THE PLACE OF ECOLOGY IN SCIENCE AND AFFAIRS

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Basically, ecology is concerned with the distributions and densities of plants and animals; hence with the external factors of the environment which limit these distributions and densities; and with the internal factors in the organisation of communities and populations which regulate these distributions and densities. To put it shortly, ecology asks "How many organisms live where and why?" Man is himself concerned in these questions, indeed vitally concerned at the present day, as will be discussed later.

To learn what is the scope of ecology as a scientific discipline and how it may affect our attitude to human affairs, we should look briefly back on its development. This is not a lengthy task, for it took shape only during the early years of this century.

THE GROWTH OF ECOLOGY

Plant ecology led the way in this development, perhaps because the composition of aggregations and associations is easier to study in organisms that are stationary. Many distinguished names are connected with this stage, of which those of F. E. Clements and A. G. Tansley should be specially mentioned. Plant ecology remained for a long time partly preoccupied with the description and classification of habitats in botanical terms and from this has sprung the detailed and somewhat confusing nomenclature of phytosociology, a subject which still absorbs much of the energy of European plant ecologists. At the same time the study of pattern and process, especially succession, in plant communities in relation to the physical environment has produced some of the most fruitful progress in plant ecology.

But, on the whole, a dynamic approach to ecology by botanists was confined to plant communities, in spite of Tansley's early contention that the *ecosystem* (i.e. the whole complex of animals, plants and physical environment together) was the proper unit of study. The tremendous impetus of population ecology, the investigation of how the numbers of any given species are regulated, seems to have passed the botanists by, with one or two notable exceptions. Experimental work has been directed largely to elucidating the ultimate limiting factors to the distribution of populations and communities.

More recently, since the end of the last war, there has been a welcome coming together of plant and animal ecologists to study whole ecosystems, especially from the point of view of energy flow—a coming together perhaps already foreshadowed in F. E. Clements and V. E. Shelford's *Bioecology* (1939).

The development of animal ecology followed, at first, the same sequence, concentrating on descriptive work which laid the foundations for community and habitat classification and on exhaustive analysis of the limiting effects of the physical environment in relation to the physiological characteristics of species. A notable pioneer at this stage was the Danish biologist C. G. J. Peterson, who showed how the animal communities on the sea bottom near Denmark fell into well-marked categories according to the physical nature of the sea-floor. In terrestrial studies, V. E. Shelford's Animal Communities in Temperate America (1913) was a landmark for many years, followed by R. Hesse's Tiergeographie auf ökologischer Grundlage (1924). Much valuable work on these lines, descriptive of communities and of environmental factors, was carried out at this time, even though it was slily observed that the only really indispensable item in the ecologist's field kit was a pH meter!

But the book which really opened up new horizons for the animal ecologist and for the naturalist was Charles Elton's Animal Ecology (1927), because it enunciated so clearly the principles of community structure and functioning. At the same time Elton insisted that first-hand, accurate field observation was allimportant in this new approach. One immediate result of his book was a burst of activity in the field, measuring communities or parts of communities, in which amateurs and professionals worked together. As an example, we may recall the quantitative surveys done by English ornithologists at this time—the index to the heron population, the surveys of heathland and woodland bird communities, organised by the initiative of E. M. Nicholson, David Lack and others.

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POPULATION ECOLOGY

But, during the 1930's and 1940's, animal ecology was largely diverted to the study of populations and a vast output of both field and laboratory work, to which amateur naturalists were still making significant contributions, converged upon the central question of how the numbers of animals are regulated in nature. Charles Darwin, partly inspired by the work of Malthus, had, long ago, pointed out that the capacity of a species to reproduce its kind is far in excess of what is needed in order to keep a population stationary in numbers. The resulting rapid turnover of members demands a delicate, self-adjusting mechanism to prevent either excessive over-population or extinction. Biometrical and actuarial ways of handling population data, developed especially for human populations by such people as Raymond Pearl early in the century, were available for tackling just such problems. Here also man is deeply involved and, at this turn of events, the study of populations must have appeared more relevant to his future than that of communities.

Several things combined to push population studies to the fore during this decade of exciting intellectual stir among ecologists before the Second World War.

