CHAPTER ONE

Opening Remarks

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Darwin first proposed a connection between biodiversity and ecosystem functioning in 1859. Interest in the topic has mainly waned—sometimes waxed—in the time interval since. In the last few decades, however, the waxing has had the upper hand, and a quick trip through an electronic archive reveals over 100 articles on this topic since 1982.

Why then a book on the subject? First, there have been significant advances in our empirical understanding of the diversity–functioning relationship in the last few years, but those results have not been compiled, evaluated, and synthesized in both a comprehensive and detailed manner elsewhere. Second, we offer new theoretical results that advance our understanding of when and under what circumstances certain forms of the diversity–functioning relationship might emerge. Third, while knowledge of consumer and decomposer influences on diversity–functioning relationships has not advanced in the last decade as much as many of us had hoped it would, some sensible recommendations for focusing research efforts can be made, and we offer those here. Perhaps most importantly, our analysis of the existing experimental record yielded some surprising results, and our attempts to explain those results and extend them with development of new theory significantly influenced our perceptions of the mechanisms governing diversity and ecosystem functioning relationships.

This book, then, is organized into three parts—a synthesis of the existing experimental and theoretical work and the interpretation of each in light of the other, new contributions to theory that extend the experimental results, and a discussion of future directions.

The first section leads with a chapter by Tilman and Lehman that presents the current prevailing theories of the mechanisms governing the diversity–functioning relationship, and the evidence for or against these mechanisms in early experimental results. The next two chapters—by Tilman et al. (chapter 3) and Hector (chapter 4)—give detailed analyses of the two most extensive diversity–functioning experiments to date, in the grasslands of Minnesota and Europe, respectively. Naeem (chapter 5) reviews the literature on trophic interactions and microbial influences on ecosystem processes, and offers suggestions for advancing the field using both theoretical and empirical approaches. In chapter 6, Schmid, Joshi, and Schläpfer offer a comprehensive review of experimental and observational studies that should serve as one of the most useful compilations of approaches and results for any serious scholar in this field. Pacala and Tilman (chapter 7) conclude this section with a discussion of the biggest surprises that have emerged in the existing experimental record, and provide some simple explanations for these surprises.

In spite of the advances made in the experimental record, however, practical limitations simply preclude experiments that can span the large spatial scales, the long temporal scales, and the representative diversity gradients and structures that are properly the concern of work in this area. Thus we use the next section, on theory, to extend diversity–functioning results to scales that are not particularly amenable to experimental manipulations—landscape-level (as opposed to plot-level) processes, the long time dynamics that govern and characterize natural systems, and multitrophic-level interactions. In doing so, we take a very specific approach. In particular, we employ a common ecosystem model and "attach" to that common model different models of species coexistence. We can thus attribute differences in outcome to differences in coexistence mechanisms, rather than to differences in approaches taken for simulating decomposition, mineralization, and so forth. The common model is general enough to accommodate many of the ecosystem processes of interest, and is presented in chapter 8. Kinzig and Pacala (chapter 9) then look at "successional niche" models—processes of succession in lightly disturbed environments or competition-colonization dynamics in more heavily disturbed environments. Chesson, Pacala, and Neuhauser (chapter 10) examine diversity–functioning relationships when coexistence is maintained by spatial or temporal heterogeneity—a patchwork of soil types, or changing climatic conditions throughout seasons, for instance. Finally, Holt and Loreau (chapter 11) examine simple models of trophic interactions and contrast their results with the previous chapters, where only the plant community was explicitly included in the ecosystem model.

In the last section of the book Balser, Kinzig, and Firestone (chapter 12) sift the literature on the influences of microbial diversity on ecosystem functioning, and offer a framework for guiding future work in this area. Lawler, Armesto, and Kareiva (chapter 13) examine the implications of these scientific findings for conservation. Finally, in the last chapter, the editors offer a synthesis of the major conclusions, and a blueprint for future research directions.

This book is not, however, the last word on the subject of diversity–functioning relationships. In fact, the characterization of any vigorous scientific field is that obsolescence begins the moment a project is conceived. So too with our efforts. In particular, when we developed the approach used in the theory section, well over three years ago now, the early experimental results all seemed consistent with a sampling mechanism—that is, dominance of polycultures by a single best competitor, and a best polyculture performance that equaled, but did not exceed, the best monoculture performance.

