Advances in ECOLOGICAL RESEARCH

Edited by

J. B. CRAGG

VOLUME 1

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The Nature Conservancy, Merlewood Research Station, Grange-over-Sands, Lancashire, England

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Preface

Ecology can be defined as the study of the inter-relationships between organisms and the physical and biological components of their environment. With such a broad field for research, ecologists, perhaps more than any other group of biologists must find it difficult to keep up with developments occurring at the many growing points of their subject. It is the intention of *Advances in Ecological Research* to present comprehensive accounts of selected topics of ecological research in such a way that biologists with a general interest in ecology as well as specialists in ecology, can obtain a balanced picture of what is taking place.

The scope of the articles to be published in this series will not be strictly limited to ecology. Advances within ecology are very dependent on changes occurring in other branches of science. It is important, therefore, that from time to time, articles surveying developments related to ecology in such subjects for example, as genetics, biochemistry, taxonomy and biometrics should be published. There has never been a rigid division between pure and applied research in ecology and many of the major advances in the subject have come from the investigation of applied problems. It is our intention, therefore, that contributions which show the application or development of ecological principles in applied biology should receive adequate treatment in this publication.

This first number contains four contributions which in their different ways discuss important aspects of ecology. Much of our knowledge of the activity of soil organisms is dependent upon more accurate assessments of their numbers and their distribution. The literature of this subject is scattered throughout many journals and the efficiencies of the various techniques are inadequately known. A. Macfadyen's review of methods for the extraction and study of soil arthropods provides information which should be of assistance not only to those concerned with arthropods but to many contemplating or engaged upon the study of other soil organisms. The main theme of M. J. D. Poore's paper is the analysis and description of plant communities. This subject as well as being the basis of plant ecology is of interest to animal ecologists and to applied ecologists concerned with the utilization of biological resources. L. B. Slobodkin in *Energy in Animal Ecology*, deals with a branch of research which is developing rapidly. Here again is a topic which goes beyond the confines of one type of ecologist. The problems of how energy is passed on from one stage in a food-chain to another and whether the efficiency of energy fixation by organisms can be increased are fundamental to the proper use of natural resources. The very long contribution by J. D. Ovington provides an integrated picture of the interrelations which exist between the biological and physico-chemical components of woodlands. This account of the many facets of the woodland ecosystem apart from being a fundamental contribution to ecological science is of special significance to biologists and others concerned with the place of woodlands in land utilisation programmes.

October, 1962 J. B. CRAGG

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Soil Arthropod Sampling

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I. Introduction

In response to the editor's suggestion this article is intended to provide practical advice on how to obtain efficient estimates of numbers of soil arthropods. The attainable efficiency of any sampling scheme depends greatly on the aims of the investigation, a truism which applies particularly to soil fauna surveys because in such work sampling effort increases steeply with the accuracy demanded. The need for the biologist to balance most carefully his demands in terms of accuracy and taxonomic range against resources of time and equipment is the more acute when he studies unevenly distributed populations, many of them belonging to groups whose taxonomy is, even now, rudimentary and possessing such a wide range of size, density and biological characteristics that the simultaneous sampling of all groups is quite impracticable. Secondly, such a variety of devices for extracting and collecting soil arthropods has already been described (see, for instance Balogh, 1958; Kevan, 1955; Kühnelt, 1961), that the novice is at a loss to know which methods are appropriate to his own work. Some of these are intended, or can be used, only for qualitative work, others apply only to a very limited range of organisms and, despite the excellent reviews mentioned, there appears to be a need for a systematic treatment devoted to the two themes mentioned, namely experimental design and choice of extracting and collecting methods.

It is essential to appreciate, that an experimental design should be conceived as a whole, that the most elegant statistical methods cannot compensate for biased sampling nor for inappropriate application and that the most complete extraction is invalidated by faulty experimental design. Nevertheless it is convenient to discuss the subject under two headings, the experimental design of the survey and the field and laboratory methods to be used, because the first has a wider application and so can be treated mainly by reference to the literature, whilst the latter are more confined in their range of interest to the present topic and therefore demand fuller treatment. In order to relate the methods discussed to practical needs the following section (Section II) suggests a number of types of soil arthropod survey and the appropriate sampling requirements whilst in the final section (Section V) an attempt at synthesis is made by considering some specific projects.