To begin with, several compartments of man's own economy, whose research activities were better financed than those of universities, had been exploring the analysis of demographic data as a help to understanding the variations in numbers of fishery and agricultural crops and of the competitors for these crops (mostly known as 'pests'). Thus already before the first World War, fishery research departments were trying to forecast harvests by a knowledge of population turnover, distribution of age-classes and so on, and, in Great Britain, this work was developed after the war by such people as Michael Graham and Sir Alister Hardy.

Economic entomology took its rise as far back, perhaps further, and the exploration of the effects of predator on prey and of parasite on host could only be effected in terms of population measurement. Many of the achievements of biological control in this sphere, beginning with the suppression, back in the 19th century, of the scale insect *Icerya purchasi* in Californian citrus orchards by the introduction

of the ladybird *Novius cardinalis* from the pest's homeland, and continuing with such achievements as the rout of the prickly pear, *Opuntia*, which had sterilised hundreds of square miles of Queensland, hit the headlines so hard that people forget the many failures and occasional catastrophes on record. Early successes encouraged the attitude of 'have a bash' and, in the long run, economic entomology may have contributed the more because its failures made people look deeper into the principles of population control.

Game management, which took its origin in North America somewhat later, was at first rather narrowly confined to economic issues (with some notable exceptions, e.g. the work of Aldo Leopold). I still treasure the passage in a published study of quail populations which ran 'for the purpose of this paper reproduction will be taken to cover the period from the egg to the gun'! But, since then, game management research has added conspicuously to our knowledge of population dynamics.

Similarly the cultivation of population research was a necessary part of many valuable epidemiological studies, the results of which helped to control troublesome diseases.

But the greatest inspiration in this field of ecology came from the interplay between theoretical ideas about how animals are regulated and experiment and observation in the laboratory and the field. On one side we have such people as A. J. Lotka, Vito Volterra and A. J. Nicholson; on the other side we recall in the laboratory the monumental work on populations of the flour beetle Tribolium by Thomas Park, on the fruit-fly Drosophila by Raymond Pearl, on grain-infesting insects by A. C. Crombie, on Protozoa by G. F. Gause, and so on. At the same time, in the field, some very detailed and laborious investigations tried to check theory with a wealth of facts, e.g. G. C. Varley studying a gall-fly, H. G. Andrewartha studying thrips, A. Milne studying ticks and a succession of researches on vertebrate populations notably mice, voles and lemmings among mammals and titmice among birds.

In spite of all this labour, the controversies raised by mathematical ecologists still remain, to a certain extent, unresolved. The concept of density-dependent regulating factors is a case in point. At its simplest this suggests that,

if the density of an animal increases, the percentage mortality must increase accordingly to prevent the population expanding explosively. In other words the rate of mortality is linked on a sliding scale to the density of the animal being regulated. The influences which can operate in this density-dependent way are comprised under competition for food and/or space and the effects of predators, parasites and disease organisms. Some ecologists think that only these density-dependent factors can regulate populations; others believe that they have no significance compared with such things as climate.

Again some ecologists seek a single fundamental principle upon which the whole mechanism of population regulation is based, while others believe that a whole complex of influences is at work. Yet another disagreement is between those who believe and those who deny that animals can, through behavioural mechanisms, regulate their own numbers at a level which does not endanger their resources (Wynne-Edwards 1962).

COMMUNITY AND ENERGY TRANSFER STUDIES

Perhaps because the results of so much effort have been disappointing, ecology has tended during the last 15-20 years to swing back to more community study. The ideas and the practice of measuring the metabolism of an ecosystem, either in terms of the flow of energy or the circulation of matter through the successive trophic levels of green plants, herbivores and carnivores and through the decomposing organisms, such as fungi and free-living microorganisms, are not recent. A. J. Lotka (1925) and A. Thienemann (1926) put forward some of the basic ideas, but not until 1940 was the first energy budget of this kind presented by C. Juday, whose subject was a freshwater lake ecosystem. Since then the study of what is now called energetics or energy transfer has expanded to all types of ecosystems, largely owing to the imagination and vigour of E. P. Odum in the United States. In this new approach plant and animal ecologists have at last to work side by side on the whole ecosystem, as Tansley foreshadowed so long before.

The proponents of this new approach are the first to admit that many of their measurements are, as yet, crude, but already many suggestive generalisations about the broad characteristics

of ecosystems have emerged. For instance, figures for primary production by green plants (i.e. the total amount of plant tissue grown per unit area and time) are not much greater in man-made or man-modified habitats, such as fields and orchards, than they are in natural habitats like woodland. This drives home the fact that the possibilities of expanding food production in the world are far less than the present increase of mankind.

