Comparison-Its Scope and Limits

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COMPARISON – ITS SCOPE AND LIMITS

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SUMMARY

At any point in time, any discipline in science tends to be seized by a particular methodology or enthusiasm and other approaches get 'dumped'. So it is in ecology – although, because of obstinate individualism, nothing is ever completely forgotten. We are currently in a reductionist, population-dominated era. Twenty-five years ago, our interests lay primarily in comparisons of species. In between, the holistic approach has had a good run with studies of ecosystems everywhere. This introductory paper reflects on this history and particularly, because of the occasion, examines the value of the process of comparison.

Key words: Holism, reductionism, autecology, synecology, inference, ecological laws, evolution, species, intraspecific variation, ecological amplitude.

INTRODUCTION

In my Summary, I use the words 'enthusiasm' and 'dumped' advisedly to imply that what happens in science is more to do with emotion than with logic. Once we spend a lot of time looking at behaviour of species, then ecosystems become important. Now, nearly any ecologist who feels he must be respectable will work on populations. Although an historian may be able to see a proximal cause for what happens – the arguments of a persuasive scientist or a novel and interesting discovery – the ultimate causes may be little other than those which give the world its flourishing fashion industry.

We have seen, therefore, a wide variety of different approaches succeeding one another in ecology since the subject was given the respectability of a title by Haeckel. Is it because of obstinate individualism, or perhaps persevering wisdom, that no approach has ever been dumped completely? The enthusiastic young will think, I am sure, that the retention of old approaches is due to obstinate, even unimaginative, individualism. The older may see wisdom in this course. This meeting celebrates the 25th anniversary of the Unit of Comparative Plant Ecology (UCPE). Few research units survive this long, so some wisdom must have been seen in its activities by the august Conservancy and Research Council which have supported it – particularly since, despite some diversity, the Unit has indeed followed the single theme of comparative ecology which forms both its title and the topic of this symposium.

It is my intention, therefore, to look at approaches to ecology, to see where they have taken us and to try to understand why comparative ecology remains a vigorous and valuable enterprise which has not been swept aside by the dictates of scientific fashion.

ON APPROACHES TO ECOLOGY

There are now a number of excellent analyses of the history of ecology. The most perceptive are those of Harper (1982) and McIntosh (1985). For the moment, it

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is sufficient to remember that, from its Greek derivation, ecology is the study of households (*oikos*, house; *logos*, study). There are therefore two components, each of which is itself divisible.

The household: it is obvious that this has a number of components, (1) the aggregation of living organisms and the way these live together and interact; (2) their background surroundings and what these provide; (3) the interactions between (1) and (2).

The study: since the word was proposed by a scientist, this implies a scientific study to obtain understanding, which can involve up to four main methods: (1) description; (2) induction, in the sense of Mill; (3) experimentation, in the sense of Bacon; (4) hypothesis/deduction, as argued by Popper (Medawar, 1979). Each of these four methods has value. We can make little progress without description. But one of the last three has to be used if we wish to discover causation, which is usually the case because we are not often satisfied just to know *what* is there; we also want to know *why*. The most sophisticated method is that in which we carry out experiments to test particular hypotheses, an approach well analyzed for science in general by Medawar (1967) and for ecology by Price, Gaud & Slobodchikoff (1984). But each of the others has its place.

Because of the nature of the material with which we have to deal, there are further distinctions in approaches to ecology which we must also recognize. Firstly, we have the following long-recognized division. (1) The holistic: where we tend to examine the household (which we may call an ecosystem) as a whole and look for activities which reflect integration within it. (2) The reductionist: where we tend to examine the properties of component species and processes, expecting by such detailed knowledge of its parts to understand the whole household.

Secondly, and in parallel with the distinction between holistic and reductionist approaches, we have the division proposed by Schroter. This arises because, whether we like it or not, species do occur almost universally in assemblages: synecology – the study of communities and their properties; autecology – the study of species and their properties.

Although the latter two pairs of terms are not totally equivalent, they each reflect a similar division of interest between the ecological world taken as a whole or taken piece by piece. In its formative years, ecology was devoted to synecology. One culmination was Tansley's remarkably perceptive survey of British vegetation (Tansley, 1939). The same approach was also followed by Odum (1975). But, at the same time, others saw the importance of studying the species which make up these communities and it is important to note that Professor A. R. Clapham, who was responsible for the founding of the UCPE, made autecology the subject of his presidential address to the British Ecological Society (Clapham, 1956). This theme carried through to the *Festschrift* published in honour of his 80th birthday (Harley & Lewis, 1984).

