Preface to the Second Edition

There is something fascinating about science. One gets such wholesale returns of conjecture out of such a trifling investment of fact.

Mark Twain, 1874, p. 156

Notwithstanding the typically amusing sentiment expressed by Twain, my hope and intent with this book is that the conjecture and ideas emerge from and by no means overwhelm a solid basis in fact. To that end, in part, this edition is thoroughly referenced to bring to the reader the most recent authoritative information, which builds upon the historical foundation cited that underpins the many theories discussed.

This second edition follows the framework of the first but is completely revised and is generally a more detailed treatment of the topics. The rationale for and goals of the initial treatise remain the same and were presented in detail in the Preface to the first edition (1991), which follows this Preface. While science and in particular molecular biology have progressed remarkably in the intervening years, the gulf between the two major branches of ecology—that of plants and animals on one hand and of microorganisms on the other—has not narrowed appreciably.

When the first edition was being written in the late 1980s, scientists and the public were attempting to come to grips with the realities of recombinant DNA and the prospect of genetically engineered organisms. This contentious debate (still in progress) had, perhaps predictably, splintered largely along disciplinary lines.[1] It set in stark contrast the two disciplines. Microbiologists, many of whom are molecular biologists, were generally confident about the new technologies, that molecular genetic interventions could be made with surgical precision, and that the phenotype emerges predictably from the genotype. Plant and animal ecologists, used to dealing with complex systems and attendant complications such as exotic species and unintended community invasions, were much less sanguine. A common refrain, frequently unspoken but omnipresent, was that microbiologists did not really understand "ecology," to which the rebuttal was that ecologists did not appreciate the reductionist rigor of microbiology or behavior of microorganisms. Actually, a closely parallel, longstanding debate had simmered within ecology between molecular camps and organismal camps. This issue was addressed years earlier by the famous paleontologist George Gaylord Simpson (*Am. Scholar* 36:363–377, 1967).

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1 For examples, see P. Berg et al. (Science 185:303.1974); H.O. Halvorson et al. (*Engineered Organisms in the Environment: Scientific Issues.* Am. Soc. Microbiol. 1985); and A. Kelman (Chair, NAS Comm. Rept. *Introduction of Recombinant DNA-Engineered Organisms into the Environment: Key Issues*. Natl. Acad. Sci., Washington, DC, 1987).

The discipline of microbiology was born with the discovery of the microscope separately by Hooke and by van Leeuwenhoek in the mid-1600s. To a large extent it remains pragmatically and philosophically distinct from macroscopic biology. There are multiple reasons for the parallel but largely separate evolution of these disciplines, not the least of which is an educational system that still rapidly channels undergraduates away from a unified and conceptual biology and into specialist subdisciplines. Inroads are being made by such avenues as molecular systematics. Likewise, since the 1970s and 80s there have been numerous examples of "macroorganism ecologists" who are using microbial systems to test ecological theory (see examples in Chap. 8). Whether the manifold emergent specializations such as transcriptomics, metabolomics, metagenomics, and the like, serve to reunite biologists or further splinter biology remains to be seen. Every biologist should periodically reread Mott Greene (*Nature* 388:619–620, 1997). It remains my hope that this text will help to provide a conceptual synthesis of ecological biology.

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October, 2016

Preface to the First Edition (1991)

The most important feature of the modern synthetic theory of evolution is its foundation upon a great variety of biological disciplines.

G.L. Stebbins, 1968, p. 17

This book is written with the goal of presenting ecologically significant analogies between the biology of microorganisms and macroorganisms. I consider such parallels to be important for two reasons. First, they serve to emphasize that however diverse life may be, there are common themes at the ecological level (not to mention other levels). Second, research done with either microbes or macroorganisms has implications that transcend a particular field of study. Although both points may appear obvious, the fact remains that attempts to forge a conceptual synthesis are astonishingly meager. While unifying concepts may not necessarily be strictly correct, they enable one to draw analogies across disciplines. New starting points are discovered as a consequence, and new ways of looking at things emerge.