There are also now data to show that the transfer of energy that occurs when animals eat plants or other animals is relatively inefficient, all but 10-20% being lost as metabolic heat or as unassimilated material. From a purely utilitarian point of view, therefore, the shorter the food chain, the more resources can be converted into human flesh; more of vegetarian man can occupy an acre than of carnivorous man.

Thus, the study of energy flow through ecosystems, and also through populations, has much to tell us and much more to promise about the general functioning and energetic equilibrium of such systems. But, without descriptions of the structure and pattern of ecosystems in terms of habitat and species organisation, it will only give us an 'impressionist' picture of such a system.

A Synthesis of Approaches to Ecology

So it seems clear to me that we are now nearing a synthesis of these different approaches to ecology. Population dynamics take us so far to solving the problems of how animal numbers are regulated but, without being set in the context of the whole ecosystem, tell only half the truth, if that. On the other hand, the smoothed picture presented by energy flow and productivity studies gives no indication of the complexity and pattern of a community's organisation and, therefore, no information about the components of the production and the paths through which the energy flows, nor about their reactions to interference or exploitation.

So the investigations of the habitat structure and species pattern of an ecosystem and of both broad and detailed paths of energy flow should best proceed together and into the results must also be woven an account of the dynamic balance of component populations. Some cross connections are already being made between these approaches. The development of ecology outlined above may suggest that, of these three complementary approaches, the description of the structure and pattern of ecosystems and communities has been the most neglected since the Second World War. This is, however, not true since a substantial and vital contribution has been made since the war by Charles Elton at Oxford, helped incidentally by the permanent and transient staff of the Bureau of Animal Population, of which he is Director.

THE WYTHAM ECOLOGICAL SURVEY, OXFORD

In 1943 the University of Oxford received the generous gift of the Wytham Estate, an area of some 1000 acres of mainly deciduous woodland, situated within 5 miles of the city centre. This has become, in effect, a nature reserve which is used by all the biological departments for research and teaching. Above all, the estate gave assurance of continuity for long-term research and offered itself as an area, about which a body of ecological knowledge could be built up. So, by good fortune, an ideal study area became available just as Elton was designing his biggest effort towards bringing the complexities of communities within the bounds of practical description and study.

The main task was that of working out a technique of recording the habitats of animals and the animals in each habitat for the whole community living on the Wytham Estate. The technique he evolved was one that could be operated by one person with one assistant and its filing system was based on nothing more complicated than needle-sorted punched cards. By now this spare system has worked so successfully that probably more is known about the flora and fauna of these 1000 acres than of any comparable area in the British Isles, perhaps in the world. Already it is a reasonable forecast that a quarter of all the non-marine British fauna is to be found in Wytham and the data about this representative area of British woodland are assembled in such a way that they can rapidly be sorted to answer a wide range of questions.

The records are entered into this system through a hierarchical classification of habitats, worked out by Elton in co-operation with Richard Miller and published by both of them in 1954. Since a habitat, however big or small, is a *place*, it can be precisely defined, but the problem is to avoid an almost infinite sub-

division into smaller and smaller botanical categories with bigger and bigger names. Elton & Miller's classification is based on structure and its skeleton can be contained within the bounds of one small index card. The use of structure means that, for example, the canopy in one type of forest is homologous with the canopy in any other type of forest so that the system is applicable, with appropriate modifications, to any part of the world.

Many kinds of data can be accommodated within the framework of this habitat classification and of its associated filing systems. The unit which Elton has used extensively is what he has called 'the ecological event'. This is any single observation of an identifiable animal doing something identifiable in an identifiable place. Thus a tortoiseshell butterfly laying eggs on a nettle leaf in an oak wood would be written straight down on a card with routine supporting information. The appropriate holes are punched and, when sufficient cards have accumulated, a picture can be constructed, based on quantitative data, of an animal's real habitat for each of its life activities. It is also possible to determine whether records in apparently 'wrong' habitats are just accidents or whether there is some unsuspected significance.

So, step by step, a complex picture has been built up for the whole estate showing what habitats are occupied by each species, when and for what purpose. Consequently the amount of overlap and possible competition between species can be discerned. Conversely, we can discover the number of species occupying each habitat and can make valuable comparisons between habitats.