II. Characteristic Sampling Requirements of Some Different Types of Soil Arthropod Survey

Since at least fifty percent of the world's arthropod fauna remains to be described there is still a great need for geographically widespread taxonomic collections to be made without regard to quantitative considerations, especially from regions outside Western Europe. However, our knowledge of the taxonomy of European soil arthropods has improved so much in the last twenty-five years that serious study of ecological problems is now possible because the ecologist can see beyond taxonomic difficulties which formerly occupied his full attention or deterred him from studying the soil fauna entirely. Thus while exploratory surveys can and should be conducted with simple, robust equipment, used on collections obtained in a haphazard manner, ecological work now demands that greater attention be devoted to sampling methods.

Ecological problems are mainly of two kinds; firstly there are those involving comparisons between species lists (sometimes of limited taxonomic range) which have been obtained from different habitats, parts of habitats or at different times, including distributional, seasonal and successional studies. Secondly we have studies that are concerned with trophic structure of communities including food chains, biomass measurements, biological interrelationships and population-size measurements within a single community. The former, which can be called community studies, tend to make greater demands on taxonomic *precision* than the latter or "trophic" type because a greater range of related species is encountered and distinctions between them are often critically important in detecting changes in community composition. In a trophic study confined to a single habitat, fewer species are encountered and general conclusions will hardly be invalidated if an isolated species is misidentified. On the other hand the trophic study may involve a wider *range* of taxonomic work because predators and competitors of different natural phyla cannot be excluded. Further, sampling accuracy is usually more important and sampling difficulties are greater because methods must give accurate information about ecologically related species regardless of taxonomic proximity. Again, the whole purpose of many trophic studies is the establishment of absolute abundance figures and this frequently includes an analysis of age structure as well.

This is not to say that the community-type study lacks sampling problems. Most soil extraction methods operate with varying efficiency in different soils, with the result that quantitative comparisons over a wide range of soil types may even require the use of a series of different techniques. Also, the ease with which even quite closely related groups — for instance chilopods and diplopods or oribatid and parasitid mites can be extracted — varies greatly, so that the use of imperfect extraction methods can seriously upset estimates of their relative abundance. (Macfadyen, 1953, 1955.) However, when allowance is made for such effects the fact remains that the community-type survey does not usually demand that numbers be expressed in terms of absolute abundance on an area or volume basis such as is essential for the trophic study. This is important because counting the fauna of sample-units is often the most time-consuming part of ecological studies and if absolute counts can be dispensed with the ecologist is free to consider alternative measurements such as records of presence *versus* absence and various types of ranking which will be discussed in the next section. For all these purposes a reasonably unbiased extraction method applied to a relatively large number of sample-units can provide more information about community differences in a limited time than a full count of numbers which will necessarily be confined to fewer sample-units. The above remarks are summarized in Table I.

TABLE I

Type of Study	Demands made on Sampling Programme Enumeration			
	Taxonomic	Precision	Covering Different Soil Types	Covering Different Groups
Exploratory	Precise	Unimportant	Comparative	Comparative
Community	Precise	Comparative	Comparative	Depending on range of study
Trophic	May demand broader range Less exacting	Absolute	Unimportant	Depending on range of study

For many groups of soil animals the perfect extraction method remains to be found and this, in the applied field may constitute an insuperable difficulty. The academic ecologist, on the other hand, is usually more interested in principles than in particular instances. He should, therefore, exercise his freedom to choose both the soil type and the animal group with which a particular type of precision can most easily be achieved. Some indication of the relative difficulties associated with the study of different arthropod groups is provided by Table II.

TABLE II

The Amenability of Soil Arthropod Groups for Different Types of Ecological Study

Arthropod Group	Relative Difficulty of Taxonomy	Suggested Method of Extracting from:		
		Litter	Grassland	Arable
Tardigrada	+	A	A	—
Diplopoda	+ +	C	C	CJ
Chilopoda	+ +	F	B	—
Symphyla	+	C	C	H
Pauropoda	+	C	C	J
Woodlice	+ +	C	C	—
Parasitiformes	+	B	B	BJ
Trombidiformes	−	C	C	CJ
Oribatei	+	C	C	CJ
Pseudoscorpionida	+	B	B	—
Aranei	+ +	EC	EC	—
Collembola	+	C	CG	CJ
Thysanoptera	+	BD	BD	DJ
Aphididae	+	CD	CD	DJ
Formicidae	+ +	B	B	—
Coleoptera (larvae)	−	C	C	J
Coleoptera (adult)	+	B	B	J
Diptera (larvae)	−	C	C	J
Insect Pupae	−	O	J	J

Key to Symbols. + + Taxonomy straightforward; + Taxonomy possible; − Taxonomy very difficult or incompletely known; A Wet funnels p. 14; B Dry funnels (fast) p. 16; C Dry funnels (slow) p. 16; D Dry funnels (Chemical) p. 21; E Duffey's extractor p. 20; F Lloyd's extractor p. 19; G Hale's extractor p. 24; H Ladell type Flotation p. 25; J Raw type Flotation p. 25; O None suitable; — Not found in this medium.

