N.Z. ECOLOGICAL SOCIETY

Report of Third Annual Meeting

It was decided at the 1953 Annual General Meeting that the Society should not hold a separate meeting in 1954, but that it should co-operate if possible in the Eighth Science Congress to be organised by the Royal Society of New Zealand. The New Zealand Ecological Society therefore became one of the Participating Bodies in the Congress and undertook the organization of two half-day symposia, which were held as joint meetings of the Botany and Zoology sections. These were: "Population Dynamics of Newly-introduced Species", held on the afternoon of Thursday, 20th May, and "Ecology of Sub-Antarctic Islands", held on the following morning. The symposia were organised in the same way as in previous years, the first half of each period being occupied by papers by invited speakers, and the second half by impromptu discussion. The formal Annual General Meeting was held on the Wednesday evening.

PRESIDENTIAL ADDRESS

The Growth of Accuracy in Ecology

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I am very conscious of the responsibility that has fallen on me to deliver this, the first presidential address to the New Zealand Ecological Society. It is perhaps customary for a presidential address to deal in broad terms with some topic related to the main objects of the body to which it is addressed. I feel that I ought therefore on this occasion to talk about ecology in a fairly general sort of way. Much as I should like to do so, I am immediately up against the fact that ecology covers such a wide field, and has so many aspects, that it would be possible for few people—of whom I am certainly not one—to deal at all competently with the subject as a whole. All I can hope to do tonight is to give you some idea about what ecology looks like, as seen by one whose working life has been largely devoted to studying the inhabitants of fresh waters, and who has probably developed a bias in favour of the quantitative approach. I ought perhaps to begin by defining what I mean by "ecology", but I'm not going to. If I did, probably many of you would promptly say to yourselves: "That's not what I mean.", and that would invalidate much of my subsequent argument.

Whatever it is, ecology is a branch of science which deals both with plants and with animals. This does not necessarily split the subject itself into two, and the formation of this and other similar societies is itself a testimony of the need to prevent such a split opening too widely. It does, however, whether we like it or not, tend to split the students of the subject into two camps. As knowledge grows it is becoming inevitable that most of us should approach the subject with a primary interest in either plants or animals, and indeed generally in some special ecological or taxonomic group. The best we can hope to do is to be aware of the impact of our selected organisms on the other sections of the living world, and, conversely, of the impact of that world on our own subjects. In what follows, therefore, I am speaking as one whose ecological world is centred on animals, with plants forming a sort of peripheral fringe, which in places is rather scanty.

In describing to you my view of ecology, I want to discuss some of the lines along which it has already developed and is, I believe, likely to continue to develop in the future. It is because it summarises one of the most important features of that development that I have taken for my title—"The Growth of Accuracy in Ecology". To provide a standard against which to assess that growth, I want to ask and then attempt to answer the question—"Is ecology an exact science?" The answer will, I think emerge most clearly if it is sought in two steps. The first step is to see how far the objects of ecological research are appropriate to a science claiming to be exact; the second step is to examine some types of ecological work which, in intention, have a claim to exactness, to see what degree of precision is actually attained.

The simplest ecological observations are probably those which record the part of the earth's surface covered by the normal range of the organism, and which describe in general terms the type of habitat in which it is usually found. Observations of this kind, which are concerned only with an end result and not with the way in which it arises, are commonly found in monographs and handbooks to particular groups, and they pre-date by far the emergence of ecology as a distinct branch of science. They remain however the basis of ecology as we know it today, and this has arisen essentially as an attempt to understand and explain the facts of distribution, although in applied work the immediate practical aims may be of a different nature. The conscious study of ecology has, rather naturally, been approached from two distinct directions. On the one hand, we may select a particular species of animal or plant and study its relation to the animate and inanimate world surrounding it. This branch is often described as autecology. On the other hand, we can take the entire assemblage, or community, of animals and plants which inhabit a particular locality or type of locality, and study the relation of the various species to each other and to their physical environment. This is often called synecology. There is, I suspect, a general tendency for plant ecologists to approach their subject from the synecological point of view, while animal ecologists more often, though not always, are concerned primarily with particular species—they approach from the standpoint of autecology. In making this generalisation I have deliberately stressed the idea that the difference is essentially one of approach, for it seems that the further our studies are advanced the more common ground will be found. The student of the community must find that as he advances he has to know more and more about each of the component species, that is, he must study their autecology. On the other hand, the student of particular species must inevitably find that his species is affected in various ways by other forms which inhabit the same environment; they may, for instance, provide food or shelter, or they may prey upon his original species. He is therefore compelled to see and to study an assemblage of organisms, which can be envisaged as forming concentric rings round the species with which the study commenced; he is therefore studying the community, although from a particular aspect. Even this concentration on one aspect may not, in practice, form such a distinction from the synecological approach as at first appears, since with the great number of species which usually constitute a community limited resources would normally compel the worker to concentrate mainly upon a few forms, generally those which in one way or another occupy a dominating position. My first point is therefore that while the rather arbitrary distinction between autecology, or the study of species, and synecology, or the study of communities, does conveniently distinguish between two main methods of approach, this distinction gradually disappears as knowledge advances.