The macroscopic organisms ('macroorganisms') include most representatives of the plant and animal kingdoms. I interpret the term 'microorganism' (microbe) literally to mean the small or microscopic forms of life, and I include in this category the bacteria, the protists (excluding the macroscopic green, brown, and red algae), and the fungi. Certain higher organisms, such as many of the nematodes, fall logically within this realm, but are not discussed at any length. Most of the microbial examples are drawn from the bacteria [defined here in the generic sense to include archaeans] and fungi because I am most familiar with those groups, but the concepts they illustrate are not restrictive.

Because the intended audience includes individuals who are interested in 'big' organisms and those interested in 'small' organisms, I have tried to provide sufficient background information so that specific examples used to illustrate the principles are intelligible to both groups without being elementary or unduly repetitious to either. Evolutionary biologists in either camp may also find the work of interest because the central premise is that organisms have been shaped by evolution operating through differential reproductive success. Survivors would be expected to show some analogies in 'tactics' developed through natural selection. The only background assumed is a comprehensive course in college biology. Hence, the book is also appropriate for advanced undergraduates.

The need for a synthesis of plant, animal, and microbial ecology is apparent from an historical overview (e.g., McIntosh 1985). Plant ecology was originally almost exclusively descriptive. It remains so to a large degree. A strongly predictive science has emerged, but one based largely on correlation rather than causation (Harper 1984). Within the past few decades it has branched into three main streams: phytosociology, population biology, and the physiological or biophysical study of individual plants (Cody 1986).

In contrast, animal ecologists have tended to study groups of ecologically similar species (i.e., guilds; Cody 1986). Although animal ecologists have probably been the most influential in developing the field of population ecology, many of their mathematical models derive from work based on microorganisms (e.g., Gause 1932), and from medical epidemiology (again involving microorganisms). Zoologists have also been the main force behind ecological theory, particularly as it applies to communities. Significantly, in both plant and animal ecology, the processes underlying patterns are usually inferred: The evidence marshalled is typically correlative rather than causative, and frequently the difference between the two is overlooked, if recognized.

Many microbial ecologists study systems. Ecology as practiced by microbiologists, however, has been mainly autecology, is typically reductionist in the extreme (increasingly often at the level of the gene), and lacks the strong theoretical basis of macroecology. Microbiology is a diverse field and microbial ecologists may be protozoologists, bacteriologists, mycologists, parasitologists, plant or animal pathologists, epidemiologists, phycologists, or molecular biologists. Approaches and semantics differ considerably among these subdisciplines. Nevertheless, microbial ecology is in general like plant ecology in its strong descriptive element. For example, often the goal is to identify and quantify the members of a particular community. Despite increasing emphasis on field research in the last few decades, microbes are usually brought into and remain within the laboratory for study under highly controlled conditions to determine the genetic, biochemical, growth rate, or sporulation characteristics, or the pathological attributes of a particular population, and how these are influenced by various factors. Thus, the major operational difference between microorganisms and macroorganisms is that the former must generally be cultured to understand their properties. It is this requirement that brings the microbial ecologist so quickly from the field to the laboratory.

To oversimplify, one could say that macroecology consists of phenomena in search of mechanistic explanation, whereas microbial ecology is experimentation in search of theory.

The foregoing picture is reinforced by observations on the parochialism evident in science. Examples include the streamlined makeup of most professional societies, the narrow disciplinary affiliation of participants at a typical conference, or the content of many journals and textbooks. Microbes as illustrations of ecological phenomena are omitted from the mainstream of ecology texts and are mentioned in cursory fashion only insofar as they relate to nutrient cycling or to macroorganisms. Discussion is left for microbiologists to develop in books on ‘microbial ecology’, which in itself suggests that there must be something unique about being microscopic. This is not meant as criticism, but rather as an observation on the state of affairs and an illustration of the gulf between disciplines. Finally, if additional evidence were necessary, one need only reflect on the current furor about the release of genetically engineered organisms. To a large degree this contentious issue has polarized along disciplinary lines: Ecologists express concern that microbiologists have little real knowledge of 'ecology'; microbiologists respond that ecologists really do not understand microbial systems. While acknowledging obvious differences between the two groups of organisms, one must ask whether their biology is so distinct that such isolationism is warranted. This book addresses that question.

