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Toward a More Exact Ecology

edited by
Peter J. Grubb
and John B. Whittaker

TOWARD A MORE EXACT ECOLOGY

The Second Jubilee Symposium to Celebrate
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TOWARD A MORE EXACT ECOLOGY

FOREWORD

The British Ecological Society was founded in 1913, the first national ecological society in the world. For our jubilee 75 years later, we decided that the time was ripe for taking stock of the achievements of our subject, and looking forward toward new developments. Accordingly, the Society held two complementary symposia in 1988. The first was planned as an assessment of the contribution of ecology to understanding the natural world, under the title *Ecological Concepts;* it was held at University College London, the venue of the inaugural meeting of the society, on its anniversary date, 12–13 April. The second was focused on the future, and called *Toward a More Exact Ecology*, aimed at considering the most fruitful current approaches and technologies, and determining the major obstacles and likely profitable lines of advance; it was held at St Catherine's College, Oxford, on 13–15 September. The two symposia volumes thus represent a vision of the ecological community's understanding of the past, present and future of the subject; it is hoped that both will be of value in the planning of future research.

R. J. BERRY
President 1988–89

PREFACE

The last major celebration of the British Ecological Society was in 1963, when it reached its 50th year. It was decided then to mark the occasion by holding a jubilee symposium at University College London, and in due course the proceedings of that meeting were published in the form of a special supplement to the Society's journals. At that time the organizers considered that there were five main areas of development in ecology: ecology and conservation, quaternary ecology, production ecology, experimental and autecological studies, and finally the community concept.

Now, 25 years on, the 75th anniversary of the Society has been marked by two jubilee symposia. As explained in the foreword, the first reviewed the history and current state of ecological ideas, and the second looked forward to exciting new developments.

In its 75 years the Society has grown from a small vegetation committee to a 'broad church' of nearly 5000 members. As it has grown, it has embraced a vast range of expertise and interests. Selecting a limited number of high-profile topics, representative of advances in the subject as a whole, is necessarily a somewhat idiosyncratic task. In the last 25 years, however, ecology has emerged from being a predominantly descriptive subject to one with a more substantial theoretical framework underpinned by evidence from experiments. In this advance, improved technology has undoubtedly played a most significant role; few ecologists could operate without a computer to hand, while some branches of the subject require very sophisticated instrumentation. But we also owe to this period much greater precision in the formation of hypotheses, a more general search for mechanisms, increasing integration of ecology with other disciplines, and increasing demands for application of the lessons learned. These trends have, in part, determined the choice of our six main topics.

We have resisted the tendency for symposia to become more and more specialized, and have brought together botanists, microbiologists and zoologists, evolutionists and behaviourists, physiologists and system modellers to identify the ways in which their particular ecological fields are becoming more exact through application of new techniques, refinement of theoretical concepts, and bridge-building over the artificial divides between cognate disciplines. In doing so, we are constantly reminded of the absolute necessity for concepts, models and experiments to be based on sound biological assumptions founded on good natural history observations.

Emerging again and again in these essays is the question of scale in investigations, ranging from those concerned with dynamics of a few square metres of vegetation to those on whole ecosystems and global phenomena. Linked with this question of scale is the inevitable divergence resulting on the one hand from the reductionism appropriate to some experimental techniques and the need to synthesize information on a vast scale, and on the other hand from the gap between ecological theory and practical management of resources. It is paradoxical that the move toward greater exactness in ecology can involve simultaneous deployment of these widely different approaches.

In addressing the whole question of exactness in ecological science we hope to show how each part of the subject can benefit from being placed in a wider framework, and perhaps to give the lie to Edmund Burke's view that 'it is the nature of all greatness not to be exact.'

We were much helped in the planning of the symposium by Malcolm Cherrett, Charles Godfray, John Grace and John Lawton, and in the editing of this volume by numerous referees. We thank Mick Crawley, Charles Godfray, John Grace and Bill Heal for leading the evening discussions. The Society is especially indebted to Robin McCleery for acting as local organizer; together with the domestic bursar of St Catherine's College and her staff, he ensured that the meeting was both very enjoyable and efficiently arranged. We are also grateful to Susan Sternberg, Rowena Millar and other staff at Blackwell Scientific Publications for their sympathetic handling of the production side.

Finally we thank our wives, Anne and Helen, for their tolerance and support while we were engrossed in our endeavours to prepare the text of this book on time.