Thirdly, the division of ecology into two has now become a division into three; into *populations* and *species* as well as into *communities*. This recognizes that the species which occur in communities are themselves made up of individuals which react together in interesting and complex ways. The range of exciting discoveries that have been made in this field is well displayed for plants by Harper (1977) and for both animals and plants by Begon & Mortimer (1986).

ON COMPARISON

In the hierarchy of methods of study, it is clear that comparison, as a specific exercise, appears early. It is true that we can describe anything without making comparisons but once we attempt induction then comparisons must be involved. Experimentation, whether Baconian or more directed towards hypothesis testing, obviously involves comparison of the effects of a particular treatment with those of another treatment (which can be no 'treatment' at all).

All this may seem trivial, because comparison is surely something which we take for granted. Yet do we really understand what we are doing? There is a simple premise of statistics that, between two observations, only one comparison can be made and that, between *n* observations, *n* - 1 independent comparisons can be made. This we term the number of degrees of freedom.

Of course it is possible to make only one observation. We could discover, for instance, that tree lupin on china clay waste, because of its associated Rhizobia, fixes 400 g N ha^{-1} d^{-1} (about 150 kg ha^{-1} $year^{-1}$). Such a bald fact, however, is useless. It is true that many people will think otherwise, probably because they will be very interested that tree lupin can fix so much nitrogen. But this interest only arises because they are tacitly making a comparison with other evidence, gained elsewhere, that most plants either do not fix nitrogen at all or fix far less. They are simply not using the fact by itself but comparing it with other facts already accumulated. Herein of course is a substantial problem, because the other facts have been accumulated by other people in other situations and may not provide the basis for legitimate comparison. This becomes more obvious if we remember that some woodland plants which do not bear N-fixing organisms in nodules nevertheless fix appreciable quantities of nitrogen in their rhizosphere. Is then 400 g ha^{-1} d^{-1} at all remarkable? The only way to decide is to carry out a proper comparison with all the material being tested in a similar manner and with appropriate controls and assessments of error (Fig. 1). Then we can see the real contribution of the legume.

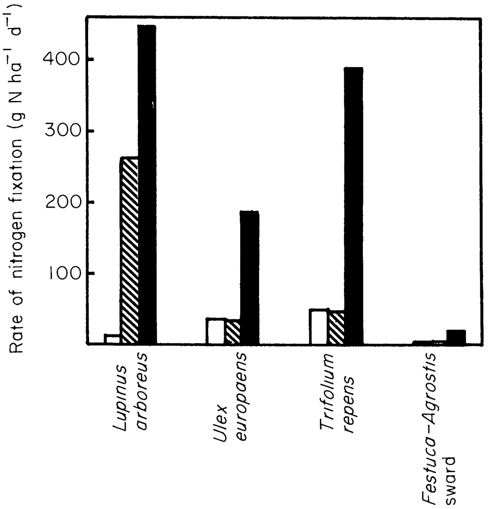

Fig. 1. A comparison of the rates of nitrogen fixation by different species of legume and by a grass sward, all growing on sand waste (rates measured successively in August 1976, October 1976 and May 1977) (from Skeffington & Bradshaw, 1980).

All of this, some will say, is totally obvious. But is it? A great deal of ecology has been, and still is, based on single observations without any proper comparisons – for example Tansley's (1939) species lists. Sometimes, it may appear otherwise because many items have gone to make up the single observation, as in the detailed description of a particular plant community or in the description of the response to density of particular animal or plant species. But few critical conclusions will be possible unless other entirely comparable evidence on other material is also available, a view supported by Strong (1980).

The response to density of a single species (Fig. 2), of course, is not entirely without interest because the experiment provides valid comparisons, and therefore evidence, about the effects of density within the single species. But we gain no idea of the significance of what we observe. There is the possibility that everything behaves in the same way. We will return to this sort of evidence and its problems later.