The data on general distribution which I have mentioned earlier as forming the basis upon which ecological study begins are essentially of a descriptive and qualitative nature. But, I suggest, the true study of ecology begins with the attempt to observe this distinction in detail and with accuracy instead of in broad general terms, and, especially, to correlate it with detailed knowledge of the life-history of the organisms concerned. Thus, for instance, instead of saying that a certain moth is found in beech forests, we record that the larvae live and feed on the leaves of *Nothofagus*; or, instead of saying that the trout is found in rapid, stony streams, we find that they can only reproduce successfully in clean gravel, such as is found only in those streams. Similarly, if our approach is synecological, instead of saying that a certain tree occurs in coastal forest, we now list the species associated with it and observe the conditions of aspect, slope and so on under which it occurs. Or, on the marine side, we no longer simply say that a certain barnacle is found on rocky shores; we say that it is found only in a particular zone between tide-marks on such shores, and that certain other species of plants and animals occur with it, and others below it. At that stage the observations are still largely of a qualitative nature, and we are concerned only with the presence or absence of our organisms, or, at the most, their density on a rough scale of scarcity or abundance. In the same way, the observations on the environment are generally of a qualitative nature. Up to this point at least it is obvious that ecology can have no pretensions to exactitude, but I would stress that I do not regard such work as inferior for that reason. In fact, observations of this kind form an essential preliminary to more detailed studies, which as a rule cannot even be efficiently planned until preliminary qualitative observations have disclosed the main outlines of the pattern.

It is from this point on that an increasing degree of precision appears in ecological work, and that techniques begin to be concerned with measurement, and not only with observation and description. It is only to be expected that at this stage the lines of ecological research should begin to diverge, but I will try to outline briefly what seem to me to be some of the main routes being followed—I would remind you again of the limitations of my outlook which I mentioned earlier. Of these lines, the one which should logically be dealt with first is that which is primarily a refinement of the descriptive methods I have already discussed. This involves the substitution of measurements for the generalized observations which were adequate in earlier stages. In autecological work, measurements are needed both of the frequency of occurrence of the species under investigation, and of the various environmental factors whose influence is being studied. It is not necessary for both classes of observation—those on the immediate subject and those on the environment—to turn from the descriptive to the measuring phase at the same time, although the fullest use of measured data on one aspect can only be achieved if the data with which they are to be compared are also expressed numerically. Studies based on the comparison of measurements of populations and of environmental factors are more simply made when the environmental factors are physical or chemical than when they are biotic, and this relative simplicity is even more pronounced in the interpretation than it is in the collection of the data. As examples of such studies, I might mention those which have correlated the occurrence of various species of flat-worms with the temperatures of the springs or other sources of the streams in which they are found: also those relating the distribution of plant species, or of plant communities, to the pH, redox potential, or other characteristics of the soil on which they grow. Measurement of biotic factors would, in the simplest case, imply observations on the numerical abundance of those species of plants and animals which occupied the same environment as the subject of study and which were considered to have an impact upon it. It would extend also to include the study of the magnitude of this impact, in such work as that designed to show either the extent to which the species studied fed upon the various possible foods available to it, or, in other cases, the extent to which the species is itself eaten by various animals.

Work of this kind, when successfully completed, presents us with results which show how the size or the density of a population varies with changes in certain environmental factors, and, in this connection, it should be noted that an arbitrary definition of the population has to be made either expressly or implicitly in each such study. These results, however, bring us to the realization that a population is not something which can be fully described by saying that there are X individuals of species Y living in area Z. We are forced to realise that the X individuals consist of so many juveniles, so many immature adults, and so many mature adults, or whatever the appropriate subdivisions of the species may be. If our species is bi-sexual, the population will also consist of so many males and so many females at each of these stages. Realization of the complex structure of the population in turn emphasizes that this structure, and hence the total size of the population, is itself the resultant of such phenomena as survival, reproductive potential and growth. One of the main lines along which ecological studies may develop from the simple measurement and comparison of total populations is that which leads to study of the structure of the population, and of the measurement of the vital statistics which bring it about. In practice such studies may be approached from either end, or from both ends simultaneously. That is, we can either analyse the population and deduce the vital statistics from the results of the analysis, or we can measure the statistics directly and then apply them to the population analysis. Often a combination of such methods may be of use since some data, such as survival and mortality rates, are most easily computed from population structure, while others, such as growth, may be more easily measured directly.