We now see experimental results that differ from these—a "transition," if you will, between a sampling mechanism to niche-partitioning or niche-complementarity mechanisms. These niche mechanisms permit an "overyielding" effect—where the best polyculture can outperform the best monoculture. This observed transition justifies some of the early criticisms of Huston (1997), Aarssen (1997), and others—namely, that what we were seeing in the initial experimental results was domination by the "weediest," fastest-growing species, a dynamic that has little to do with any interesting features of diversity–functioning relationships. These experimental outcomes also force us to revisit the earlier analyses of MacArthur, where just such niche complementarity and overyielding were predicted to occur.

Nonetheless, the early experimental results, and the overly harsh discreditation of MacArthur's work, led us to focus on possible sampling mechanisms over niche-complementarity mechanisms. Thus, while we include some complementarity mechanisms in the theory section (see, particularly, chapter 10), we overlook other classes of models that might have proved useful in interpreting observed relationships and extending experimental results. We return to this point in the concluding chapter.

In retrospect, we should not have been surprised by this transition from sampling to niche complementarity. As ecologists, we know that systems away from equilibrium (as planted plots in experimental manipulations certainly are) can be characterized by two (or more) distinctive time dynamics—an initial, rapid response that has to do with early growth dynamics, and a longer-term response governed by competitive interactions and population dynamics. (Pacala and Tilman elaborate on these points, and offer formal mathematical representations, in chapter 7.) Thus, we should have expected potentially significant changes in outcomes as time wore on. Nor should we have been surprised by the emergence of niche complementarity—we know that species coexist, and we understand that this coexistence can mean changes in performance that do not "balance out" between monocultures and polycultures.

In addition, the analyses presented in this book illuminate some conspicuous exceptions to the generally expected result that ecosystem functioning will increase with diversity, and that the performance of the best polycultures will equal or exceed the performances of the best, but more depauperate, communities. In particular, there is some experimental evidence for declining functioning with increasing diversity, and this same pattern emerges from the theories developed for communities where coexistence is maintained by successional niches or interference competition. These outcomes can be understood by considering the relationship between competitive ability and the performance of certain ecosystem processes. Ultimately, the influence of diversity per se on ecosystem functioning should depend on those mechanisms permitting coexistence in particular systems, and on how those strategies that permit competitive superiority or dominance in these coexistence battles influence performance at both local and landscape scales. For instance, are competitive rank and performance of certain functions "parallel," with the superior competitor being the superior performer? Or are they "orthogonal," with no discernible relationship between competitive ability and performance? Might a superior competitor have high local performance but low landscape performance due to low abundance and suppression of other types? How do these relationships between competition and performance depend on scale, or on the coexistence mechanism operating, or on the ecosystem process being examined?

These emerging insights into the more complicated dynamics and mechanisms governing diversity–functioning relationships provide one of the most compelling reasons for further study in this area—namely, that disentangling the influences of diversity on ecosystem functioning, across space and time, requires that we deepen our understanding of the answers to some of the most compelling questions in ecology. How do species coexist? Why do we see so many together, and why don't we see more? How do insights into patterns and processes derived at one spatial and temporal scale translate across other scales? How do communities assemble, how do they disassemble, and how do these rules change when humans decide to rearrange their surroundings? (See Levin 1999 for a wonderful exposition on many of these questions.) Ultimately, then, the study of biodiversity–ecosystem functioning relationships is no more and no less than the study of some of the most fundamental questions in ecology.

Finally, though, we are citizens as well as scientists, with an interest in sustaining critical ecosystem processes and species integrity, which are under increasing assault from the sheer magnitude of the human endeavor. We therefore cannot ignore the social, ethical, and political implications of our work in this field—what it might mean for the design and control of managed systems, for the likely responses of ecosystems to global change and the policies needed to mediate those responses, for the choices we must make in the species triage we conduct every day. We only touch on some of those implications in this volume, but as scientists and as citizens we are acutely aware of them. We do hope, after all, to leave a world that sustains human well-being, and to leave a world in which tomorrow's scientists can answer the questions we fail to answer today.