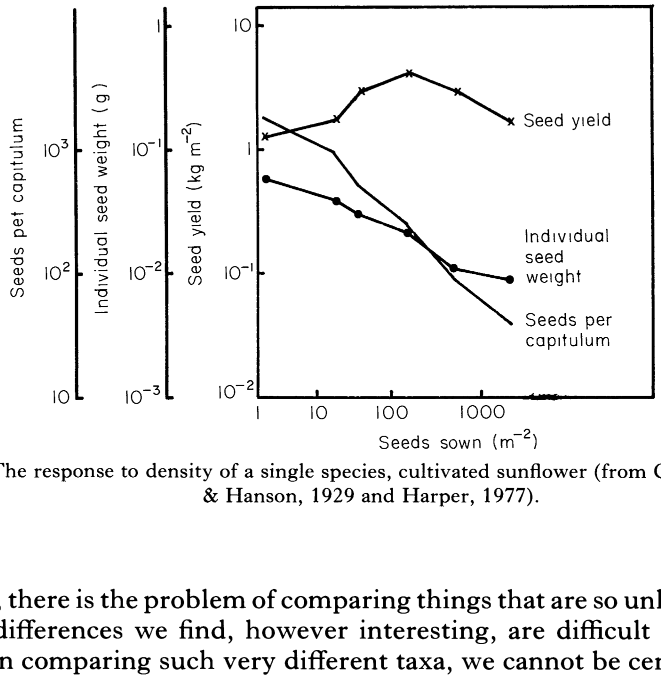

Fig. 2. The response to density of a single species, cultivated sunflower (from Clements, Weaver & Hanson, 1929 and Harper, 1977).

Finally, there is the problem of comparing things that are so unlike and unrelated that any differences we find, however interesting, are difficult to make sense of because, in comparing such very different taxa, we cannot be certain of the origin of the differences. The comparison of the temperature responses of *Urtica dioica*, an angiosperm, and *Brachythecium rutabulum*, a moss, for instance (Fig. 3), is very interesting but we must be cautious in using the differences we find to provide a full explanation of their coexistence. The differences could have historic origins and have little to do with current ecological relationships. This important point is returned to, both at the end of this paper and that by Grime & Hodgson (1987).

ON INFERENCE

Let us now assume that we have made a series of comparable observations from which we hope to make certain inferences. If we have made a number of observations, we may infer some general conclusion. But let us beware, because the process of inference has considerable limitations.

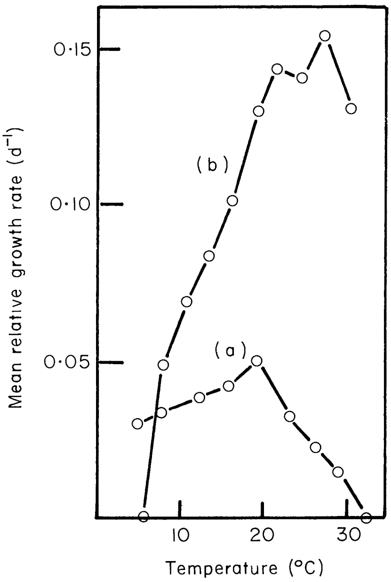

Fig. 3. The effects of temperature upon the mean relative growth rate (30 d basis) of (a) *Brachythecium rutabulum* and (b) *Urtica dioica* (from Furness, 1978).

The first and most obvious limitation is related to the number of observations and to their origin. If only two things are compared, despite great and interesting differences, being found, there is absolutely no way of determining their generality. The next two examples taken might show a completely reversed behaviour. The solution to this is, of course, well understood and is accessible to statistical analysis. The statistical significance of any comparison is related to the number of independent observations involved, the degrees of freedom. A very low number of degrees of freedom will make it difficult to achieve a significant result. The requirement is for more comparisons, which in the case of Figure 3 would mean extending this work to other species. This is the great strength of the work carried out at Sheffield. This extension must, however, involve material which, within the comparison being examined, is chosen at random and is therefore unbiasedly representative. All this is simple to do but still often not done. It does involve more work, which is not possible in all cases. This is where good Research Council or other support is invaluable.

The second limitation is the asymmetry of proof argued by Popper (1959). If we observe something which agrees with an idea, then the conclusion is that the idea is *not disproved.* But we cannot conclude that the idea is *proved.* If we observe something which disagrees with an idea then, providing we have exposed our idea to 'a cruelly critical test', what Galileo called '*Il cimento*' (Medawar, 1979), we can conclude that the idea *is disproved.* In statistical analysis, this is translated into the null hypothesis approach. Because this approach is so widely used, and because we can also make a probabilistic assessment of the error in what we conclude, I believe that the problem of asymmetry of proof has become less of a trouble for biologists. But it indicates that we must continue to produce ideas and conclusions that are testable by refutation, which means using *imagination* in constructing hypotheses.

The third and most important limitation are the troubles that can occur in attributing particular effects to particular causes because of confounding variables, recently well discussed for animals by Clutton-Brock & Harvey (1979). If we observe that a particular species, such as white clover, disappears at high altitudes, we may perhaps infer that it is more sensitive to lower temperatures than other species. But, in this case, we would be very wrong because although, for instance in North Wales, white clover generally disappears above an altitude of 500 m, it can also be found growing vigorously there even at altitudes of 1000 m on special soils which have an adequate supply of bases maintained by the geological substrata. The apparent altitudinal zonation is not due to the direct effects of climate but to associated soil effects. In statistical parlance, we must beware of silly correlations.