By now many specific research projects have also been carried out in Wytham, both by the staff and students of the Bureau of Animal Population and by those of other groups, notably the Edward Grey Institute of Field Ornithology and the Hope Department of Entomology. So there is fed into the system also a mass of information on life histories, distribution and habitat preferences of particular species, as well as analyses of sub-communities, such as dead wood or litter, and studies on population dynamics. The fruits of much co-operative effort are not easy to assimilate but an extensive account of present achievements has been written by Elton and is now in the press.

For the pattern of future development of ecology as a scientific discipline Elton's ecological survey of Wytham Estate has these particular lessons. First, it reveals—incidentally—the multiplicative effect of many ecological projects going ahead in one place. Secondly, after all the wanderings of attention among ecologists during the last 40 years between community description, population dynamics and ecosystem energetics, it re-asserts that knowledge of the structure and pattern of communities, however complex, is both feasible and fundamental. Thirdly, it suggests that the study of this structure and pattern and of the dynamics of component populations should go together with the study of energy flow on the same ecosystem. It is obvious that any of these approaches has much to give the others.

The last, and most important, lesson that we learn is that the ecological study of communities and ecosystems on these lines could be rapidly expanded throughout the world, both by the simple establishment of more such survey centres and by the increased use of modern methods of processing data. Of course, there are the usual dangers of rushing the pace of such expansion and, against these, safeguards would be necessary. Until, however, the investigations enter a comparative phase, it will be most difficult to tackle the vital problem of how man should assess and manage, from a world-wide viewpoint, the resources of his environment which remain to him.

ECOLOGY AND HUMAN AFFAIRS

We can, at this point, turn to examine the relevance of ecological researches to human affairs. Two features of the world scene demand urgent attention—the proliferation of the human population and the effect of man's activities upon the health of the world ecosystem. Both these features belong to one problem, just as the foregoing considerations have shown that no specific piece of ecological research is really meaningful except in the context of the ecosystem. Nevertheless, it is simpler, in the first instance, to examine the two features separately.

We have already noticed that the process of converting plant tissue into animal tissue is 'wasteful' in that much energy is lost to the ecosystem as metabolic heat, so that the bulk of animal material at any one moment in an ecosystem is always very much less than the

bulk of plant material. A few rough comparisons will set the scale of the problem we are considering. For simplicity's sake let us limit our comparisons to vertebrate animals. Probably one of the most highly productive of terrestrial ecosystems in terms of animal flesh present at any one time is the East African savanna of grasslands interspersed with trees and shrubs with its highly specialised community of large herbivorous mammals (the so-called 'big game'). Recent estimates put the standing crop of these animals in one locality at about 13,000 kg/km² (Talbot & Talbot 1963) and it is unlikely that any other terrestrial ecosystem ever exceeds this; most of them will fall far below it.

But, if we compare the figure for one species of animal alone—namely man—in England and Wales, we find it soars to 18,000 kg/km². This is quite a lot of man and, indeed, as many of us believe, a dangerous lot of man. The world at the moment has far more energy fixed in the form of human flesh than is found in natural ratios of animal:plant biomass or is healthy for the equilibrium of the world ecosystem.

Nor is this the worst: not only is the population of man increasing but also the rate of increase is increasing. Between 1800 and 1850 the percentage increase in the world's population was 30; from 1850 to 1900 37%; from 1900 to 1950 the rate had advanced to 55% and recent estimates for the year 2000 indicate that by then a rate of 150% will have been reached.

In other words the increase is perilously near to a geometrical one. Ecologists are familiar with the sigmoid or flattened S-shaped curve to which the growth of populations conforms. The first half of the curve, showing geometric increase, denotes that the resources of the environment are still unlimited; the second half, gradually levelling off to an equilibrium value, shows the gradual depletion of resources until birth and mortality rates are approximately equal.

Thus we must expect the human population to level off before long and since, of the factors which normally achieve this in nature, man has already minimised the effects of predators, parasites and diseases, the levelling off can only be obtained through competition for food and/or space. The effects of these factors are

already plain to see, in their early stages, in many parts of the world. Their full impact can scarcely be pleasant.

