visited, considered and exemplified. The second significant contribution of the book is that it is a superb example of ecological thinking that blends theory and empiricism. We desperately need strong examples of this approach, and this book is written in such a clear and engaging prose that I believe this message will reach many ecologists.

The manuscript does present new analysis (the trait analyses in section II, the SDM and population growth analyses in section III, etc). It also offers a synthesis of concepts and analyses that is unique in its conceptual and methodological breadth while remaining focused on a single experimental system. Few authors can offer such a deep and broad walk through ecological ideas, and these two have (once again) proved to be excellent docents and guides to important concepts and an ecosystem that may be unfamiliar to many readers. Even though pitcher plants may be unfamiliar, their introduction in the context of general ecological problems and concepts makes them immediately familiar.

3. To what extent will it be useful to readers outside the main field of scholarship or to general readers?

I think this book would provide a rich introduction to ecological science and thinking for any reader. I think the authors are correct when they state that they are lucky to be working with such a charismatic organism, and I think the organism's charisma could carry their message of ecological thinking to a wide audience. That said, I'm not sure that the title will be sufficiently inviting to ecologists. For some reason, the idea of reading a book about a single species might not make a book rise to the top of the to do list. I do hope readers pick up this book, I think they would find it engaging and interesting.

4. Is the scholarship sound?

Yes, absolutely, references are comprehensive throughout and general – not restricted to the *Sarracenia* literature. This is yet another aspect of this book that is useful for ecologists and students – it is a guide to the general literature on important ecological concepts, from nutrient limitation to food web theory.

5. Is the content effectively organized? Is it well written.

The book is extremely clear and well written, and the organization is generally sensible and clear. The authors have made excellent use of headings and subheadings.

Overall (as noted below in my chapter by chapter comments) I have mixed reviews of the overall structure of sections comprised of a general chapter, a 'small world' chapter and then a scaling up chapter. The strengths of this approach is that it's creative and new (to me), it gives adequate space to the general concepts. Those general chapters are excellent texts and references on their chosen topic. The weaknesses (more severe in some sections than others, as noted below) is that the reader can get lost in the first chapter of each section without knowing how it will connect to the data and analyses to come in subsequent chapters. On balance, I don't have a clear recommendation. I think it could be ok to stick with the structure and improve it by adding signposting and roadmaps early on. Alternatively, a more concise structure in which the concepts and examples are blended might be more effective, but would require a substantial amount of revision and I'm not sure in the end would be much more effective if it results in fewer but longer chapters. So I leave this decision to the editors and authors.

6. Please comment on the importance of this book in relation to other books published in its field (including any published by PUP). Does it overlap? How?

I am not aware of another book like this one in ecology. To me it is unique, and is written by two of the best people to write this – experts in ecology and pitcher plants. I love reading books

by experts in their area, and this book is certainly attractive and unique for that reason. I can't think of books with substantial overlap.

Specific notes and feedback made as I read the book:

Xviii – it is great to name the undergraduates working that summer, but is there a way to tell the story without making Shannon Ladeau and Francesca Meier's work seem marginally important or unimportant? Perhaps it could be added that they were each encouraged to explore a different system, and the pitcher plant system emerged as a good one. Alternatively, add a note about the other two students' successful research outcomes. I worry that students would read this and get the impression that they are guinea pigs for their supervisors, or that if they don't do well they might be named in a book as having go-nowhere research!

Presenting the datasets and code for the analyses in the book is simply outstanding! It's a great example, and also enhances the value of the book as a learning resource.

I think the introduction is excellent – scaling is a critical idea for this book, and necessary to show readers right away how pitcher plants are windows into understanding our biosphere. The first chapter summarizes different approaches to scaling in a concise, clear and accurate way. I have no suggestions to improve this chapter, it is fantastic. I wish this were available now for students in my undergraduate class and graduate students in my lab to read! I am very excited for the rest of the book, as I finish chapter 1.

The book also excels at explaining and demonstrating how to use empirical studies in the context of ecological theories. This approach is critical now more than ever, because ecologists are not only trying to observe nature out in nature, but also to understand how their understanding from observations can be used to predict larger spatial and temporal patterns in the context of global change. Ellison and Gotelli have demonstrated the best way to do this – they show this in a fractal way in their book: within each chapter, within each section, and across the outline of the entire book beginning with their chapter on scale.

Chapter 2 conveys the love of nature, and one particular part of nature, that most ecologists will connect with. The natural history, and the history of the natural history, of their study system is indeed fascinating, and the authors' enthusiasm for it shines through in their writing. Though very different from the first chapter, this chapter is equally engaging and inviting. I'll admit that I skimmed some of the pages on taxonomy and its history here; this could possibly be removed if length is an issue, though I would vote to keep it. I suspect it will be interesting to people working with the species, and it is an important reminder that these issues of distinction and identification are present in all systems we work in. The botany section of chapter 2 is essential, I think, to understanding the ecology in later chapters. I'll admit I also skimmed the section (2.3.2) that lists taxonomy of the inquiline food web, but I do think this section should stay; it is a good example and illustration of this system and is foundational material for later chapters. The dispersal and colonization section (section 2.4.2) was fascinating and one of many

examples throughout the book in which the authors present observations and understanding of their system in the context of general patterns and theory (i.e., by using Reid's paradox to frame the discussion of *Sarracenia* dispersal). They also beautifully weave in their own experiments and observations to present a complete picture. By seamlessly integrating knowledge derived from theory, observations and experiments, this chapter conveys ecological research and understanding at its finest.