The choice of category is, of course, somewhat arbitrary and the fact that a particular extraction method is advocated does not imply that no others can be employed; in particular, as will be shown in Section IV, many potentially useful separation principles remain to be tried and the efficiency of existing methods is not known for many groups.

III. The Design and Execution of a Survey

A. Statistical Aspects

The main objective when planning a soil survey should surely be to obtain the required information with a minimum of labour. To achieve this, experiments must be devised in such a way that clear-cut hypotheses are tested and the right number of sample-units is used in relation to the desired degree of accuracy. Both these requirements are usually difficult to meet in practice. In community work one cannot know beforehand which species will occur in a given locality nor how abundant the critical species will be. The number of replicates required to show significant differences is also unpredictable because it depends on total density and on the patchiness of distribution of the animals. In the case of laboratory-based surveys it is possible to carry out a preliminary survey and to obtain rough estimates of density and patchiness on which a rational sampling scheme can be based, but under expedition conditions when the survey is of limited duration there is usually no option but to fix the number of sample-units in the light of previous experience or to take as many sample-units as possible consistent with the labour available. Even here a choice between taking many small or fewer large samples must be made.

When a preliminary survey is possible the mean number m and its standard error s can be calculated in the normal way (see, e.g. Snedecor, 1946). Some idea of the number of samples required in order to achieve a given degree of accuracy can be found (see Snedecor, p. 456 ff.) by substituting in the formula for fiducial limits $m + \frac{ts}{\sqrt{n}}$ where s is the standard error per individual observation and in which t for any given probability level can be obtained from statistical tables.

The question of size of sample-unit, especially when some kind of core borer is used, is often fixed beforehand by the apparatus available. However, there are two statistical considerations involved here, firstly that if the population is distributed in patches, it is essential that the sample-unit area should be small in comparison with patch size, especially if the properties of the patchy distribution are being investigated (see below). If the aim of the survey is to obtain an efficient estimate for a given amount of labour of say the density of a particular species, and if the patchiness of the distribution is only of incidental interest, then the sample-unit area should be such that the ratio of standard error of mean to mean is least. Secondly, it is necessary to balance the advantages and disadvantages of using relatively large numbers of smaller units which usually involves handling less soil but larger numbers of actual cores and pieces of laboratory apparatus. All kinds of practical decisions such as distance from the laboratory and transport facilities are involved here but a useful example of a comparison of this kind is given by Finney (1946) which is also quoted by Healy (in press).

In the example of a wireworm survey conducted by Finney two different sample sizes were tried and in each case the mean and standard error were calculated. By plotting s/m against m and joining the points by eye an expected value of s for any given value of m can be obtained. Since the number of units required to give the same precision are in the ratios of the squares of the s/m ratios the relative advantages of using different sample sizes can be assessed. In this particular instance there proved to be little advantage in using 2 in diameter cores rather than 4 in diameter ones.

Decisions about sample size will, of course be very much influenced by whether or not abolute numbers are to be determined, that is, whether the survey is of the "trophic" or "community" type as discussed in Section II. Most ecological work done under expedition conditions is of the second kind and is often aimed at detecting and delimiting characteristic species groupings and relating these to environmental factors. Although it has quite commonly been the practice to count all specimens contained in each sample-unit, various expedients can be employed to derive quantitative information from samples without necessitating complete counts. In continental Europe it is usual to estimate numbers to the nearest order of magnitude or to employ an arbitrary abundance scale as has been done by Gisin (1943) and Strenzke (1952) although rather little use is made of these ratings. Presence or absence can be recorded and used to calculate "frequency" (i.e., proportion of sample-units in which a given species occurs). Frequency and mere presence are the basis of correlation tables (or "Trellis diagrams") which are used for community analysis in Scandinavia particularly, for example in the work of Kontkanen (1950, 1957). The recording of the simultaneous occurrence of several species in this way provides a means of determining the extent to which their distributions are associated or complementary. The more modest studies of this kind are content with analysis of correlation between two species at a time, for example, the work of Cole (1949). A recent development however has been the simultaneous correlation analysis of presence or absence of a large number of species by Williams and Lambert (1959, 1960) with the aid of a computer. This involves the complete sampling of a large gridded area and recording species lists for each grid square. The squares are then classified on a hierarchical system which separates those species groups whose distribution is least significantly associated using all possible combinations of species. In this way previously unsuspected correlations between vegetation pattern and environmental factors are detected.