Objections have been advanced to this dismal conclusion. Perhaps, some new discovery, such as cheap and safe production of atomic energy, or the harvesting on a large scale of food from the sea, will increase the 'carrying capacity' of the world for people. Apart from the fact that the discovery of new resources merely stimulates an equivalent shift in birth or survival rates, the law of the minimum must operate and a stimulated increase may encounter a deficit in a fresh resource. A very sober report on the situation (World Population and Resources by P.E.P. (Political & Economic Planning)) states that some of the world's material resources, such as phosphorus and fuels, give even more cause for anxiety than shortage of food.

Some demographers suggest that peoples and nations tend to evolve from a primitive state in which their numbers are stationary and the birth and death rates are high, through an unsettled state of rapid increase, to a highly civilised and industrialised state which is again stationary but with low birth and death rates. One need only reply that we are still far from such a happy state and what, we may ask, will be the condition of the world by the time that this state is reached?

Even if we accept the policy of a controlled birth rate as an answer to the problem, we still have to face the thorny question of the level at which it should be controlled and we cannot escape inquiring what is the verdict of ecological research on the present health and future prospects of the world's ecosystems. We would have surer information if the development of research suggested above had made further progress but several trends are already clearly detrimental. To some of them methods of cure and prevention can be suggested.

THE ENGLISH LANDSCAPE

The example of England is instructive. England is happily situated climatically with a rainfall well distributed round the year and a geologically old landscape which changes very slowly. The removal of its primeval forest cover over the last two millenia has created no urgent problems of soil erosion or water conservation. A wise system of agricultural

land-use, developing during the last few hundred years or so into mixed farming over most of the lowlands and sheep walks, and more recently afforestation, on the higher ground of the north and west, has gone far to providing a stable regime, living on the income of the earth's fertility. Originally both landowners and tenants were imbued with the tradition that the land was more important and more enduring than they were and their highest ambition was to pass it on to their successors 'in good heart'. This tradition produced a scene which was not only agriculturally, and perhaps ecologically, efficient but also aesthetically pleasing and stabilised with duties and customs which bound the rural community together. Both literature and architecture of the time breathe the spirit of these settled traditions.

Such ecological stability was due to various factors in the whole traditional practice of husbandry, some of the most important being the small size of the units (fields, spinneys, ponds and so on), their diversity (especially after rotations were introduced) and the richness, ecologically speaking, of the boundaries between them. Thus any part of lowland England would have grass and arable fields mixed with woodlands and marshes and outlined with hedges and trees, these last two items containing a particularly rich fauna.

If anything is specially characteristic of this stable English landscape, it is the boundary ditch and hedge. Traditional treatment of hedges, which are composed predominantly of hawthorn, with many other subsidiary species, was to let them grow to a height of 12-20 ft., then to trim them down to 3-4 ft., leaving sturdy poles every 3-4 yd. These poles were chipped near the base, so that they could be bent almost parallel with the surface of the ground and woven around thin posts to make a living and impenetrable barrier.

This process is known as 'cutting and laying' and a hedge which has been so treated a few times establishes a rooting system out of proportion to the size of the hedge. It binds the soil and conserves moisture as well as reducing wind speed near the ground.

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and herbs, with trees at intervals allowed to grow to full stature and often with ponds straddling the boundary between two fields. The many miles of such a linear habitat carry an extremely rich fauna, to the importance of which I shall return later.

The radical changes which began to assail this long-persisting equilibrium were the accompaniments of industrialisation, which led to the import of cheap food and the export of manufactured goods. Not only were large areas of living space needed for the rapidly expanding population but the viable unit of the large estate with its tenant farmers broke up and farming became more a business than a way of life.

Since, at the same time, labour was drifting away from the land, technical advances, including greatly increased mechanisation, were called in to help. This meant many changes away from the old system, changes which are still being carried out. Hedges are rooted up and replaced by wire fences, fields are thrown together, marginal land sometimes on steep slopes, is brought into cultivation, woodlands are felled and so on—I need not detail the whole dreary process. Finally has come the complex problem of toxic sprays and dressings, which would appear to have attained the acme of efficiency but have led us to think furiously not only about straightforward danger to life and health but (through the accumulation of residues and unexpected side effects) also about fundamental damage to ecosystems. Thus food chains are simplified and shortened and habitats are unified. Even if this outlook makes the utmost use of the world's resources, it can scarcely be making the wisest use. The old term husbandry has little application nowadays.

