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Herman H. Shugart
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Part 1

Introduction

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1 · *The importance of understanding ecosystem change*

Semper in adsiduo motu res quæque geruntur.
(All things are caught up in ceaseless motion.)
Lucretius

We live in a technological era that is propelled by a special, and perhaps unique, form of creativity in which the imagining of difficult problems – How can we communicate over large distances? How fast can we move people or things from one place to another? Can we develop a material that transmits energy with the most efficiency? Can we eradicate smallpox? Can we map the entire genetic contents of the chromosomes of humankind? – seems to inspire technological solutions to these problems. We routinely conceive and solve problems that would have been considered in the realm of magic and witchcraft less than ten generations ago.

But for all our ability to generate, and eventually solve, the problems we present ourselves, we have stumbled in solving environmental problems. Why is this?

Modern technology excels in solving well-posed, clearly defined problems. Most people who deal with environmental problems will certify that environmental problems are rarely clearly defined or well posed. Indeed, they are often maddeningly to the contrary. In the environmental area, yesterday's logical solution can become today's problem. Unfortunately, as the human population increases, in part as a result of our ability to solve other problems such as people dying from infant mortality and curable diseases, environmental problems seem to become more difficult and larger in their spatial extent.

Since the mid-1970s, ecological problems, inherently regional and global in scale, have emerged. These involve understanding the response of ecosystems to spatially extensive environmental change. Many of these

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ecological problems are public concerns and, as such, have gained pen names; recent examples are 'Acid Rain' and 'The Greenhouse Effect'. Public interest in such scientific issues can be fickle. There is a news reportage of the 'Environmental Disaster of the Week' that invites the cynicism of a jaundiced readership. At the root of these and other issues is a central scientific challenge: how can we extrapolate our understanding of underlying biological, chemical and physical processes to larger land areas over long time frames? This is the kernel of the problem. If we can engage this issue, hopefully we can then pose environmental questions in a context that will allow us to apply our technological and scientific muscle towards solutions.

For example, we have a wealth of research results that have created a basic understanding of how oxidizing pollutants, such as ozone and the gaseous oxides of sulphur and nitrogen, affect the functioning of leaves. We have a degree of understanding of the analogous responses of whole plants to these pollutants. But we need to know how to extrapolate this detailed understanding to predict the potential effects (if any) of these pollutants on the species composition, productivity and functioning of the vegetation over a region. Nevertheless, it is difficult to demonstrate unequivocally that brown spots on leaves (that we can associate with air pollution) are the cause of large-scale die-backs of trees.

Similarly, we understand the responses of single plant leaves to elevated levels of CO_2 under different temperatures, light levels and humidity conditions (at least for certain species of plants). But, in a world with increases in atmospheric CO_2, how do these responses translate into alterations in forest or crop productivity? Equally difficult is the reciprocal problem, how do changes in productivity of forests (and other terrestrial systems) change the rates that atmospheric CO_2 is removed from the atmosphere? How does variation in the uptake of CO_2 by terrestrial ecosystems influence the atmospheric levels of CO_2?

Like Lucretius, quoted at the beginning of this chapter, we live in a time with an awareness of the omnipresence of changes. We are compelled by scientific interest and by the need to solve environmental problems to understand these changes better. We need to know how the Earth's systems work because we are affecting these systems through our actions and we have not yet solved the problem(s) of understanding the consequences.

The prime objective of this book is to communicate an understanding of the prediction of the 'ceaseless motion' of the Earth's vegetation: the large-scale dynamics of the terrestrial surface of the Earth in response to a

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changing environment. Important tools to explore such changes are computer models that can be used to predict ecosystem responses. The quantitative modelling of the dynamics of the vegetation covering the Earth's terrestrial surface under current and altered environmental conditions can be used to reconstruct the response of terrestrial ecosystems to past change and to predict responses to future changes.

One of the difficulties in treating a subject matter as broad as terrestrial ecosystems and their response to change is avoiding writing a general ecology text. There are several scientific themes that will emerge as this book develops. These are largely concerned with perspectives or points of view involved with the development of global or large-scale ecology. However, these issues are far from unique to large-scale ecology. Indeed, they are important for a wide range of scientific disciplines.