This sort of thing is a particular problem with observational, correlative evidence, even when a large number of comparisons is involved. Experiments designed to determine the particular effects of a particular factor, which are not very difficult to carry out in the case of plants, usually overcome this problem. But sometimes this is not so. For example, from the profound effects of the simple fertilizer treatments which emerge from the Park Grass Experiments (Brenchley, 1958; Thurston, 1969) it seems very easy to attribute appropriate causations. Yet it would, even now with so much progress in plant ecology, be a very brave person who could infer *exact* chains of causation from the differences in species composition which are evident between the different plots – because of the multifarious effects of fertilizers on an ecosystem. Pigott (1982) rightly argues that further experiments are the only answer. Tilman's work (1984, 1985), indicating the interrelations between competition for nutrients and for light, is therefore an interesting step forward.

ON ECOLOGICAL PRINCIPLES

Despite all the problems that surround our methodology, no-one can deny that we have made progress in ecology. Many will measure this progress by the number of general laws we have produced. Open any textbook and you will discover many generalizations, whether in mineral nutrition – such as the classical response of plant species to increased nutrients (Fig. 4), or in population biology – such as the

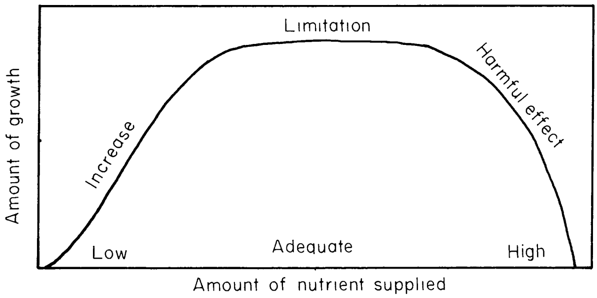

Fig. 4. The general relation between any particular nutrient or growth factor and the amount of growth made by the plant (from Russell, 1973).

– 3/2 law of density-dependent self-thinning (Yoda *et al.*, 1963). Nearer to home, we have had the elaboration of the calcicole/calcifuge concept by Grime & Hodgson (1969) and the development of the C–S–R theory of plant strategies (Grime, 1977, 1979). All of these generalizations are very important, not least because they provide a framework of understanding.

The list of such generalizations is long. It will certainly be interesting to see (from a survey, see Bradshaw *et al.*, 1986) which ecological 'concepts' are considered important enough by members of the British Ecological Society for inclusion in their 75th Anniversary Symposium in 1988.

But is progress only to be related to the number of successful generalizations (which we will grandly call principles) which we can establish? Teachers and writers of textbooks may feel this way. The search for general principles is very important, no doubt. But the ecological world has reasons which make the search for *exceptions* equally important.

ON EVOLUTION AND SPECIES

The living material we examine is the product of evolution. This evolution is determined to a major extent by the environment. The starting point was the physical environment. As we know, there was, and is, not just one physical environment but an infinite set of them, owing to simultaneous variations in many different factors. Evolution is therefore going to set off in many different directions. Then, once this simple sort of evolution has begun, each physical environment will be complicated by the presence in it of the products of the primary evolution. Once a simple habitat offering one environment is occupied by a single species then there immediately appear two sub-environments, the space already occupied by the species and the space which is not.

Of course this is an oversimplification, because each of the spaces is itself divisible into a whole range of micro-environments. But the crucial point is that nature has offered, since life began, an immense and complex range of physical and biological environments within which evolution has occured. We may think of these environments as a two-dimensional matrix, which is complex enough. But the reality is much more complex, involving an array of niches each of which is, in the terminology of Hutchinson (1965), a multi-dimensional hyper-volume.

The great characteristic, then, of the evolutionary products of this enormous array of environments is its enormous complexity and diversity. This was well recognized by Darwin, and especially noted in the final chapter of *The Origin of Species by Means of Natural Selection* (1859), so there is nothing novel in the idea:

> It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us.

But what is surprising is that, as ecologists, we have spent so much of our time looking for general principles which, for the species, means similarities in behaviour. Surely in doing this we are, wittingly or unwittingly, overlooking that great attribute of evolution, and therefore of the 'households' we study, namely the *diversity* in species which arises from the life of species within communities and therefore from evolution (Bradshaw & Mortimer, 1986).