Chapter 3 starts off with a lengthy overview of basics of nutrient limitation and stoichiometry. Is this necessary? If this book is for graduate students, presumably they've had this before or could be referred to a textbook for the basics. The review is comprehensive in terms of content, and cites many of the important and classic references, and deserves to be read! But if the manuscript needed to be shortened, this seems not fully essential to the '*Scaling Sarracenia*' story. Could chapter 3 begin, perhaps, right at section 3.2.3 – sections 3.2.1 were hard to follow because it wasn't clear why they were essential to the point about evolution of carnivorous plants. That comes in 3.2.3. Clearly the sections leading up to this are laying the groundwork, but as a reader, it wasn't clear to me that I was going to need to read quite a few pages before getting to the explanation of evolution of carnivorous plants. It seemed to me that one could begin the chapter at 3.2.3, and omit much of the preceding sections, but weave in a brief reference to the global trait spectra when needed to understand how *Sarracenia* are unique.

The purpose of the subsequent section – 3.2.4 Anthropogenic activities alter nutrient fluxes – was also not entirely clear. It seems the relevant point in this section comes a few pages into the section, on page 101: 'the physiology and life history of *S. purpurea* make it especially useful as an indicator of atmospheric N deposition'. With a tighter focus on this point, the section could be shorter while still using *S purpurea* to view global change in nutrient fluxes.

Chapter 4 begins with a clear statement of purpose and signposts to where it's going; this is very helpful. The structure of this chapter is clear and efficient, and the ratio of content to length is good. the sequence of sections that focus on the authors' work in *sarracenia* and then in other pitcher plants works well.

Chapter 5: this chapter was somewhat well signposted, but also felt a bit long. I'm not entirely sure whether the details on trait databases are necessary up front; that did help to convey the novelty of the analysis in this chapter. However, I found myself thinking that this whole section of the book (Part II) could be shorter – even to the point of being one chapter that includes a comparison of carnivorous plants with others, drawing up on the highlights of the analysis in chapter 4 but not going through it in such detail.

Section III: Excellent – clear, informative, educational, and just the right length. Though it follows the same structure as section II, it is clearer why we are learning about population growth models and SDMs – it's to conduct this exercise with *Sarracenia*. So the introduction of concepts, tools and *Sarracenia* ecology in this order works more effectively here than in section II.

Section 6.3: Here I take the authors' first sentence to be a statement about the general use of SDMs: "We consider here three other issues that also have been neglected in SDMs but that we think should be included in them or addressed by users of them". I suggest adding a few words here to make clear that the subject is SDMs used across all kinds of taxa – this is a general problem and you are going to present a step toward a solution and illustrate with *Sarracenia*.

Chapter 7: this is an illustrative example of an analysis of population growth and possible trajectories and I think will be interesting and valuable to graduate students. It is clearly explained, and I take the references to code to mean that code to support these analyses is available, and I think students will use this as they try to learn these methods. This is a strong chapter.

Section IV. I think this overview of the community concept is important and interesting (great for students to read!) and references the appropriate classic literature. Here is a place where a little more signposting would help the reader – something like, 'before we explore the communities that rely on *Sarracenia* for habitat and food, we consider what it means to study a community...(and why do we take this detour?)'. This section falls somewhere between Section II and Section III in terms of how a reader is guided through the pages. Again, the first chapter is essentially a textbook on the very general topic of understanding communities (this is an excellent guide!). But why we are doing this first, in terms of how we will then join this knowledge with empirical knowledge of *Sarracenia*, is not yet clear to me as a reader, and therefore I'm tempted to skim the chapter and think that I will come back here later when I know what I need to know. So it's seeming too long. I stress again, though, the chapter is an excellent overview and I will strongly encourage students to read it and study it! But its place and purpose in this book at this point is not as clear as it could be.

That said, now that I'm part way through chapter 10, I really like how this fits together! So I'm not sure I would change the structure – it's creative, and I think effective. Even if a bit unusual.

Chapter 11 is excellent.

Section V: This section contains another great overview / review of tipping points that will serve graduate students well as they develop a general understanding rooted in the classic papers. I think this is very important, and this is an excellent resource. I also found their use of their work in the *Sarracenia* to test and illustrate these concepts to be interesting, useful and engaging. Still, this section felt a bit like section II – it could perhaps be one chapter instead of a long section. The conceptual overview and the test against *Sarracenia* experimental results could perhaps be woven together to be overall more concise and effective.

Chapter 12: introduction is in need of a roadmap for why we are suddenly reading about tipping points.

Chapter 14 – perhaps because this is more in my own area of expertise, I find this introduction to be not as comprehensive as others have struck me as being. Specifically on section 14.2, the statements describing the biodiversity / ecosystem functioning research are too general. Though much BEF work was in grasslands, hundreds of studies have been in soil, freshwater and marine systems. So, ‘mostly in temperate-zone grasslands’ may be numerically correct, but there is a substantial body of research in other systems involving food webs and structures distinct from temperate grasslands. Furthermore, the classic BEF design used by Tilman and modeled by hundreds of other studies does go a long way to disentangling composition and species richness effects by ensuring replication of richness levels across species compositions. Many designs avoid having the highest level of species richness include all species in the experimental pool, reducing the potentially confounded relationship between richness and composition. Examples include (but are not at all limited to) work by Duffy, Bruno, Stachowicz, Bracken in marine systems, and Fox, Bell, McKie, and others in freshwater. Many of these studies experimentally test factors other than diversity in factorial experiments (reviewed by Hooper et al 2012 Nature, O’Connor et al 2017 Oikos, Gamfeldt et al 2015 Oikos).

Correcting these details does not change the chapter’s direction and purpose, but does correct some of the misconceptions broadly held about BEF.

Overall, though, this chapter presents an interesting and thought-provoking argument about how biodiversity-ecosystem functioning thinking can be merged with technologies to better understand the relationships between diversity and function, and I think this is spot on and great reading. This one includes the general background with the *Sarracenia* results (in the same chapter), and it reads well.