Preface: On Unifying Approaches in Ecology

The vigorous growth of ecology from its origins in the late 19th century and early 20th century has been accompanied by its gradual fission into several distinct subdisciplines. The unified view of ecology that was present in a book like Lotka's *Elements of Physical Biology* (1925), which introduced many of the theoretical approaches that are still followed today, has given way to more specialized research programs. Although specialization is to some extent inevitable to make science more precise and predictive, it also creates problems. The conceptual frameworks of the various areas tend to become increasingly divergent over time, hampering communication across the discipline as a whole. This divergence is nowhere more apparent than between two of the major subdisciplines of ecology, i.e., community ecology and ecosystem ecology. These two subdisciplines have grown largely independently, each having its own concepts, theories, and methodologies. *Community ecology* is to a large extent an outgrowth of *population ecology*. It is mainly concerned with the dynamics, evolution, diversity, and complexity of the biological components of ecosystems; its starting point is the population and its interactions with other populations. *Ecosystem ecology* is mainly concerned with the functioning of the overall system composed of biological organisms and their abiotic environment; its starting point is the flow of matter or energy among functional compartments.

The separation of these subdisciplines is understandable insofar as they partly address issues at different hierarchical levels and different spatial and temporal scales. But it is harmful insofar as it is an obstacle to their unity and mutual enrichment. In the real world, populations and communities do not exist in isolation; they are parts of ecosystems, and, as such, they are subjected to constraints arising from ecosystem functioning, such as energy dissipation and nutrient cycling. These constraints can deeply alter species interactions and community properties, as we shall see in this book. On the other hand, ecosystems do not exist without their biological components; the latter impose their own constraints on ecosystem processes, as the disruptions generated by some biological invasions attest.

In a way, community ecology and ecosystem ecology provide two different perspectives on the same material reality. Real ecological systems are not either "communities" or "ecosystems," they are both one and the other at the same time—it is just the way we look at them that makes them communities or ecosystems. There is today a clear need for integration of the two subdisciplines. Reunifying these perspectives is an important scientific challenge, not only to progress our fundamental understanding of natural and managed ecosystems but also to allow human societies to develop appropriate responses to the global ecological crisis we are entering as a result of growing human environmental impacts on the Earth system. These impacts include destruction and fragmentation of natural habitats, pollution, climate change, overexploitation of biological resources, homogenization of biota, and biodiversity loss, and affect indistinctly the composition, dynamics, and functioning of ecosystems.

Ecosystem ecology, with its emphasis on higher-level complex systems, has also traditionally been divorced from evolutionary biology, with its emphasis on individual fitness and selection. Yet, ecosystem functioning is shaped by evolution, just as evolution is shaped by the constraints that arise from ecosystem functioning. Fully understanding the functioning of ecosystems and predicting their responses to environmental changes require incorporation of an evolutionary perspective, just as a complete theory of evolution cannot be achieved without consideration of ecosystem functioning.

The need for integration of population, community, ecosystem, and evolutionary ecology has been increasingly recognized during the last 20 years. There have been a number of attempts at doing so from a variety of perspectives, such as those provided by hierarchy theory (O'Neill et al. 1986), linking nutrient cycling and food webs (DeAngelis 1992), linking species and ecosystems (Jones and Lawton 1995), complex systems theory (Levin 1999; Solé and Bascompte 2006), linking biodiversity and ecosystem functioning (Kinzig et al. 2001; Loreau et al. 2002b), ecological stoichiometry across levels of biological organization (Sterner and Elser 2002), and the metabolic theory of ecology (Brown et al. 2004). Each of these perspectives has contributed to addressing part of the problem. But a broader synthesis of the various subdisciplines of ecology is still lacking.

But is such a synthesis possible, and what does it involve? There seems to be a proliferation of "unified theories" in ecology currently, which raises the question whether this is a feasible, or even desirable, enterprise. As a matter of fact, there are a number of different unifying approaches in ecology, each of which has both merits and limitations.

First are approaches that seek *generalizations across hierarchical levels of organization based on elementary physical and biochemical constraints.*

Although there is a limited set of fundamental physical and biochemical laws that constrain all biological and ecological systems, their number is sufficiently large that a variety of unifying approaches have been developed historically. These include approaches based on energy and thermodynamics (energy budgets, entropy, metabolism, temperature, etc.), materials and biochemistry (ecological stoichiometry), structure and topology (fractals, network theory, etc.), and dynamics (complex systems theory, catastrophe theory, self-organized criticality, etc.). Each of them has made important contributions to ecology and other sciences by uncovering similarities in patterns and processes among vastly different systems, scales, and hierarchical levels of organization. Their limitations match up to their success. By focusing on one specific constraint or set of constraints, they explore that part of reality that can be explained by these specific constraints. For instance, the metabolic theory of ecology is able to account for a range of macroecological patterns related to body size and temperature (Peters 1983; Brown et al. 2004). This suggests that elementary physiological constraints related to body size and temperature are powerful enough to govern a number of large-scale ecological patterns. All patterns in ecology, however, cannot be reduced to the influence of body size, temperature, or physiology. Ecology is the science of the complex interactions that bind the organisms and their environment together. Simple physical and physiological laws cannot be expected to provide a full understanding of these complex interactions since they express general constraints that are independent of this complexity. Other forces and constraints govern many other ecological patterns and processes over a wide range of spatial and temporal scales.

