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Fundamental Processes in Ecology
an Earth Systems approach

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An Earth Systems Approach

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The answers to nearly all the major philosophical questions are either found in or illuminated by the science of life, especially ecology, whose stated goal is the elucidation of the relationship of organisms to environment.

Lynn Margulis (in Margulis and Sagan, 1997, p. 311).

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Preface

> A work of synthesis is not only difficult, it is also not part of the pattern of a career in modern science.
>
> Nisbet (1991, p. xvi)

This volume is a book-length expansion of a paper originally published in *Biological Reviews* during 2003. That paper summarized an approach to thinking about academic ecology at the scale of the whole Earth based on the following astrobiological thought experiment; 'for any planet with carbon-based life, which persists over geological time scales, what are the minimum set of ecological processes that must be present?' In the context of all the changes that we are making to our planet, such an Earth Systems approach to ecology appears timely—if only to highlight what we don't currently understand. In addition, I believe that there are great benefits in rethinking very fundamental ideas from a novel perspective and asking questions about some of the traditional emphases of ecology: such as why are so many of our journals filled with huge flocks of birds when microorganisms are so much more central to the things we need to understand?

Attempting to put ecology into this much wider context requires the synthesis of information from biology, chemistry, physics, geology, and astronomy; few readers can be expected to be fluent in the language of all these parts of science so I have included an extensive glossary (which also summarizes the geological time scale). As the epigraph to this preface suggests, such a work of synthesis was considered both difficult and unfashionable by Euan Nisbet at the start of the 1990s when he wrote his own, more applied, book on the Earth—today it is no less difficult and probably even more unfashionable, at least within British science. The problem is that such synthetic work requires no expensive laboratory or groups of research students or post Docs and as such it does not generate the large research grants, rich in overheads, for the scientist's University or Institute. The influence of such work is also very difficult to quantify, at least on a short time scale, this makes it almost useless to the accountants of research 'quality'. As such, many academic administrators consider this kind of work completely pointless—I am lucky that at least some of my senior colleagues at Liverpool John Moores University have been tolerant of my overhead-free theoretical work. I would probably have been in danger of losing my job at many British Universities for following this approach to research.

I don't expect anyone to agree with all the ideas and suggestions in this book—that includes myself as I will have no doubt changed my views on at least a few points of detail before publication! I will consider the book successful if it provokes people into reconsidering the core ideas of ecology and hopefully in so doing causing some of them to generate new and interesting ideas themselves. At the very least the reference list should be a useful way into a diverse literature, both for ecologists interested in the wider context of their subject and for scientists from other disciplines interested in what ecology can offer their subject.

Many people have contributed towards the writing of this book. First my science teachers must take some responsibility for my approach (hopefully this will not dismay them!): I would particular like to highlight the role of my father, Lionel Wilkinson in my science education. In addition, both Humphrey Smith and David Keen were influential at Coventry Polytechnic while Brian Huntley and John Coulson were especially important while I was at the University of Durham. Fred Slater (curator of Cardiff University's biological field centre) was influential in giving me the opportunity to 'play' with a wide range of taxonomic groups in the late 1980s. It gives me great pleasure that the science discussions with my father are still ongoing and that in recent years I have returned to collaborative work with Humphrey Smith in his 'retirement'. Yrjo Haila, David Schwartzman, and Tyler Volk provided helpful comments on the paper that was the forerunner to this book (Wilkinson, 2003). Jim Lovelock, Hannah O'Regan (my wife), and Tim Lenton provided comments on early drafts of the majority of chapters; Tim in particular provided many detailed suggestions in spite of his own heavy work load. Tom Sherratt, Andy Young, and Ian Sherman also provided invaluable comments on some of the chapters. Tom has been an especially important collaborator in theoretical work since the end of the 1990s, some of our joint work being facilitated by financial support from The Royal Society of Britain. Three of the graphs used in this book have been redrawn from other authors' work; I thank Jim Lovelock, Graeme Ruxton, Tom Sherratt, Mike Speed, Bland Finlay, and Tom Fenchel for permission to use their work in this way. My former research student Steve Davis helped with the production of Figs 4.1 and 4.5; the photographs are my own.

David M. Wilkinson

Liverpool
January 2006

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Part I Introduction

In fact, the conditions necessary for life on the earth have not been ‘naturally’ there but have been shaped by life itself.