Ecologists deal with systems of great complexity and science is currently oriented towards description with an interest in detail. At times, there seems to be a fascination with the production of counter-examples to generalities. Ecological studies are often conducted at relatively small space scales. Karieva and Anderson (1988) found that 95% of the studies that they surveyed from leading ecological journals were conducted on study plots of less than 1 ha. Half of these studies used plots of 1 m^2 or smaller.

Also, ecology is strongly an observational science. Observations are the currency of the science. Ecologists traditionally argue against a particular theory (or claims for generality) by the production of counter-examples. The ecologist's seeming fascination for counter-examples is reinforced by the increased importance of the role of statistics in modern ecology and the emphasis in statistical procedures of asserting that a particular assemble of observations negates a stated hypothesis. In statistical tests, one does not 'prove' things in the sense of demonstrating them to be true. Rather, results are judged to be highly unlikely if a hypothesis called the null hypothesis, H_0, is true. In application, statistics is mostly about demonstrating that calculated features such as averages of samples (and other calculations) are not likely to be the same. This is not the equivalent to proving that they are different. Progress in a statistically based science proceeds by formulating appropriate hypotheses and then collecting observations to reject these hypotheses. The creative aspect of the science is to identify which hypotheses to examine.

Across ecology, an exchange of theories with examples and counter-examples drawn from different systems at inappropriate time and space scales has fuelled several acrimonious and continuing arguments. For

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example, the fundamental nature of succession, the importance of competition in structuring communities, or the importance of internal feedbacks in the regulation of a range of ecosystems have been debated continuously, some might say *ad nauseam*, without resolution. One factor providing fuel to these non-illuminating fires may be in the mismatch in time and space scales of the sets of observations being used to test theory.

A fundamental motif that will arise in the initial chapters of this book is that it is important to match the time and space scales of important phenomena. Time and space scales are usually expressed in terms of the ranges over time or space in which the changes in the phenomena are measurable and observable. Scale-related issues will emerge in understanding ecosystems and their spatially explicit analogue, the biogeocoenosis, and in relating environmental variables to the biology and ecology of plants and vegetation. Further, time and space scale will figure prominently in understanding the dynamics of ecosystems that occur as heterogeneous mosaics.

The importance of the appropriate blending of phenomena, time and space to gain understanding is not in the least unique to ecology. Rather, it is an integral part of most scientific investigation, theoretical, observational or experimental. For example, in particle physics, one ignores the effects of gravity because the gravitational forces are small relative to other forces; in astrophysics, gravitational forces are a central concern. Although the nature of gravity constitutes a topic of considerable interest for physicists, whether it is right or wrong to ignore gravitational forces at certain scales generally is not an issue of debate. The same type of inclusion or exclusion of important considerations in problem formulation also occurs in ecology. For example, in most ecological population models, the age-structure and sex-ratios of the populations are usually not considered explicitly. Other examples will be discussed in the development of models used to assess the consequences of large-scale environmental change.

Part 1 of the book deals with the omnipresence of change at a variety of time and space scales. This is followed by a historical review and a discussion of the ecosystem concept: a systems concept defined on problems of interest and tempered by considerations of space and time scales. One of the aims of these introductory chapters is to impress on the reader that understanding global change is an issue of both applied and basic interest. Another is to persuade the reader to adopt the use of the term ecosystem in its rich historical definition for its power in framing problems involving synthesis of information.

This is followed by Part 2, which reviews some of the basic concepts

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used in understanding and interpreting large-scale responses to environmental changes. This section introduces ecological modelling, a topic that will emerge in the later chapters of the book. Ecological models are a great array of physical and/or mathematical analogies to ecosystems, but generally they are manifested as computer programs thought to imitate central aspects of ecosystems. Because the time and space scales involved with some focal problems in understanding large-scale ecology are beyond the lifetimes or the logistic resources of ecologists, ecological models have developed as tools for projecting the consequences of observations or theories about how ecosystems may change over time. The degree to which these predictions can be believed actually to occur hinges to some extent on the degree to which these models can reproduce known features of ecosystems in a model-testing mode. For this reason, some effort in later chapters will be spent on issues associated with model verification and validation.