ON SPECIES COMPARISONS

From comparisons of species, we can deduce a very simple idea: that although some ecologists may, and indeed should, look for great principles of general applicability, others must look for the exceptions, or indeed, at situations where there do not appear to be great principles at all. Some may feel that I am trying to lead them towards a sort of latter-day obscuritanism. Maybe I am, but I am in deadly earnest in warning that, if we concentrate on the generalities of ecology, we will miss some of its most elegant lessons, those which come from the inexorable principle that evolution automatically leads to diversity.

A target in ecology must, then, be understanding this diversity of species. As Clapham (1956), Grime (1984) and others have argued, this should mean looking at diversity in morphology, in physiology, in life-cycle and in any other attributes which determine the ecology of species. Perhaps the first step must be an examination of distribution, because what is this but the primary defining attribute of the ecology of a species?

Immediately, however, we realize that, for the reason already given, we have to be involved *in comparison* because we can have no idea about the significance of a particular species' distribution unless we have one for a second species with which to compare it. At the same time, this comparison cannot be based on evidence which is so general that there is no precision – '*Arrhenatherum elatius* is usually found in rough pastures and hedgerows on neutral soils' or '*Agrostis capillaris* is found on a wide range of pastures on neutral or acid soils' – because no exact comparison is possible. This leads to a requirement for precise evidence on distribution, which is so rarely available. Sheffield's *Ecological Atlas of Grassland Plants* (Grime & Lloyd, 1973) was a conspicuous exception (Fig. 5). It not only illustrated the value of precise data but also what can be gained when several species are compared on a common basis – and not just a few but 50 or 100 or, in the case of the latest compendium (Grime, Hodgson & Hunt, 1987), even more.

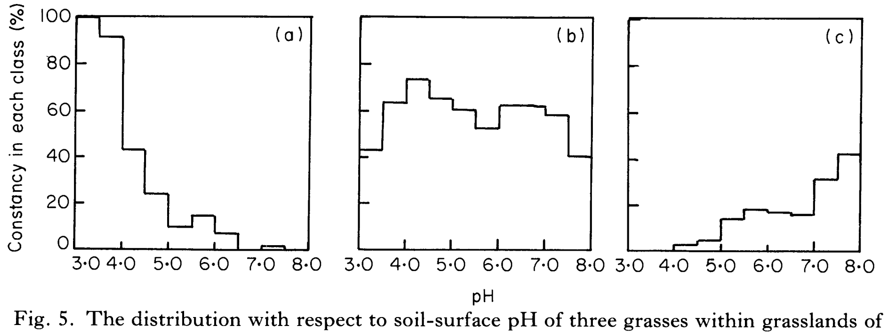

Fig. 5. The distribution with respect to soil-surface pH of three grasses within grasslands of the Sheffield region: (a) *Deschampsia flexuosa*, (b) *Festuca ovina*, (c) *Brachypodium pinnatum* (from Grime & Lloyd, 1973).

However, these sorts of data are obviously only a starting point. The pH value is a factor which affects many other characteristics of the soil, each of which is often capable of varying independently of pH – so obvious for calcium and nitrogen for instance. We have good evidence that not only do species have their own particular responses to each of these, but also that these responses do not go in parallel (Bradshaw *et al.*, 1958, 1964) as Figure 6 demonstrates. The responses of *A. elatius* and *Festuca ovina* discussed by Rorison (1987) show that there are even further complexities.

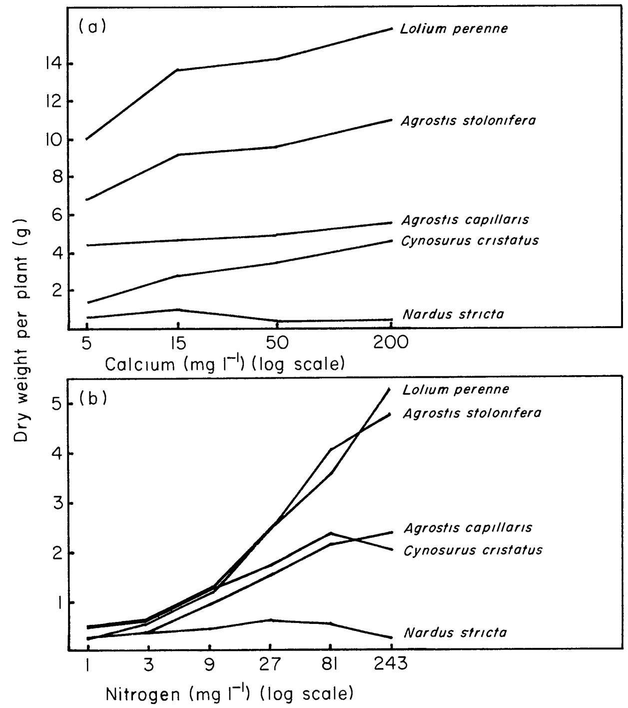

Fig. 6. The response of five grass species to calcium (a) and to nitrogen (b) (from Bradshaw *et al.*, 1958, 1964).