Haila (1999a, p. 338)

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1. *Introducing the thought experiment*

1.1. The entangled bank

The subject matter of ecology appears confusingly complex, one of the most famous images of this complexity in the scientific literature being Charles Darwin's description of an entangled bank (Fig. 1.1). In the closing pages of *The Origin of Species* he wrote, 'It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about and worms crawling through the damp earth.' (Darwin, 1859, p. 489). Some years ago in an essay in the journal *Oikos* I argued that Darwin's image ignored many of the most important parts of the system, such as the microorganisms in the soil and the mycorrhizal fungi in the plant roots (Wilkinson, 1998). Indeed, while Darwin stressed the animals (birds, insects, and worms), it is the plants, fungi, and, most importantly, the microbes which are involved in the majority of ecosystem services (Fig. 1.2). Indeed, for most of the history of life on Earth ecology was entirely microbial, although today microbes are surprisingly rare in our general ecology textbooks. In the 1998 essay I wrote, 'To a first approximation the animals are of no importance to the functioning of the system.' Possibly I was slightly too hard on the animals and their lack of functional importance. As Joel Cohen (pers. comm.) has pointed out to me, although animals may not be required for most of the important ecosystem processes, they should be regarded as potentially important catalysts, as their presence may greatly speed up the *rate* of these processes. For example, Darwin's worms are probably catalysing the microbial breakdown of leaf litter.

Ecological systems such as Darwin's entangled bank (composed of myriad species of microbes, fungi, plants, and animals; all interacting with each other and their abiotic environment) are clearly difficult to understand and challenging to explain to students or the wider public. It is instructive to ask, *how has academic ecology attempted to order this complexity?* I believe the answer to this question can be most easily seen by looking at university-level general ecology

Fig. 1.1: Archaeological evidence suggests that hedgerows have been a part of the British landscape since at least late prehistoric times—here a hedge marks out one side of a 'strip field' of probable medieval date behind the village of Great Asby in Cumbria, northwest England (see Clare, 1996). In some parts of Britain they are traditionally established on hedgebanks, which are constructed of earth or stones, these are common in southwest England but also found much more widely across the country. Before metalled road surfaces many British roads formed eroded troughs often edged with hedges on the tops of their banks, so-called holloways (Rackham, 1986: Muir, 2004). In summer these banks can be alive with life, Darwin probably had similar hedges in mind when he constructed his famous metaphor of an 'entangled bank'—which he shortened to a 'tangled bank' in later editions of *The Origin of Species*.

texts. As Stephen J. Gould (2002, p. 576) wrote in his *magnum opus* 'yes, textbooks truly oversimplify their subjects, but textbooks also present the central tenets of a field without subtlety or apology—and we can grasp thereby what each generation of neophytes first imbibes as the essence of the field . . . I have long felt that surveys of textbooks offer our best guide to the central convictions of an era'.

1.2. **The entity approach**

How do textbooks organize ecology? In most cases as a hierarchy of entities (I am indebted to Haila (1999b) for the term 'entities' in this context). There appears to be a reasonable consensus about how to classify these ecological entities in a hierarchical manner: going from genes through individuals, populations,

Fig. 1.2: A biological soil crust (cryptogamic soil) in the Utah Desert, USA. Such crusts often have filamentous cyanobacteria as an important part of their structure, along with mosses and lichens. These crusts are very important in many arid and semi-arid systems around the world; especially in controlling hydrological aspects of the soil and preventing soil erosion (Lange *et al*., 1992). They provide a rare example of a system where the ecological importance of microbes is clearly visible to the unaided human eye. Mainstream ecology has tended to concentrate on macroscopic organisms (Fenchel, 1992; Wilkinson, 1998), however, there is now some sign of a slight increase in microbial papers in several ecological journals, although this work has yet to feature in many ecology textbooks. Microbial studies are crucial for the development of an Earth Systems ecology, as such they feature prominently in this book.

species, communities, ecosystems to the biosphere (e.g. Colinvaux, 1993; Smith and Smith, 1998; Krebs, 2001; Stiling, 2002; Begon *et al*., 2006). A hierarchical approach, from population to community ecology, was also used to structure the *Principles of Animal Ecology* (Allee *et al*., 1949), one of the key textbooks in the mid twentieth century. This approach has an even longer pedigree in plant ecology with an important early text (Warming, 1909) using a different entity-based strategy, being arranged around various plant communities. Indeed an entity approach is an obvious way of organizing natural history into species, habitats, biomes, and so forth. An early exception to these approaches was Charles Elton's classic text *Animal Ecology* from the 1920s (Elton, 1927), which he organized, at least in part, around concepts; such as 'succession', 'parasites', and 'dispersal'.