Following an introduction to ecological modelling, Part 2 then covers some of the more important ecological paradigms used in large-scale terrestrial ecology. Niche theory, the mosaic nature of landscapes and plant/environment relations at relatively large spatial scales are discussed. These are large topics. Each has been the subject of entire books and will probably continue to be so. Intentionally, the chapters in this section are relatively non-mathematical – although several of the topics (niche theory, spatial dynamics) have been advanced greatly by mathematical treatment. The emphasis is on the conceptual roots of the topics and their origins as ecological constructs, rather than on the mathematical analysis associated with these topics. The concepts in this second section are the bases for models used to simulate large-scale response of terrestrial ecosystems, which is covered in the third section of this book.

Part 3 discusses ecosystem models, the testing of these models and their implications regarding the functioning of large-scale ecosystems. The leading chapter of the section, Chapter 8, will introduce individual-based models and will emphasise the ecological features embedded in the models. Chapter 9 discusses some of the possible consequences of the dynamics of these models at the population level and for natural landscapes. Chapter 10 will introduce landscape and larger-scale models and the consequences that proceed from the application of the models to issues involving change.

Finally, in Part 4, a model-based evaluation of some of the consequences of global change will be presented. In this section, the prediction of landscape responses to changes will be developed using ecosystem

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models with different underlying assumptions – particularly regarding the spatial interactions and the influence of such interactions on overall system dynamics. Chapter 11 will discuss mosaic landscape models and their use in understanding change of terrestrial ecosystems. Chapter 12 will review some of the progress being made in spatially interactive landscape models, and Chapter 13 will focus on results from models that are based on the assumption of a homogeneous landscape. Dynamic changes in the structure and function of ecosystems are treated at increasingly larger spatial resolution through the text. Therefore, the final chapter (Chapter 14) will close with some of the important global issues in terrestrial system dynamics.

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2 · *The omnipresence of change*

Two hundred years ago, Thomas Jefferson described the bones of an extinct ground-sloth, *Megalonyx* (Wistar 1799), that, because of its large claws, he took to be some sort of giant carnivore (*Megalonyx*, large lion). Mr Jefferson felt that the animal was still alive someplace in North America and reasoned,

> . . . the bones exist: therefore the animal has existed. The movements of nature are in a never-ending cycle. The animal species which has once been put into a train of motion, is probably still moving in that train. For if one link in nature's chain be lost, another and another might be lost, till this whole system of things should evanish by piecemeal. . . . If this animal has once existed, it is probable that . . . he still exists. (Jefferson, 1799)

Jefferson instructed Lewis and Clark, when they were sent west to explore the Louisiana Purchase, to watch for and report on large animals like the *Megalonyx*. The logic that Mr Jefferson used paralleled that of other eighteenth century intellectuals who saw extinction as an affront to the Creator. Grayson (1984), in a rich historical review of the topic of extinction, quotes Jefferson (above) and also Pope (Pope, *Essay on Man*, 1733–4),

> Vast chain of being, which from God began,
> Natures aethereal, human, angel and man,
> Beast, bird, fish, insect what no eye can see,
> No glass can reach! From infinite to thee,
> from thee to Nothing! – On superior pow'rs
> Were we to press, inferior might on ours:
> Or in the full creation leave a void,
> Where one step broken, the great scale's destroy'd:
> From Nature's chain whatever link you strike,
> Ten or ten thousandth, breaks the chain, alike.

These arguments for a constancy in nature, of an unbroken natural chain, survive in popular ideas about the 'balance of nature' and of the antiquity of certain ecological systems. However, most educated people today have little difficulty imagining that species have become extinct or that environmental character was quite different in some previous time. The ideas of an 'ice age' or a 'time when dinosaurs ruled the earth' are commonly understood phrases and, as such, are exemplars of a general appreciation of prior environmental change.

Ecologists are also aware that environments were different in the past. Given this appreciation of past differences, it is surprising that ecological theory abounds with analyses of what ecological systems should be like at equilibrium, and that ideas about ecological succession and landscape change often are posed in terms of a constant environment.* Further, the concept that a wilderness or constant primal state is 'natural' pervades many of our policies on managing parks and nature preserves.