Of course, I have taken England only as an example but what one might call this ecological entropy is going on all over the world. Some countries are, like England, destroying equilibria carefully built up by man. Others are starting from scratch and destroying natural equilibria. The main difference is that some of these latter countries like Canada, the United States, Australia and New Zealand, have still a good deal to play with in the way of unexploited, or partially exploited land and can still afford to set aside large areas for study, the results of which will benefit other countries, which can no longer afford to work on so large a scale.

CONSERVATION IN THE BROAD SENSE

So among all these pressures—of wildly and diminishing increasing populations resources, of competition and friction, of cold wars and hot tempers—we have to seek what Elton has called 'some wise principle of coexistence between man and nature, even if it has to be a modified kind of man and a modified kind of nature'. Since the seeking of this solution is urgent, we cannot leave it to an evolutionary process of trial and error but must have recourse to some hard, concentrated scientific research and thinking. The organisation and functioning of ecosystems, which it is the main task of ecology to elucidate, underlie the practical system of organising human affairs which can be subsumed under the title of conservation. The phrase which I have just quoted from Elton was given by him as his definition of conservation.

In fact, we might venture, approximately to call conservation applied ecology. In this broad sense the term conservation transcends smaller compartments of it. It has been used sometimes to mean little more than soil conservation, sometimes merely preservation, e.g. of an animal or habitat threatened with extinction, sometimes living on income and not on capital. I prefer to think of conservation as concerned with the health of ecosystems in relation to man's proper needs.

As we have noted previously, ecology as a scientific discipline has established itself only during the present century and, in spite of its clear relevance to human affairs, has not yet attracted the scale of support which it merits. Nevertheless, there is much that can be done. I recall the dictum of the Director of a Dutch ecological research institute just after the last war, when resources of all kinds were scarce in that corner of Europe. 'Ecological research,' he said, 'pays the greatest dividends because the outlay is limited to a man and a bicycle.'

THE NATURE CONSERVANCY

In England the government has come, though tardily, to support this mixture of fundamental and applied ecological research, which I call here conservation, guided partly by an urgent document from the British Ecological Society, sponsored by Professors Tansley and Pearsall and by Charles Elton, among others. The Nature Conservancy was set up under Royal

Charter in 1949 on the basis of a report by the Huxley Committee and immediately set about the task of preserving, by purchase or agreement, areas typical of British natural or semi-natural habitats. These Nature Reserves, by the end of 1958, covered over 130,000 acres, which is a remarkable achievement in a country so torn between competing claims for land-use.

These areas are 'reserves' in the fullest sense, since their management and use are regulated almost entirely by the Nature Conservancy. Entry by the public may be prohibited entirely, may be allowed by permit or may be free to all comers. Thus those reserves, which need to be kept almost as 'museum specimens' of disappearing or radically altered habitats, can be preserved from disturbance or management other than what is necessary to maintain them in statu quo.

Still other nature reserves are 'outdoor laboratories', where observation and experiment are carried out by the staff of the Conservancy and by other scientists. The conditions are much the same as in the Wytham Estate near Oxford, mentioned previously. Such areas are guaranteed to be reasonably free from disturbance and are available for a certain amount of experimental manipulation.

Finally, there are many areas throughout Britain, often quite small, which have some particularly interesting characteristic which would vanish if normal development were allowed. Such places are scheduled as Sites of Special Scientific Interest and local planning authorities must give notice to the Conservancy of any proposed development at such a site. These may range from a quarry famous for fossils to a part of a much loved landscape like Arthur's Seat above Edinburgh, which was preserved from being quarried under this scheme.

Thus, the Nature Conservancy has been far from idle during the short period of its existence. It has already acquired fair samples, though most are small, of representative habitats including those that are near to their primeval state, though for obvious reasons these are few in number. The volume of research upon conservation problems done upon these reserves is growing fast and benefits from the policy of having laboratories near to reserves.

COMPLEXITY AND STABILITY

We can now consider a little more closely what Elton meant by 'a modified kind of nature'. In his book, The Ecology of Invasions by Animals and Plants (1957), he details many case histories of plants and animals introduced into new countries and environments, spreading and increasing with explosive force and producing desperate economic, as well as ecological, catastrophes. Obvious examples are the rabbit and the water hyacinth. He points out that these explosions are due partly to the increased speed and volume of transport around the world, so that ecosystems are subjected to a constant bombardment of new species trying to force a way in, and partly to the simplified nature of many man-made or man-modified ecosystems. Apart from this, the breaking down of geographical barriers will mean that ecosystems which evolved in isolation may be wide open to invasion by organisms which have been reared in a more competitive environment. The success of so many plants and animals introduced into New Zealand is a case in point. It is clear therefore, that we have to accept the inevitability of some of this levelling process, this 'modified kind of nature', but can we influence wisely the course of this modification?