An entity-based approach has great strengths in describing systems. It is probably also inspired by a strongly reductionist tradition which believes that the lower levels in a hierarchy contain all the information needed to understand the higher levels. Reduction has been so successful in tackling many problems in the past that the philosopher Mary Midgley (2001) has argued that there has been an unfortunate tendency for some scientists to think that it is not only necessary but also sufficient to explain any scientific problem. In this view community ecology is just population ecology writ large, so that an understanding of communities will provide everything required to understand the biosphere. An interesting recent example of this approach is by Allen *et al*. (2005) who describe a 'bottom-up' model which attempts to make predictions about the global carbon cycle based on the effects of body size and temperature on individual organisms. However such bottom-up, reductionist, approaches may have limits when faced with all the complexities of the entangled bank. In studying a complex system it is often its organization that is most important. Ernst Mayr, in his last book, illustrated this point with the following physiological example: 'No one would be able to infer the structure and function of a kidney even if given a complete catalog of all the molecules of which it is composed' (Mayr, 2004, p. 72). In an ecological context, Lawton (1999) has argued that the many complex contingencies in ecological systems may limit such an approach, forcing us to rely less on reduction and experimental manipulations, especially at the level of community ecology.

1.3. **A process-based approach**

An obvious alternative to the hierarchical entity approach would be to emphasize processes, especially if the goal is conceptual understanding rather than a narrative description of the natural world. Such an approach immediately raises a crucial question: what are the fundamental processes in ecology? While many authors appear to agree on the broad outline of an entity approach (genes to biosphere), no such consensus is available for ecological processes. This book is a provisional attempt to address this difficult question.

The type of approach used is important as it can govern the kinds of ecological questions a researcher asks. Consider peatland systems, the entity approach suggests questions about the number of different peatland types. Such questions date back to Linnaeus in the eighteenth century, who appears to have been the first person to publish lists of plant species from different types of bogs (Du Rietz, 1957). Much more recently the British National Vegetation Classification has defined 38 peatland plant communities to be found in Great Britain (Rodwell, 1991). A process-based approach to peatlands would more naturally lead to very different questions, for example about their role in carbon sequestration and its climatic implications (e.g. Klinger *et al.*, 1996; Clymo *et al.*, 1998). A recent analysis of ecological research papers published over the last 25 years suggests that there is a growing increase in studies of processes (Nobis and Wohlgemuth, 2004). If the approach taken can affect the question asked then it can clearly affect our understanding of the Earth. If a more processed-based approach is to be considered then it becomes important to develop a reasonably rigorous way of defining key, or fundamental, ecological processes.

One possibility would be to ask ecologists what processes they consider important. In the run up to the 75th anniversary of the British Ecological Society a survey of its membership asked them to rank a list of ecological concepts in order of their importance (Cherrett, 1989). The resulting top five concepts were; ‘the ecosystem’, ‘succession’, ‘energy flow’, ‘conservation of resources’, and ‘competition’. It is interesting that some of these overlap with those used by Elton (1927) in his early attempt at a concept-based ecology text. However, Cherrett’s concepts differ from what I mean in this book by ‘fundamental processes’; for example, ‘conservation of resources’ only applies to a planet populated with intelligent organisms that can plan ahead. Other concepts discussed by Cherrett, such as the idea of nature reserve management or maximum stainable yields (by harvesting humans) are also clearly not fundamental ecological processes but important applied concepts for a planet with intelligent life.

An alternative strategy would be to attempt to approach fundamental ecological processes experimentally using mesocosms. However, it is unclear if such systems are large enough (and they clearly operate over an unrealistically short time scale) to answer such big conceptual questions. The largest of these experimental systems has been the 1.3 ha Biosphere 2 closed-environment facility in Arizona, USA. However, so far, the main theoretical contribution of this mesocosm has been to illustrate the difficulties in maintaining stable ecological systems, even on a year-to-year basis (Cohen and Tilman, 1996). Therefore, even the largest mesocosm apparently does not provide a realistic system for experimental study of many major ecological processes.