Simplifying theories that link previously unrelated properties within a hierarchical level represent a second type of unifying approach in ecology. The "unified neutral theory of biodiversity and biogeography" developed recently by Hubbell (2001) and others is an example of such an approach. This theory radically simplifies the description of communities by assuming all species to be equivalent, and thereby obtains simultaneous predictions for a range of community properties that were previously described by different models. Its strength is that it provides a consistent set of testable predictions that can serve as null hypotheses in community ecology. Its corresponding weakness is that it deliberately ignores the many demographic and functional traits that determine the ecology of species, and hence it remains confined within a specific description of reality.

A third type of unifying approach in ecology, and in science in general, consists in *merging the principles and perspectives of different disciplines* to create a synthesis that goes beyond the boundaries of each discipline. This is the approach that I champion in this book, based on previous efforts by DeAngelis (1992) and others. In many ways this approach is orthogonal, and hence potentially complementary, to the previous ones. Instead of seeking generalizations within or across hierarchical levels based on a specific perspective and a specific set of constraints, I seek to lay bridges between different perspectives and different sets of constraints. Such an approach also has limitations since it cannot pretend to build a single unified theory of ecology. But I accept this limitation happily. In fact, I believe that a monolithic unified theory of ecology is neither feasible nor desirable. Natural systems are too complex to be reducible to a unique description. My goal is to generate new principles, perspectives, and questions at the interface between different subdisciplines and thereby contribute to the emergence of a new ecological synthesis that transcends traditional boundaries. Working along these lines leads to a range of theories on different topics, although these theories obviously have to be compatible and complementary.

Accordingly, this book is the expression of an evolving research program. In this book, I synthesize a decade or so of theoretical work at the interface between population, community, ecosystem, and evolutionary ecology and set it within a coherent framework. Many questions have found answers in this work, but many new questions have also emerged from these answers. The book addresses both the answers and the questions.

I start by revisiting the basic principles that underlie the approaches of population and ecosystem ecology in chapter 1 and show how mass and energy budgets can be used as a basis for unification of these approaches in building community and ecosystem models. Chapter 2 provides a synthesis of the many existing theories of species coexistence, with a focus on their often overlooked implications for community-level functional properties. This chapter covers a relatively classical topic in ecology, but it does so from a slightly different perspective than usual, and the material it contains serves as a basis for several subsequent chapters. The functional consequences of species coexistence are further discussed in chapter 3, which examines how species diversity within a trophic level—a community property that is increasingly threatened by human environmental impacts—affects ecosystem functioning. The relationship between biodiversity and ecosystem functioning has emerged as a vibrant new research field during the last 15 years or so and has greatly contributed to fostering the integration of community ecology and ecosystem ecology that I champion. As a result, this theme runs through the whole book.

Many of the studies on this topic, however, have considered artificially simple systems with a single trophic level, thus ignoring the vast complexity of real ecosystems with their myriad trophic and nontrophic interactions between species. Chapter 4 provides some theoretical foundations to start to address this complexity. It analyzes the relationships between species interactions, biodiversity, and ecosystem functioning in food webs and interaction webs. There has been a long-standing debate in ecology over the relationships between the stability and diversity or complexity of ecosystems. This debate has resurfaced recently within the context of biodiversity and ecosystem functioning research. Chapter 5 provides new perspectives on this topic by explicitly distinguishing and linking stability properties at the population and ecosystem levels.

Up to chapter 5, only part of ecosystem functioning is considered—usually biomass and productivity of one or several trophic levels. Chapter 6 extends the scope of analysis to the overall functioning of ecosystems. It presents a coherent theory of material cycling and of its role in ecosystem functioning and shows how and when an indirect mutualism between autotrophs and heterotrophs arises from nutrient cycling at the ecosystem level. Chapter 7 puts all these results into a spatial context. It examines how biodiversity, ecosystem functioning, and the relationship between them are affected by spatial flows of nutrients and individuals across ecosystem boundaries, and the constraints that arise from these flows in metacommunities and metaecosystems. Last, I explore the evolutionary dimensions of ecosystem functioning in chapter 8. This final chapter discusses how natural selection leads to evolution of ecosystems and ecosystem properties and provides rigorous bases for the development of a much needed evolutionary ecosystem ecology.

Throughout the book I make use of relatively simple mathematical models to build and support my theories. I limit myself to their most salient, clearly interpretable results, leaving more detailed treatment to specialized publications. As a result of this choice, I have decided to leave aside some important issues, such as the interactions between several limiting nutrients and their consequences for ecosystem functioning. Although I take an active interest in this topic, its theoretical treatment requires more complex, stoichiometrically explicit models, which are beyond the scope of this book. Sterner and Elser's (2002) book provides a comprehensive overview of ecological stoichiometry, albeit from a more empirical perspective.

The book covers a wide range of topics. But these topics are strongly related to each other and follow a logical progression, from competitive communities, which are small subsets of ecosystems, to entire ecosystems, and from small scales to larger spatial and temporal scales. My book does not pretend to provide a comprehensive treatment of all the issues related to these topics, let alone a final resolution of these issues. Its main purpose is to show that merging the principles of population, community, evolutionary, and ecosystem ecology opens up new ways to look at reality, thereby offering new insights into a wide range of key issues in ecology and new theoretical weapons to face the mounting ecological crisis. I am convinced that we need a more synthetic ecology and hence a more synthetic ecological theory. If this book contributes to spread this conviction, I shall regard it as successful.