Appreciation of the significance of the vital statistics which determine population size and structure, and the development of techniques by which these statistics may be measured, open the way for study of the influence upon them of environmental factors. In the development of ecological studies along this particular line, this stage is probably the farthest that has been reached in most of the main fields. Indeed, the vast majority of the problems which open up when even the simplest naturally occurring population is considered from this point of view is such as to ensure that this phase of study will provide occupation for many ecologists for a long period. It would be impossible to attempt to catalogue the problems which arise in this field, but their variety and complexity is evident when we consider that they include, among many others, all the phenomena associated with competition and predation, and the effects on fecundity and growth of physical factors such as light and temperature.

The progress of research in this stage—the correlation of vital statistics with environmental factors—appears to differ in two important respects from that involved in the stages which led up to it. The first of these is that emphasis is changing from description to explanation: the other is that research is no longer a matter principally of making observations and measurements and correlating the results; it is now becoming necessary also to build up a body of generalised theory which can be used, first in planning the observations, and afterwards in interpreting the results. I do not claim that the nature of ecological research changes abruptly and completely in these two respects when the stage now being discussed is reached, but I do believe that there is a progressive shift of emphasis, and that this moves particularly fast at the stage when research begins to concern itself with the effect of the environment on those characteristics of the organism which determine its population structure.

Some degree of expansion of these two points may be desirable. The idea, that ecological research tends to develop from description towards explanation is complicated by the difficulty which often arises in distinguishing between a description and an explanation. We have most of us, I suspect, been warned when young not to think that when we described something we have explained it, but we are not so often told how to distinguish between the two. I suspect that much depends on the point of view, and that a given fact may change its status as research develops. To illustrate what I mean I should like to refer back to one of the examples I used of the earliest stage of ecological research: that is, the moth which is found in beech forests. The early entomologist who observed this fact and wondered why was well satisfied when he discovered that the larva fed on *Nothofagus*—there was the explanation! Today another worker becomes interested in the same species. He looks up the literature to see what is known about it and finds that this habit has been recorded; it is therefore described as a *Nothofagus* - eating species. It is for this characteristic that the new worker seeks for an explanation; he tries to find out why the eggs are laid in places from which the young larvae can reach *Nothofagus* leaves; how the larvae select these leaves from other objects about them; whether they can and will eat other food in the absence of *Nothofagus* and so on. Thus, the same fact which was legitimately an explanation to the earlier worker appears only a description to the later. I suspect therefore that in saying that the most advanced field of work which I have described is concerned more with explanation and less with description than those which led up to it, I may only be reflecting the fact that, simply because it is the most advanced field, it poses the largest array of inviting problems, and provides the minimum of completed observations to form the foundations for further advances. If I may digress for a moment, I would add that I believe that the warning against confusing description and explanation should really be directed against labelling already recorded phenomena with new and elaborate names, and particularly against imposing on them complex schemes of classification with resounding terminology, in the belief that one is thereby explaining them. I fear that there are few fields of science in which this warning is more frequently necessary than it is in ecology.

The other characteristic of the study of environmental effects on vital statistics which I mentioned was the increased attention which has to be given to the development of generalised theory at this stage. Here we are faced with a genuine effect which arises from the nature of the phenomena we are studying, and not from our point of view. In the earlier stages of ecological studies we are concerned with the special characteristics of particular species and with simple variations of environmental factors. We need in our study no more than a simple working hypothesis as to the nature of the relationship we are studying, which can be used to direct our observations, and subsequently accepted, rejected, or modified. In the later stages however we are concerned with the combined effect of a number of environmental factors on various vital statistics which may again react on each other in determining the actual nature of the population. Here the complexity of the relationships to be studied for a single species may greatly outweigh the differences between species, and progress may be made by the building up of hypotheses based on foundations formed from studies of a variety of different forms. To use an analogy, which may sometimes be no analogy but the actual truth, the hypothesis may resemble a mathematical equation which can be made applicable to a number of species simply by varying the constants. It is only necessary to turn to a review of the literature of such a topic as predator-prey relationships, or population-regulation, to realise the extent of the generalised theory which has developed, and the way in which it over-rides specific boundaries.