Of course, the ecological world is more than pH or nutrients. It is salt and temperature and water and light and a host of other physical factors. It is not difficult to set up comparative tests to see how species differ in their response to these, and remarkable differences can be found (Jarvis & Jarvis, 1963). It may be more difficult to discover how much species are affected by these factors in the field. Indeed, it is remarkable how little critical evidence there is on the relation of distributions of species to any critical physical factor. There is, for instance (with recent notable exceptions, see Rorison, 1987), very poor evidence for even such an important nutrient as nitrogen. So how can we begin to understand the factors involved in the distribution of species? Yet these species are the products of evolution and therefore of the natural selection which arises from specific environmental conditions. So we should be able to relate what we find in species to what we find in environments. But it will not necessarily be easy.

ON THE REST OF THE ENVIRONMENT

We have just argued that the environment of a species is not solely determined by the simple physical factors which occur on site. It is also profoundly shaped by how many, and what, other organisms are there too. The other plants, can, of course, be members of the same species. Indeed, these may be the most common determinant of the micro-environment of any individual. These organisms ultimately have effects which must be physical. But it is convenient, because of their origin, to distinguish them as biological.

This biological component of the environment may profoundly affect plant responses to the physical components. This can be well seen from the work of Werner & Platt (1976) on the distribution of *Solidago* species in relation to moisture (Fig. 7). The presence of other species alters the distributions considerably.

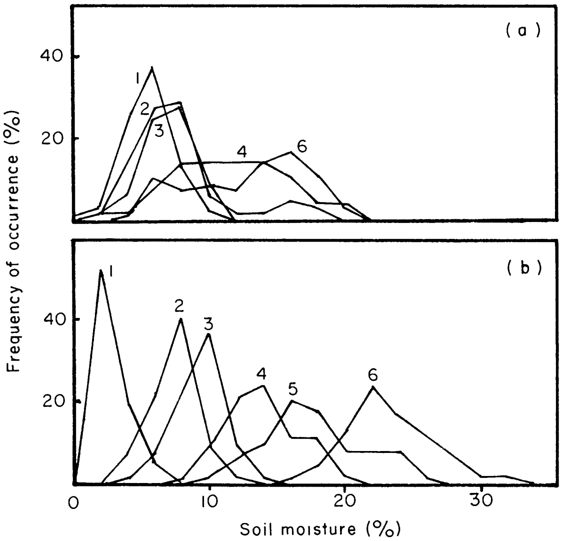

Fig. 7. Differences in the distribution of *Solidago* species in relation to moisture, in a successional old field (a) and in a mature prairie (b) (from Werner & Platt, 1976). *Solidago* species: 1, *S. nemoralis*; 2, *S. missouriensis*; 3, *S. speciosa*; 4, *S. canadensis*; 5, *S. gigantea*; 6, *S. graminifolia*.

The trouble is that these biological components of the environment are tremendously variable. Own density can, for most species, vary between very wide limits. So also can the density of other species, quite apart from their actual occurrence. If we are anxious to discover the response of a species to its own density (Fig. 8) and compare this with that of other species to *their* own density, we shall have to carry out the necessary experiments in order to demonstrate the generality of the $-3/2$ self-thinning law. However, now it is not the similarities in behaviour of the various species which become interesting, but their differences. The similarities may be no more than the results of in-built physical or physiological constraints within which the species must operate. The differences support the ecological interest. These do indeed seem to make sense (White, 1980) and make us realize that the differences in response are of ecological significance.

It is much more difficult to compare the behaviour of individual species in relation to the presence of others, if only because of the great number of these and their combinations. It is remarkable what complicated differences in response are found when only three species are grown in all possible combinations (Haizel & Harper, 1973). Even with two species, the interactions owing to 'same species' are difficult to unravel from those of 'other species' (Jolliffe, Minjas & Runeckles, 1984). The difficulty in relating such results to the distribution of the subject species is one salutary aspect of this sort of comparison.