PETER J. GRUBB
JOHN B. WHITTAKER

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I. INTRODUCTION

Holling (1966) considered the attributes of a good ecological study to be realism, precision, completeness and generality. In the introductory paper, exactness in ecology is defined as accuracy or precision and perfection or completeness of understanding, leading to an increased ability to predict. Exactness may be qualitative or quantitative, but it will be underpinned by sound mechanistic understanding, which may be possible at an ecological level, but will often be supported by physiological or chemical and physical observations.

It is proposed that an ecological principle is a proposition that is always true and has a mechanistic basis, whereas a generalization is a proposition that has a high probability of being true but need not have a theoretical basis. Definition of as complete an array as possible of principles and generalizations will undoubtedly lead to a more exact ecology, but so will the art of asking new or neglected questions. Sometimes this will be by new approaches to old questions, for example by ecological physiologists exploring what sets the limits to the distribution of an organism rather than over-emphasizing adaptation, or it may be by the coming together of disciplines previously pursued separately, as in the recent exciting developments in evolutionary and behavioural ecology. If there is any tendency for these to be somewhat reductionist in nature, this is surely balanced by ecologists working on ecosystem and large-scale applied problems requiring adjustments of scale with which we are only just beginning to learn to cope.

The ways forward are diverse. Exactness need not be the prerogative of the mathematical ecologist, and valid generalizations may be made by anyone with mechanistic insight into patterns of nature. Ecology will advance most effectively when its wealth of intellectual diversity is combined in a community of effort. That should be better understood by ecologists themselves than by most other scientists.

REFERENCE

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1. TOWARD A MORE EXACT ECOLOGY: A PERSONAL VIEW OF THE ISSUES

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INTRODUCTION

The objectives for the meeting, as set out by the Organizing Committee, were: 'to review the most exact studies in a selection of fields within ecology, to consider the approaches and technologies which are being most fruitful at the present time, to determine the major obstacles to progress, and to make suggestions for the most profitable lines of work in the future.' It is certainly not my intention to 'set an agenda', as some would say, because the fields covered are too diverse for any one person to deal with. Rather, I have the three following major objectives: to put forward some very general ideas about the theme of the symposium, to place the topics chosen for analysis in some kind of perspective, and to mention some of the important topics not allocated a place in the programme. Inevitably the perspective provided is an essentially personal one, but I hope it will serve as a basis for useful reflection by others.

The first part of this paper deals with the meanings of 'exact ecology', and the issue of prediction in ecology. The second part deals with exactness in various approaches to ecology: in studies on the distribution and abundance of organisms, in evolutionary ecology, in community ecology, and in ecosystem and applied ecology. The third and final part offers a viewpoint on the issue of empiricism and the naturalist tradition.

THE MEANING OF EXACT ECOLOGY

According to the *Oxford English Dictionary*, the word 'exact' is used to express two kinds of idea. The first is 'accurate' or 'precise', and the second is 'consummate, finished, perfect'. I believe that it is helpful to consider this symposium as concerned with both of these senses of 'exact'. Certainly we are concerned with improving the accuracy and the precision of ecological studies, and some contributors will emphasize this aspect, but I believe that we are also concerned with the issue of perfection, which might perhaps be restated as 'completeness of understanding'. That, in turn, might be taken to be reflected in an increased ability to predict.

Advances in accuracy and/or precision

There are several areas of ecological study in which major advances in accuracy and/or precision are being made at the present time through development of new techniques. The one area chosen for discussion at this meeting is that of measuring the rates of physiological processes in free-living plants and animals. Here the greatest general problem has been the 'inaccessibility' of the organism. Even for plants, which do not run, swim or fly away when you start to study them, the issue of inaccessibility is real, because as soon as you enclose some plant part to measure, say, the rate of output of water or uptake of carbon dioxide, you change the conditions and you fail to measure the rates that would occur in the absence of your apparatus. A great deal of effort has been expended by ecologist physiologists to overcome this problem. One approach has been to determine the rate of uptake of CO_2 into whole stands of plants by aerodynamic methods which do not involve enclosure of plant parts, but this approach is useful only in certain kinds of vegetation, and in any case cannot yield information about individual plants or plant parts. To obtain that, enclosure is necessary, and then it is essential to control the environment of the plant part being studied so as to keep it like that of the unenclosed parts. Pioneering work of this type, done in the Negev Desert of Israel in the 1960s (Koch, Lange & Schulze 1971), ultimately provided information of great value in testing ideas on the optimization of changes in stomatal aperture which control the ratio of water lost to CO_2 taken up (Cowan & Farquhar 1977), so illustrating our second meaning of a more exact ecology — a more complete understanding. Long's paper in this volume on measurement of gas exchange in plants brings up to date the story concerning both meanings of exactness.