In this address I have so far traced what seems to me the line along which ecological research has developed in reaching population studies as we know them today. I have followed this line first since it is in a way the most logical development from the generalised "presence-or-absence" type of observation with which ecology begins. At various points along the path I have suggested that branching may occur, and that there are other important lines of development. Of these perhaps the most significant is the study of the individual organism. Obviously not all studies of the behaviour or other characteristics of individual organisms can be regarded as ecological, but those which deal with their behaviour under natural conditions, or which are carried out under experimental conditions with the object of interpreting the results of previous ecological studies, are clearly also of an ecological nature. The need for individual studies may arise at any stage in the line of development. Its application at an early stage was illustrated in my example of the moth larva feeding on *Nothofagus*; the development of this study to the stage of finding out why the eggs are placed conveniently to the leaves, and why the larvae select those particular leaves would be best performed by observations on individual insects. Individual studies can lead from stage to stage in the same way that occurs in those centred on populations. Thus, field observations might show that in a given stream there was a progressive change in the specific composition of the mayfly fauna as places of increasingly rapid current were examined. In seeking an explanation of this observation, the investigator might find by experiments with individual nymphs that each of the species which successively dominated the fauna was able to withstand a faster flow of water before it was swept away. This result would provide an explanation of the original observation, but it would in turn raise the problem of why the species had different powers of resistance. This would lead the investigator to examine the nature and then the method of operation of the structures by which the nymphs attached themselves to the substratum. In this example, the chain led from one problem, which was approached by individual study, to another which was best dealt with in the same way. But the result of individual studies may equally well feed back into the line of population studies, and make possible further advances on this path. For instance, in discussing the type of problems which arose when the influence of environment on population structure was examined, I took as an example the effect of light and temperature on fecundity and growth. These problems are ones which can all be fruitfully studied by the investigation of individual animals under experimental conditions, but the results of such studies will not only provide answers to the problems from which they arose, but they will also give a starting point for further advances in the understanding of the population as a whole.

In the examples I have just quoted I have been referring to the effects of physical and chemical factors—the inanimate environment—on the organism. But there are also many biotic factors which can best be dealt with by study of individual organisms. Perhaps the best example of this is that given by the problems of range and territory which occur in various forms among many vertebrates, and possibly not a few invertebrates. These effects, which must have considerable influence on the density, and so on the size, of populations, can undoubtedly be best studied by detailed observations on individual animals under natural conditions. I suspect that a botanical field in which study of individuals would give useful data regarding the operation of biotic factors might be that concerned with intra-specific and inter-specific competition for light and space.

To sum up: what I have said must make it evident that I regard the study of ecology, like any other true science, as a process in which almost every observation does not merely answer —if successful—the problem it was intended to solve; it also places before the investigator, or other students of the same field, a number of new problems which were not previously apparent, and which cannot be solved without further investigation. It is in this way that the subject advances and continually expands, and I have tried to indicate in this talk some of the principal lines along which the advance has occurred. I am well aware that there are many important branches of ecology of which I have made no mention. Sometimes it may be because of my lack of appreciation of their significance, but I believe that it is usually because they form only one of the lines of work in progress at one of the stages in development which I have suggested. I feel, however, that I should make some mention of the fairly recent relationships which have appeared between ecology on the one hand, and genetics and evolutionary studies on the other. I suggest that from the ecological side this contact can be regarded as the latest stage so far reached in the line of development which proceeds through studies of the individual organism. As such a line is followed, sooner or later we must come to an answer which is, in effect, "because it's the nature of the beast". In my example of the mayfly nymphs of rapid streams, the final correlation of distribution in relation to water velocity with the structure of the adhesive organs seems to reach this point, and in such a case further exploration must take us into the field where ecology joins up with genetics and evolution studies.

In my view therefore ecology develops by the comparison and correlation of the responses of organisms with environmental factors in greater and greater detail, and with ever-increasing accuracy. We begin with a stage of general description; from this we go on to detailed description; this takes us to the direct comparison of single, simply-determined quantities; and finally we reach the stage of the simultaneous study of many inter-related factors and responses which form a complex which can only be interpreted and analysed by the use of a theoretical concept as a model.