Work of this kind has not yet been done for soil animals but it should be noticed that since only presence is being recorded very small sample-units should be possible — and indeed required, so as to make certain that a proportion of units will be without animals. Under some circumstances this might facilitate taking the large numbers of sample-units which such an analysis demands.

A different approach to community analysis has been suggested — and illustrated — by Fager (1957) who records for each sample-unit the rank order (i.e. the order of dominance) of each species. With the aid of rank correlation analysis developed by Kendall (1955) the affinity of different sample groups can be determined and standard errors can be estimated. Again, the size of sample-units can be considerably reduced compared with those required for complete counts and statistical significance of the results can be established. Also the counting labour can presumably be lessened because a relatively cursory inspection will often suffice to establish order of dominance. When samples regularly contain large numbers of small animals and smaller numbers of large ones, for example oribatid and parasitid mites, it will be desirable to analyse each main group separately.

Sequential analysis [for practical details of calculations see Waters (1955)] is another technique not yet applied to community studies of soil, but which appears to offer substantial savings in labour, and which demands relatively small samples. In cases where a particular species is already established as a valuable indicator and sets of sample-units are being examined for affinity in terms of this species, sequential methods should provide a means of reducing the number of sample-units *examined* to a minimum, although it is unlikely to reduce substantially the number of units taken from the soil in the first place. A somewhat similar method was developed by Capstick (1959) for detecting significant differences between aliquot samples with minimum labour.

A final point to be remembered in connection with the size of sample-units in community studies is that when they are made too small the rarer species are likely to be excluded altogether. It is frequently observed that the commoner species are not those whose distribution is the most useful indicator of faunistic groupings and, as shown by Hairston (1959) it is important to include the less common species. It seems, therefore, that any attempt at a complete community analysis may require either parallel samples with units of different sizes or else the collection of rather numerous sample-units for the rare species and the use of aliquot parts of these or a sequential analysis scheme for obtaining statistics on the commoner ones.

The importance of deciding at the outset whether or not absolute abundance figures are essential should now be apparent. If they are (trophic studies) preliminary samples must be taken to determine the ratio of variance to mean and thus to establish whether distribution is patchy (=aggregated, =contagious, =underdispersed) and, if so, what must be done to measure and allow for patchiness. When patchiness has been demonstrated it is usual to attempt to fit the field data to a theoretical distribution containing terms representing the mean numbers per unit area and the mean size of the patches. The first of these can be used in trophic studies but the asymmetrical distribution invalidates statistical tests which are based on the assumption of a normal distribution and to ignore the patchiness is to discard valid biological information. Distributions which have been fitted to soil sample data include the Poisson, which describes the frequency of random (i.e. non-patchy) events. According to this distribution, which rarely applies in natural soils variance and mean are equal. The negative binomial (see Bliss and Fisher, 1953; Anscombe, 1950) is a distribution related to the Poisson but incorporating the two hypotheses that the population is logarithmically distributed within patches and that these patches occur at random. In addition to m, the mean, the negative binomial uses an extra parameter k which is given by $s^2 = m + km^2$ (when s^2 is the variance). As k approaches infinity the distribution becomes identical with the Poisson whilst as k approaches zero the distribution becomes more clumped.

In practice, as Healy (in press) has shown, k can be determined from preliminary sample data by plotting standard deviation (ordinate) against mean (abscissa) for increasing sample size. The point on the horizontal axis cut by the regression line (drawn by eye) gives an approximate value for k which can then be used with the definitive samples to describe spatial distribution.

Methods for testing the closeness of fit of data to distributions of this kind are discussed by Anscombe (1950), Waters (1955) and Quenouille (1950) while Hartenstein (1961) describes a practical study on aggregated soil arthropod populations.

When data obtained from populations which do not fit a normal distribution are to be subjected to statistical tests such as those used to determine significantly different population levels, the raw data cannot be used because such tests are based on the assumption of normal distribution. In this case the data must be "transformed" by functions which will vary with the type of distribution. Data which fit a Poisson distribution should be converted to their square roots (Snedecor, 1946). When the data fit symmetrically into the groups 0–1, 1–2, 2–4, 4–8, 8–16, etc. logarithms should be taken (Quenouille, 1950) and data which fit the negative binomial should be transformed by log $(x+k)$.