THE TEACHING OF QUANTITATIVE ECOLOGY

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Like the term "cytology" which, in the 1930s, came to mean the study of little more than chromosomes, "quantitative ecology" is used in both a general and a more particular sense. In the restricted sense it has come to be equated with the virtuoso techniques of community analysis pioneered by Curtis, Goodall, Williams & Lambert and others; that is, primarily the application of multivariate statistics to ecology. In the more general sense, on the other hand, quantitative ecology has for its province the quantification of all ecological perception; that is, the replacement whenever possible of subjective estimates by objective measurements, of prejudice by fact, of judgment by logic. This is not to say that judgment can, or should be, eliminated or that ecological intuition should be decried, but merely that the aim of quantitative ecology is to refine all the normal ecological procedures of gathering and manipulating data and drawing conclusions, to the point where judgment will be as soundly based as it can be.

It is convenient to maintain the distinction between these two levels of meaning which correspond largely to univariate and multivariate statistics and hence, broadly, to autecology and synecology. Although both are part of quantitative ecology in the widest sense, they differ in the degree of previous training which they demand of a student (or for that matter of a teacher) and hence differ in their appropriate position in the university curriculum.

The teaching of quantitative ecology at university demands some justification and this leads immediately and inescapably to a consideration of the much more general problem of the whole function of the university. Here there is no escape from personal opinion, no answer which is incontestably right. I would argue that the primary function of the university is to train students for the professions, and that this is, in fact, only a more specialised version of the schools' function which is to train pupils for their future occupations in general. This implies that the business of, for example, the science faculty is to turn out scientists; the business of a botany department to train students as botanists. Most of them, admittedly, will not become botanists but the justification for teaching them is still the same. I believe it is wishful thinking, and often second-hand thinking, which holds that the job of a university is merely to teach students to think. If it were true, then the curricula are ill-designed indeed for their purpose and successes are few and far between. My own feeling is that the job of university staff is to train students by imparting the power to generalise within the restricted field of their chosen course of studies. That is, students should be provided with the appropriate combination of instruction and practical experience which will allow them to extrapolate and interpolate. It follows that the course of studies largely determines the kind of mind that results from it because it determines the field within which this power of generalisation is developed. That is why universities have long insisted, and rightly insisted, on well balanced and carefully controlled degree courses instead of accepting uncritically any mélange of the appropriate number of units. The subjects studied by a student must, in fact, be contiguous enough to constitute an intellectual field and recognition of this principle is behind the customary aggregation of university departments into faculties. Even the highly experimental courses in some new universities seem to follow the same principle, as far as an outsider can judge; and the courses are intellectually contiguous however much they may run across the grain of traditional disciplines.

This power of generalisation is, to me, the primary distinction between training and education, between true learning and mere technology; more generally, it provides a large part of the distinction between universities and technical colleges of the old sort, and perhaps even between the trades and the professions. Knowledge or skill which is incapable of generalisation, which ends with itself and from which no extrapolation is possible, is not educational; and in designing a university curriculum it is surely vital to ensure that these cul-de-sac skills, which lead nowhere, are kept to the minimum. For example, biological microtechnique, microscopy, ability to use apparatus of any sort (even computers) are tools of great power but no more than tools and we must be restrained in our teaching of them.

Judged by this criterion of giving the power to generalise within a limited field, quantitative ecol-

ogy comes out very well. More than perhaps any other biological discipline, ecology attempts to elucidate the underlying laws governing the pattern of distribution of living organisms in time and space; that is, it is concerned with building up precisely that power to generalise which I believe to be the hallmark of academic education.

But having satisfied the requirement that it is the right sort of subject for university work, quantitative ecology must meet yet another condition before it can find acceptance in a university curriculum; it has to find a niche in the curriculum where it can do its work profitably and fit in with other subjects to produce a balanced course. It is here that the duality of quantitative ecology is important, for univariate and multivariate ecology must obviously fit into different niches. Ecology as a whole is such a general topic that it demands the widest possible prior training and the widest possible interests throughout the whole realm of knowledge if it is not to be merely trivial. The greatest danger seems to me to be in teaching ecology too soon, to people whose field of training is not yet sufficiently wide. There are strong arguments against the teaching of ecology at all at undergraduate level, lest it degenerate into a set of precepts and preconceptions which could destroy the intellectual sprightliness which is vital for any ecologist faced with the immense variability of living communities. But given ecological instruction at this level as a *fait accompli*, there seems to be least danger in teaching general, univariate, strictly quantitative ecology first and leaving multivariate ecology, including most community studies whether quantitative or not, until at least honours level, if not post-graduate.

The best position for univariate quantitative ecology in a university course is again a matter for judgment, but my own feeling is that ideally it should come in the vacation between first and second years when those students who are going to continue in botany to advanced level can be given, through it, a useful introduction to simple statistics and rigorous observation and deduction. Such a course need scarcely touch on communities as associations of plants and animals but should investigate the simplest relationships between individual species and habitat factors.