Reverting to my original question as to whether ecology is an exact science: the first part of the answer seems to be that in intention, at any rate, it gradually becomes one as it develops. In the early stages in any field attention is concentrated on obtaining the broad outlines of the picture in general descriptive terms. As progress is made, greater detail is sought, and increasing use is made of numerical data and quantitative relationships. Numerical data, to be of value, must be as accurate as it is practicable to make them, and thus the aim of exactitude comes more and more to the fore. Similarly in non-numerical data an increasing degree of precision must be sought.

The second part of the question was how far ecology succeeds in those parts of the field where exactitude is an aim. Obviously there is no one general answer to this question, and it would be impossible to discuss in detail the success achieved in each of the various fields where there is some claim to exactitude. All I can hope to do in the time available is to mention a few relevant points which seem to me to have fairly general significance in this connection.

The first point which occurs to me is that the value of exactitude does not apply only to numerical data. Apart from the obvious fact that observations of any sort are actually harmful rather than useful if they are incorrect, it is also clear that the usefulness of even correct observations increases as their precision increases. It appears to be only gradually becoming realised by ecologists how much this applies to the application of taxonomy to ecological work. We have all seen much published ecological work in which the forms dealt with have very inadequate systematic identification, and I suspect that most of us will have published such work ourselves. In studies involving large numbers of specimens belonging to a wide range of major groups it is often virtually impossible for the single worker to become sufficiently familiar with all groups to be able to handle the material with sufficient speed. Where the organisms are, so to speak, part of the background of the study, lack of specific identification may have little effect on the value of the work; but, in studies directed towards some characteristic of the particular organism, or where the organism, though regarded as part of the environment, may operate through some feature which may vary between one closely-related species and another, the need for rigorous specific identification becomes apparent. Without it, results which may be misleading or even contradictory may arise when an attempt is made to duplicate previous work, or to extend it to related forms. Realization of this danger seems now to be rapidly spreading, but failures in this respect in many early ecological studies, as well as in some of the present time, limit the achievement of that degree of exactitude which is desirable.

Much ecological work is concerned with the influence of physical and chemical environmental factors on various organisms. Measurement of these factors can sometimes raise peculiar problems. In general the actual measurement of humidity, or temperature, or pH, or whatever it may be, can be made by the standard methods developed for the purpose. The results therefore should have the degree of accuracy for which the technique was designed, and this may be selected to suit the needs of the study. This degree of accuracy will in fact be obtained if the result is accepted as a measurement of that quantity at the place and under the conditions where it was actually made. In ecological work we usually proceed to correlate it with some feature of the organism, on the assumption that we have measured the actual impact of that factor on the organism. This assumption is not always justifiable; current velocities measured on the surface of a stream do not, for instance, give a good measure of the impact of water-flow on animals living among the stones of a stream-bed; nor does measurement of sunlight in the open tell us much about the illumination received by plants growing nearby on the forest floor. Errors as gross as this are usually obvious, and often, but by no means always, avoided. Smaller errors of the same sort may be insidiously hard to detect and avoid, and I feel that they provide another major source of limitation on the exactitude of ecological techniques.

One of the major techniques of quantitative ecology is now that concerned with the size or density of animal or plant populations. The variety of techniques employed is large, and a very substantial literature has developed regarding the statistical theory of the techniques and the estimation of the errors involved. The great majority of these methods are based in some way or other on random sampling, and as a result substantial sampling errors are very often involved. By their very nature these techniques, which are generally still the best available to us, give results which have a degree of uncertainty far in excess of that normally encountered in those fields of science which by common consent are termed "exact". I believe it is unlikely that any substantial improvement can be made in this respect as long as we continue to be limited to the use of sampling techniques in the forms in which we have them today. The greatest possibility of advancement seems to me to lie in the application to these problems, to a much greater extent than at present, of the results of studies of individual organisms. These studies should ultimately lead to such an improved understanding of the way in which the individual members of a population are distributed that much that seems now to be random may be shown to be responses to environmental factors, both biotic and physical, and, as such, susceptible to more accurate measurement. There seems a real hope that such a development would so reduce the random features of the distributions as to produce substantial increases in the accuracy of our techniques of population measurement. It is evident that if there are sources of inaccuracy in even the most advanced fields of ecological research which are as prevalent as my three examples seem to be, then it becomes impossible to sustain the claim that ecology is now an exact science. But we must not forget that it is one of the youngest branches of biological science. Its aims, and the knowledge which it seeks, become ever more precise as it develops, although much still remains to be done in the generalised descriptive fields which provide the foundations. Its techniques are also new, and in process of adaptation from those developed by the older sciences. Ecology is not an exact science today, but it is moving in that direction, and I believe the day will come when its claim will be as well recognised as that of many other branches of science to which we now accord that title.