Of course, many of these views are expediencies intended to provide answers for simplified cases and insight into more difficult cases. If one does not know what the behaviour of an ecological system is in a constant environment, then how can one hope to predict its behaviour in a changing environment? Before one can expect to appreciate the dynamic response of ecological systems, it is appropriate to know what the system is like in an unchanging state.

What is known now and is becoming clearer in its details as more information is collected is that the earth environment has been quite dynamic over almost any time scale one might consider. This chapter will provide some examples of changes at some of these time scales. Later, in Chapter 3, it will be noted that one expects changes at frequencies in time to excite responses from different ecological processes.

Long-term variations in climate

When considering the variation in climate over the period of time during which higher forms of life evolved (~800 million years ago), one can see either catastrophe or constancy. The constancy is in the sense that the Earth's temperature has remained relatively constant and in the range that supports life, despite a 25% increase in the intensity of solar radiation (Lovelock and Margulis 1974). Catastrophic events are seen in the seemingly periodic mass extinctions of forms of life. Raup and Sepkoski (1984) claim that there have been nine such extinctions with periodic

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* Solbrig (1994) points to the 'Newtonian paradigm', that all of nature was interpretable in terms of a few laws in a 'clockwork' universe, as a contributor to the eighteenth century concept of the balance of nature. He also notes this view as an influence on most scientists until fairly recently.

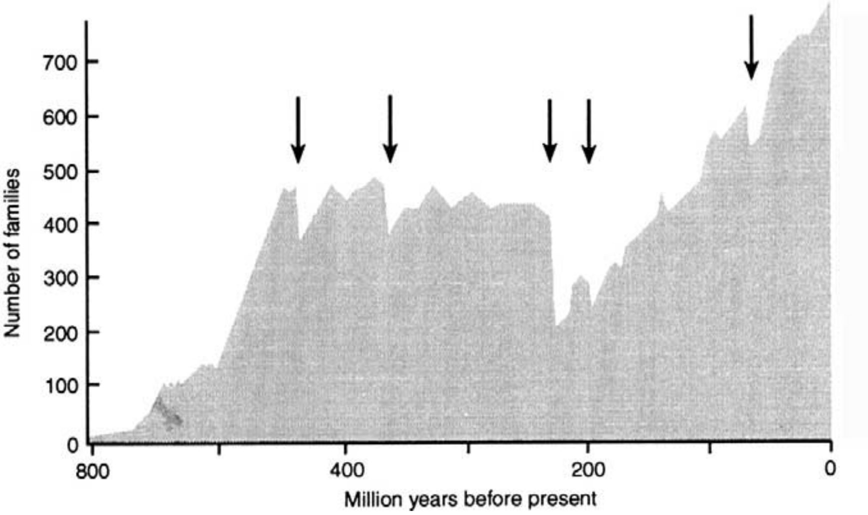

Figure 2.1. Extinction events over the past 800 million years from families of marine animals. Arrows indicate what were interpreted by Erwin *et al.* (1987) as major extinction events in the geological record. From Erwin *et al.* (1987).

components of around 33 million years and 260 million years. Figure 2.1 illustrates the number of families of marine animals living over the past 800 million years and shows several phases of extinction. The largest drop in numbers of marine animal families occurred in the Permian period (*c.* 245 million years ago) when the number of families dropped by over 50% and the number of known genera was reduced by around 80%. Such drops in the existence of higher-level taxa imply losses of species as high as 96% (Jenkins 1992). While the topic is hotly debated (Jablonski 1986), the periodicities seen in extinctions (Fig. 2.1) conform to large events on the Earth's surface (tectonic events, sea level changes, changes in the magnetic poles) and evidence for meteor impacts.

One of these extinctions of recent interest appears to have occurred at the end of the Cretaceous Period, 65 million years ago. It involved the extinction of about half of the living genera at the time (Alvarez *et al.* 1980; Ganapathy 1980). This included microscopic aquatic plants and animals of various kinds, marine and flying reptiles, and dinosaurs. However, land plants, crocodiles, snakes, mammals and many kinds of invertebrate survived (Lewin 1986). There is (and will likely continue to be) a debate as to the cause: an asteroid impact (Pollack *et al.* 1983) or volcanic eruptions have been suggested as two possible causes. Harrington (1987) observed that these cataclysmic events may obtain their periodic