The whole of ecology is concerned with the detection and interpretation of pattern in living organisms — pattern in time and space on all scales, from the imperceptible but fundamental pattern investigated by Greig-Smith and his school at Bangor to the broad regional patterns of the plant geographers. Curiously, the type of pattern which has attracted least attention is both the most obvious and the easiest to investigate — the clear pattern shown by small patches of vegetation on a scale of metres, rather than either centimetres or kilometres. The environmental and morphological factors involved are, it is true, likely to be compound rather than single at the physico-chemical level, but are no less informative for that. Mosaics of this sort are all around us and are easily investigated by simple transects across the ecotones and, if necessary, regression analysis of plant abundance on environmental factors. More graphically, the plotting of isonome lines, i.e. lines of similar density, frequency, cover, etc. from a grid of samples, may be quite revealing. This sort of simple univariate investigation seems to me to be an ideal introduction to quantitative ecology and permits the basic measures of plant performance — cover, density and frequency — to be thoroughly instilled. The Bangor style of subdivided quadrat (25 one dm. sq. quadrats in a 0.5 m. sq. grid) is a most useful tool for such simple work on individual species or communities.

The two main risks in the early introduction of quantitative methods are that students will be too bored by repetitive sampling and discouraged, if not actually frightened, by the prospect of mathematics or statistics. Paradoxically, one of the best ways of avoiding the first of these problems is to work under difficulties; not in a field centre but from a hut or tent, even in unpleasant conditions. For New Zealand students, at least, this kind of physical challenge seems to act as a stimulus. As for the second, the most effective way of countering the common dread of mathematics is, again paradoxically, to use a computer. A programming language such as FORTRAN seems to have none of the implications which make so many students shy away from even the most elementary conventional mathematics, and the logical construction of the language is both disciplinary and satisfying. The biggest single advantage in the use of quantitative techniques, whether in morphological measurement or plant enumeration, is the rigour — not so much of deduction but of observation — which it enforces. This is especially true in dealing with cryptogamic vegetation, wherein the eye has a convenient habit of missing forms that are hard to identify. But if the ecologist has to account for all the plants in a quadrat there is no escape and he

benefits from the experience.

But what of quantitative ecology in the other more sophisticated, multivariate sense? Is it to be reserved for post-graduate studies or is there any part that can be taught and is worth teaching at under-graduate level, especially to those whom W. T. Williams brilliantly describes as "innumerate"?

There are at present three main lines of advance in this field. First, the pattern analysis developed by Greig-Smith at Bangor; second, community classification by association analysis and other methods developed mainly by Goodall and Williams & Lambert; and third, community ordination developed originally by Curtis' school at Wisconsin. One further point at which quantitative ecology looks as though it might produce a new and vigorous offshoot is associated with Olsen and others in America and consists of mathematical model-building for ecosystems. This approach is impressive and some day may well provide a major breakthrough in ecological understanding.

The first of these topics, pattern analysis, admittedly involves only variance analysis, but the handling of the technique and the interpretation of the results requires a fair amount of statistical understanding. Its great disadvantages for undergraduates are that it is enormously time-consuming and that there is no guarantee that the results at the end will reveal much more than is intuitively obvious. I have found it most difficult to make effective use of it in teaching.

The other two topics, however, association analysis and ordination, are well within the reach of the best undergraduates and reasonably easy to teach. Admittedly the mathematical background may be rather hard for many students to grasp but the principles are simple; even the concept of the plant community being a hyperellipsoid in multi-dimensional space is easy enough to grasp as a simple extension of a two-dimensional ellipse.

There are two schools of thought about the teaching of community ecology. The usual one is to start by intuitive recognition and description of communities and proceed through objective methods of describing them to the finer and finer investigation of the components, ending up at the association between individual pairs of species and the spatial patterns shown by them. The other school holds that the patterns and interrelationships between two or a few species should be investigated first and then the idea of a community built up as an extension of this. My own opinion is that although the latter is the logical way, not many ecology courses would go on long enough to reach the community level. Perhaps the most productive approach is to start with neither the abstract community nor the individual species but with a stand of vegetation within which sub-samples can be classified, ordinated, and mapped on the ground and the results compared with subjective judgment. The excitement and novelty of these methods and their power of uncovering general principles are so great that they seem to be worth employing empirically, even when their mathematical foundations may not always be clear.

These very general methods of investigating community structure seem to me much better suited to the principles of university education suggested above, than the customary list of pre-judged individual communities, their composition and habitats, which feature prominently in ecology courses throughout the world. By far the greater part of biology has to be accepted by even the best of students without verification. Life is not long enough to allow learning by personal experience alone and too much iconoclasm is more unprofitable than too little. But communities are so variable, our knowledge of them so meagre and established ecological principles so rare, that there is here an unrivalled opportunity for teaching by investigation and discovery as well as by precept. This is no mere luxury, for the future of ecology depends in great measure on retaining freshness and flexibility of mind. As Sir Hector Hetherington (1953) said: "An indispensible element in the intellectual experience of every serious student is that somewhere he should encounter the dimension of depth, should discover for himself how deep down, beyond his reach, go the questions which enter into his handling of any significant matter. To that end, let him somewhere find himself at the limit of his visible resources, facing an issue with which, as best he can, he must come to terms. Research, in that sense, is a superb and fortifying discipline."

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(a select list)

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