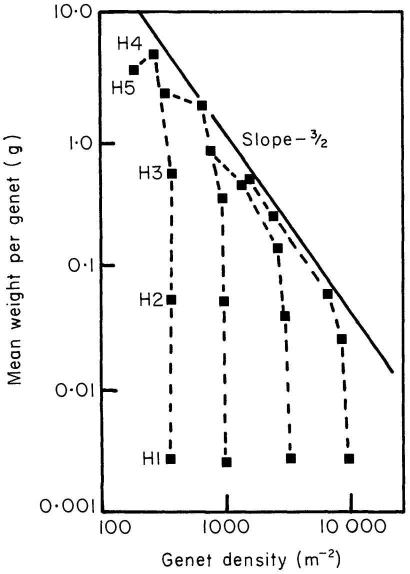

Fig. 8. Self-thinning in populations of *Lolium perenne* planted at four different densities. H1–H5 represent five successive harvests (from Kays & Harper, 1974).

Here I have put my head into the hornet's nest of competiton. What is so difficult is to find a simple way of testing the total effects of the biological environment on species. The most elegant is the reciprocal transplant, where two or more species are planted both into their own and the other's habitat(s). This was first used in a recorded manner by Bonnier (1890) but, alas, it was misused because the material was not well enough maintained and recorded so that species 'transformations' occurred (Clausen, Keck & Hiesey, 1940). Since those early days, the method has mainly been used to test intraspecific rather than interspecific differences. However, Schoen *et al.* (1986) have used it to compare *Impatiens capensis* with *I. pallida.* Interestingly, they found that differences in survivorship and fruit production were attributed primarily to features of the site of the transplants rather than to neighbours. A similar picture was obtained by other investigators (e.g. Fowler & Antonovics, 1981; Snow & Vince, 1984). But more critical work is needed, such as that where performance of transplants is examined in the presence and absence of vegetation (Wilson & Keddy, 1986). Perhaps the most elegant and penetrating use of the reciprocal transplant has been with populations of *Anthoxanthum odoratum* in the Park Grass experiment, which is discussed in the next section.

It is not possible to do justice to what is to be extracted from these sorts of comparison because of the sheer complexity of environments. At this point, it is perhaps necessary to remind ourselves that far too little has been done to define the distribution of species in terms that take into account *all* the characteristics of their environments. I personally find, for instance, that the recognition of either *r–K* types of adaptation (MacArthur & Wilson, 1967; Pianka, 1970) or C–S–R types of adaptation (Grime, 1977, 1984), even as parts of a continuum, are too likely to lead us to miss essential, important, attributes of differences in adaptation to be valuable tools when used on their own. We should use them for exposing anomalies and complexities and as a stepping stone to further analysis.

However, this does not excuse us from attempting a definition of the characteristics of the distributions of different species using as many attributes as we can. The first step may be in terms of the obvious overall characteristics of their habitats, as is so beautifully explored in the new Sheffield compendium (Grime *et al.*, 1987, from which Figure 9 has been abstracted). But if we are to achieve proper understanding, it is clear that a reductionist approach will be required to define the habitat preferences of species in precise physicochemical terms.

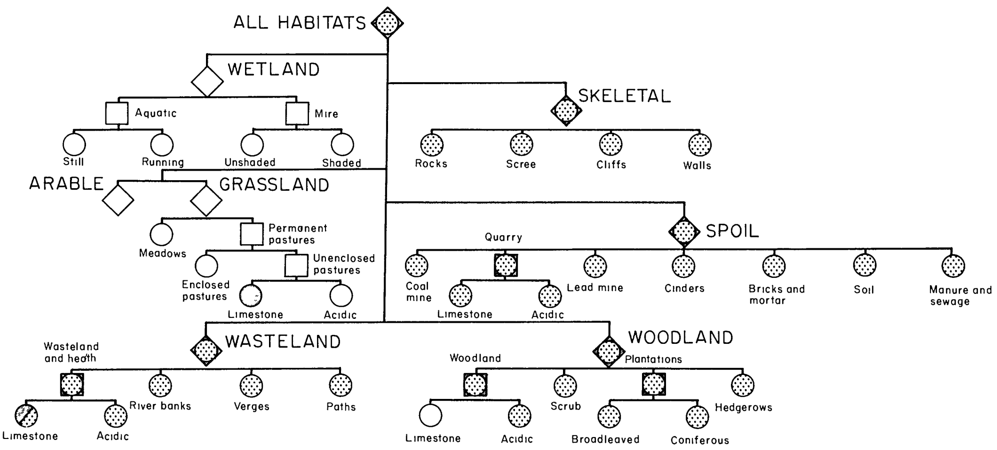

Fig. 9. Two contrasting distributions in the Sheffield flora. Habitats in which *Primula veris* occurs in 5 % or more of the survey sample (dark stipple) are far fewer and more specialized than the habitats which support comparable occurrences of *Chamerion angustifolium* (pale stipple) (abstracted from Grime, Hodgson & Hunt, 1987).