I have referred to the comparative ease with which invaders can reach pest proportions in monocultures, like grain-fields or even-age plantations of trees. On the other hand, the more complex ecosystems seem to be able to repel invaders in spite of the increasing pressure. Tropical forest is probably the extreme example of complexity with its diversified spatial organisation in three dimensions, its multiple layering, its mixture of different tree forms and species and its interspersed subhabitats composed of epiphytes, lianes and parasites.

Tropical forest is also efficient from an energetic point of view. Material is turned over rapidly and the decomposing organisms are so active that dead material is swiftly broken down and made available to green plants again. One of the surprises in store for any ecologist reared in temperate regions is to see the lack of humus and leaf litter in a tropical forest.

Both botanists and zoologists have demonstrated the fantastic richness and interdependence of species in this ecosystem and it is no doubt this complexity and stability (or, to use a more modern term, homeostasis) which makes it so difficult for invaders to get a foothold.

If we are wise enough to learn from these contrasts, we have already picked up some guidance as to how to modify nature—always preserving, or even creating, the utmost diversity in terms of habitats and species and promoting a fast flow of energy through the trophic levels of the communities concerned.

So it becomes apparent that the intuitive diversification of the English countryside which is now being partly dismantled had a straightforward utility, as well as being aesthetically satisfying.

THE NEED FOR MORE ECOLOGICAL RESEARCH

But it is a poor business if we cannot do better now by ecological research than was done centuries ago by intuition. Here we can pick up again the conclusion we reached earlier, when discussing the pattern of future development of ecology, namely that the study of communities is fundamental and that the analysis of species abundance, inter-relationships and organisation is an all-important part of community study. Only by making this detailed kind of analysis can we arrive at a measure of the complexity and integration of communities, which give them their resistance to disturbance. The more widely spread and efficient this kind of research becomes in the world, the more it will be possible to learn about the health of ecosystems by the comparative method and to judge for specific circumstances how nature should be best modified.

For this, study areas of both natural and modified habitats are needed. I have already mentioned briefly what is being done in England by the Nature Conservancy but, although a range of man-modified habitats can be provided, the only natural ones to be found are usually hardly natural and are always small.

So we watch with keen interest the development of nature reserves and national parks in countries which still have large tracts of relatively undisturbed, primeval habitats. These are the places where it is pre-eminently important to make measurements and to carry out experiments and, even in these areas, time is not unlimited and the human population grows apace.

We can see, then, some lines of approach whereby ecological research may lead us to the right kinds of modification to apply to nature. But all this stir and energy will not prevent catastrophe unless we also know the right kind of modification to apply to man. At the moment, ecologically speaking, the only kind of modification we need pay attention to, is the ability to regulate his own numbers. The means are now virtually in our hands, so it remains for us to will the end (which is not an ecological problem) and then to tackle the thorny question of how many and where. Through all the clamour and confusion of competing claims between races and nations, ideologies and religions, it seems to me that ecology only, at the moment, offers an objective answer—that the ratio of organisms in the trophic levels of any ecosystem has an optimum range, the boundaries of which are not to be transgressed. But in all our present troubles and perplexities, let us at least be clear that we need desperately more ecologists, more research institutes, more field stations and nature reserves and more teaching of ecology, even if these things nowadays demand more outlay than 'a man and a bicycle'.

SELECTED BIBLIOGRAPHY

Andrewartha, H. G., and Birch, L.C., 1954. The distribution and abundance of animals. Univ. Press, Chicago.

Anon, 1947. Conservation of nature in England and Wales. H.M. Stationery Office, London. (Original report of the 'Huxley' Committee which stimulated the formation of the Nature Conservancy.)

CLEMENTS, F. E., and Shelford, V. E., 1939. Bioecology. Wiley, New York.

Crombie, A. C., 1947. Interspecific competition. J. Anim. Ecol. 16: 44-73.