For those working with animals the problems are plainly more severe. However, the use of radio- and acoustic-telemetry has hugely increased the quantity of information available about rates of physiological processes in free-living vertebrates, and has incidentally transformed the quality of our understanding of the ways in which the animals concerned are suited to their environment and way of life (Butler, this volume). The use of an indirect technique — 'double labelling' of the water supplied to animals — has yielded independent information of great interest on the particular question of respiratory rates, which are vital for our understanding of many different issues in evolutionary and behavioural ecology (Bryant, this volume).

Other kinds of measurement that might reasonably have been chosen for review at the meeting are listed in Table 1.1. In several cases it might

TABLE 1.1. Areas of current advance in accuracy and/or precision through development of new techniques, not discussed at length in this symposium

Area of advance	Selected references
Determination of genetic identity by 'finger-printing' of DNA or RNA	Schaal (1988)
Determination of animal movements by radio-tracking	Kenward (1987)
Determination of changes in cover and other properties of particular vegetation-types on land, and determination of ever-changing patterns of surface temperature, productivity, etc. of the oceans through remote sensing by satellite	Curran (1985); Platt & Sathyendranath (1988)
Determination of sources of metabolites and rates of metabolism, and determination of past climatic conditions by use of stable isotopes	Peterson & Fry (1987); Bryant (this volume); Gray (1981)

be argued that the techniques which have recently become available do not merely increase attainable accuracy, but make possible the answering of questions that simply could not be tackled before.

Outstanding barriers to the attainment of greater accuracy and precision

Just one field within ecology will be considered here, by way of illustration. The results of pollen analysis have changed fundamentally our understanding of the status of present-day plant communities (West 1964; Watts 1973), and our knowledge of the pace and extent of change in them (Davis 1976, 1986; Walker 1989), but there are innumerable cases where our knowledge of what happened in the past is limited by our inability to identify plants from their pollen further than to genus or even family.

Also striking is the impossibility of reaching any very accurate quantitative reconstruction of past vegetation because of the variation between species in their output and dispersal of pollen, and because of variation in the degree of preservation. In the investigation of many deposits the feasible resolution in the time dimension is also severely limited, although in favourable cases changes over a few decades can be followed in detail (Bennett 1986). Our recognition of limits to both qualitative and quantitative exactness in this particular context leads me to make some general remarks on these two types of exactness.

Qualitative and quantitative exactness

As shown in Table 1.2, the two kinds of exactness are concerned in both the description of the status quo and any forecast about the effects of change in one or more conditions. Qualitative exactness is what we are concerned with in establishing the genetic identity of the individual, the pathway of energy or nutrients through an ecosystem (including not just the animals but also the micro-organisms in such intractable material as soil), the biochemical nature of the mechanisms in, say, plant–herbivore interactions, and the identity of the currency in evolutionary trade-offs or in mutualisms such as those described by Pierce in this volume.

TABLE 1.2. A simple classification of variables studied by ecologists according to the kind of exactness involved

Involving qualitative exactness
(a) Descriptive of the status quo
Genetic identity of individual
Pathway of energy, molecule or atom
Mechanism of interaction between parties
Currencies of trade-offs and mutualisms
Setting for any detailed analytical or experimental study
(b) Forecasting effects of changed conditions
Abundance of x: decrease or increase?
Involving quantitative exactness
(a) Descriptive of status quo
Extent, number, rate
(b) Forecasting effects of changed conditions
Extent, number, rate

I would add to this list the more controversial issue of defining the setting for ecological studies. I once asked Professor Heinz Ellenberg, Honorary Member of the British Ecological Society, what he thought was the most important contribution of European phytosociology to the world's ecological tradition, and he said 'qualitative exactness'. In answering in this way, he had no illusions about achieving absolute exactness in phytosociological work, but he considered as inexcusably inexact the specifications of ecological setting all too often found in British and North American papers reporting otherwise valuable work, for example 'dry oakwood' or 'wet grassland'. For those who doubt the value of Ellenberg's point, I recommend that they read his account of investigative ecological studies placed in a phytosociological context in