A synthesis of microbial ecology and macroecology could be attempted at the level of the individual, the population, or the community. There would be gains and losses with any choice. Even the use of all three hierarchical levels would not ensure absence of misleading statements. Relative to the individual, comparisons based on populations or communities offer considerably increased scope and allow for inclusion of additional properties emerging at each level of complexity (e.g., density of organisms at the population level or diversity indices at the community level). Parallels based, for example, on supposed influential (i.e., organizing) forces in representative communities would be precarious, however, because unambiguous data implicating the relative roles of particular forces such as competition are usually lacking. The data that do exist have been variously interpreted, often with intense debate. Moreover, the same type of community may be organized quite differently in various parts of the world. For example, barnacle communities in Scotland (Connell 1961) are structured differently from those in the intertidal zone of the California coastline (Roughgarden et al. 1988). Entirely different pictures could emerge depending on the communities of microbes and macroorganisms arbitrarily selected for comparison.

Thus, I have decided to focus comparisons at the level of the individual. This implies neither that the individual is the only level on which selection acts, nor that shortcomings of the sort noted above do not exist. However, I consider the individual (defined in Chapter 1) through its entire life cycle to be operationally the fundamental unit of ecology in the sense that it is the primary one on which natural selection acts. Strictly speaking, natural selection acts at many levels, and a proper analysis of this issue requires that a distinction be made between what is transmitted and what transmits (Gliddon and Gouyon 1989). Efforts to relate the former (genetic information, broadly construed to include genes and epigenetic information) to a particular organizational level in a biological hierarchy extending from a nucleotide sequence to an ecosystem have engendered lively debate (e.g., Chapter 6 in Bell 1982; Brandon 1984; Tuomi and Vuorisalo 1989a, b; Gliddon and Gouyon 1989; Dawkins 1989). Without extending this controversy here, I note that at least my choice of the individual as the relevant ecological unit in this context is consistent with the conventional ecological viewpoint expressed by naturalists from Darwin onward (e.g., Dobzhansky 1956; Williams 1966; Mayr 1970, 1982; Begon et al. 1996; Ricklefs 1990). Comparisons of traits at the level of the individual can then be carried either downward to the corresponding genes—

which have passed the screen of natural selection—or upward to assess the role of selection of traits at the group level.

This book proceeds first, by developing a common format (in Chapter 1) for comparing organisms; second, by contrasting (in subsequent chapters) the biology of macro-and microorganisms within that context; third (and also in the subsequent chapters), by drawing ecologically useful analogies, that is, parallels of interpretive value in comparisons of traits or 'strategies' between representative organisms. The first two phases can be accomplished relatively objectively; the third is necessarily subjective. There are situations where macroorganisms provide the wrong model for microbes or vice versa. I have tried to avoid forcing the parallels and have stated where close parallels simply do not exist.

All citations appear in a bibliography at the end of the work. Where books are cited in the text, I also specify, when appropriate, the specific chapters or pages concerned, in order to assist the reader in locating the relevant passages. Finally, at the conclusion of each chapter, a few suggestions are made for additional reading on each particular topic.

This is a book mainly of ideas. I find that the study of analogues is instructive and productive, not to mention interesting and frequently exciting. There is considerable speculation and a strong emphasis on generalizations, which I hope will prove stimulating and useful to the reader. Inevitably, there will be exceptions to any of the general statements. I am not particularly concerned by these oddities and think that it would be a mistake for the book to be read with the intent of finding the exception in each case in an effort to demolish the principle. However, this is not the same as advocating that it be read uncritically! MacArthur and Wilson (1967, p. 5) have said that even a crude theory, which may account for about 85% of the variation in a phenomenon, is laudable if it points to relationships otherwise hidden, thus stimulating new forms of research. Williams (1966, p. 273) points out that every one of Dalton's six postulates about the nature of atoms eventually turned out to be wrong, but because of the questioning and experimentation that resulted from them, they stand as a beacon in the advance of chemistry. Finally and most explicitly, Bonner (1965, p. 15) states,

> *It is, after all, quite accepted that in a quantitative experiment, a statistical significance is sufficient to show a correlation. The fact that there are a few points that are off the curve, even though the majority are* [sic] *on it, does not impel one to disregard the whole experiment. Yet when we make generalizations about trends among animals and plants, such as changes in size, it is almost automatic to point out the exceptions and throw out the baby with the bath* [sic]. *This is not a question of fuzzy logic or sloppy thought; it is merely a question whether the rule or the deviations from the rule are of significance in the particular discussion.*

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