Elton, C., 1927. Animal ecology. Sidgwick & Jackson, London.

ELTON, C. S., 1958. The ecology of invasions by animals and plants. Methuen, London.

ELTON, C. S., 1965. The pattern of animal communities. Methuen, London. (A broad account based on the Wytham Ecological Survey.)

ELTON, C. S., and MILLER, R. S., 1954. The ecological survey of animal communities; with a practical system of classifying habitats by structural characteristics. J. Ecol. 42: 460-496.

Gause, G. F., 1934. The struggle for existence. Williams & Wilkins, Baltimore.

Graham, A., Ed. 1956. Sea fisheries. Their investigation in the United Kingdom. Arnold, London.

Hesse, R., 1924. Tiergeographie auf ökologische Grundlage. Fischer, Jena.

- Juday, C., 1940. The annual energy budget of an inland lake. Ecology 21: 438-450.
- Lack, D., 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- Lotka, A. J., 1925. Elements of physical biology. Williams & Wilkins, Baltimore.
- Nicholson, E. M., 1957. Britain's nature reserves. Country Life, London.
- Odum, E. P., 1959. Fundamentals of ecology. 2nd edition. Saunders, Philadelphia & London.
- Park, T., 1962. Beetles, competition and populations. Science 138: 1369-75. (A compact summary of a vast amount of work.)
- Pearsall, W. H., 1964. The development of ecology in Britain. Brit. Ecol. Soc. Jubilee Symp.: 1-12. (With a valuable list of references.)
- P.E.P. [Political and Economic Planning], 1955. World population and resources. Allen & Unwin, London.
- Peterson, C. G. J., 1918. The sea bottom and its production of fish-food. A survey of work done in

- connection with valuation of the Danish waters from 1883-1917. Rep. Danish Biol. Sta. 25: 1-62.
- Shelford, V. E., 1913. Animal communities in temperate America. Bull. Geogr. Soc. Chicago 5: 1-368. (Reprinted 1937, Univ. Press, Chicago.)
- Soloman, M. E., 1964. Analysis of process in control of insects. In *Advances in ecological research*, vol. 2. Ed. Cragg, J.B. Academic Press, London & New York. (A critical evaluation of work done on insect population dynamics and control.)
- Talbot, L. M., and Talbot, M. H., 1963. The high biomass of wild ungulates on East African savanna. Trans. 28th N. Amer. Wildlife Conf.: 465-76.
- Thienemann, A., 1926. Limnologie. Jedermann, Breslau.
- Varley, G. C., 1947. The natural control of population balance in the knapweed gallfly (*Urophora jaceana*). J. Anim. Ecol. 16: 139-87.
- Wynne-Edwards, V. C., 1962. Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh & London.

FOOD OF THE OPOSSUM TRICHOSURUS VULPECULA IN PASTORAL AREAS OF BANKS PENINSULA, CANTERBURY

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INTRODUCTION

Previous work on the foods of the brushtailed opossum (Trichosurus vulpecula) in New Zealand has been concerned with the choice of plants taken in indigenous bush. Although clover was sometimes recorded as a preferred food the conclusion was reached that opossums "are not grass-eating animals" (Mason 1958), and that "the opossum is not, and will never become an important grassland pest" (Howard 1963).

Present research on Banks Peninsula, Canterbury, from November 1963 to August 1964 shows that although opossums appear to be more numerous close to favourable bush, they often occur many miles from any native or exotic forest. Under these circumstances opossums feed largely, if not exclusively, on plants serving as food or shelter for domestic stock. Clover, grass and pasture plants form a large part of their diet throughout the year.

Opossums are very numerous on Banks Peninsula. By day they often shelter in such places as gorse hedges, old willows, macrocarpa shelter belts and rock crevices, and emerge at night to forage in nearby fields; they also cause much annoyance by raiding gardens and orchards.

Much of Banks Peninsula is rugged with many peaks up to 2500 ft. and ample cover is available on the rocky hillsides. Although the peninsula supports large dairy and beef cattle herds as well as many sheep, there is still much bush including totara (Podocarpus totara), lacebark(Hoheria angustifolia), konini (Fuchsia excorticata), fivefinger (Neopanax arboreum), and mahoe (Melicytus ramiflorus).

The original bush is now mainly restricted to gullies, shaded slopes and scenic reserves, although there is some secondary growth.

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