ON WHAT CAN HAPPEN WITHIN SPECIES

It is rather simplistic to argue that comparative ecology shold mainly involve an examination and understanding of differences between species, because evolution has created a diversity which we must understand, if we do not also remember that these different products of evolution in different environments must have had their origin within species.

What happens *within* species can therefore be just as much part of comparative ecology as what is found *between* them. Yet, on the whole, this has been more the concern of people interested in evolution, although they may call themselves ecological geneticists. The great value of comparisons based on different populations of a species is that any differences are far more readily related to the environments in which the populations occur, and are much less confounded by changes in characteristics acquired at some time past and of little relation to the present environment in which the species occur.

The differences found within species may not be as extreme as those found between species, which could be a disadvantage. But the specificity of their relationship to the environment occupied by the populations concerned is a great advantage. At the same time, all such evidence helps to put our ecological observations into an evolutionary context. As Harper (1982) points out, all 'ultimate' biological explanation has to be in evolutionary terms.

This has been argued on a number of occasions. The recent symposium in Mexico (Dirzo & Sarukhan, 1984) provides a wide range of powerful examples. Perhaps the most eloquent and apposite case is the analysis of the Park Grass populations of *A. odoratum*. These populations indeed reveal, almost better than anything else, the subtle complexity of the environments produced by the simple fertilizer treatments (Snaydon & Davies, 1982). The reciprocal transplants, which were repeated for different pairs of plots and are therefore of general validity, then show just how fundamental those differences are to the survival of the different populations (Davies & Snaydon, 1976) (Fig. 10). Heavy metal tolerance (Baker, 1987) provides another eloquent example, for a more barbaric type of habitat, and *Phlox* (Schmidt & Levin, 1985) shows just how complex and subtle the adaptations can be.

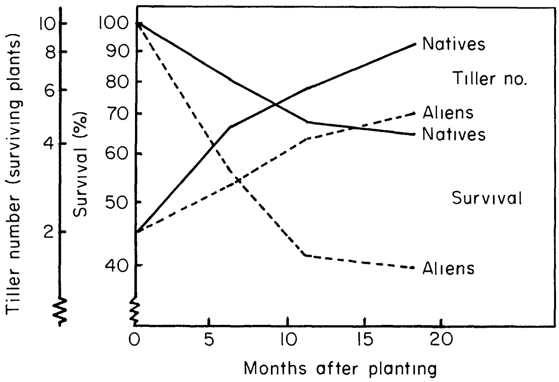

Fig. 10. The survival, and tiller members of surviving plants, of *Anthoxanthum odoratum* transplanted reciprocally into their native and into alien plots in the Park Grass experiment (from Davies & Snaydon, 1976).

Comparative ecology, to understand the diversity of environmental pressures and the characteristics of species which enable them to cope, has here a powerful tool. At the same time, population differences emphasize the evolutionary underpinning of comparative ecology.

On Ecological Amplitude

However, this diversity within species has another significance. It allows the species to extend its range of ecological amplitude. Nowhere is this more clear than in *F. ovina*, whose normal distribution is remarkably wide (Fig. 5). It possesses populations whose differences in behaviour are as extreme as those possessed by normal calcicole and calcifuge species (Snaydon & Bradshaw, 1961). This dependence of ecological amplitude on genetic variation is obvious in many species (Bradshaw, 1984).

To understand the ecology of a species properly, we have therefore to look at this genetic flexibility, expressed in the form of population differences, and consider, as with *Holcus lanatus* (McGrath, Rorison & Baker, 1980), what it tells us about ecology rather than evolution. It will give us more work but, without it, our analyses of species differences may well be erroneous.

I have the temerity to say that this line of enquiry can, and should, be extended downwards to the study of differences between individuals, simply because these are the components of populations and are the ultimate objects of adaptation. There is now strong evidence that variation between individuals provides a crucial contribution to the behaviour of populations and, therefore, of species (Allard & Adams, 1969; Burdon, 1980). It is, of course, also the raw material from which population and species differences evolve.

However, the ecological behaviour of species is not only affected by genetic flexibility. It is also profoundly influenced by phenotypic plasticity. Almost

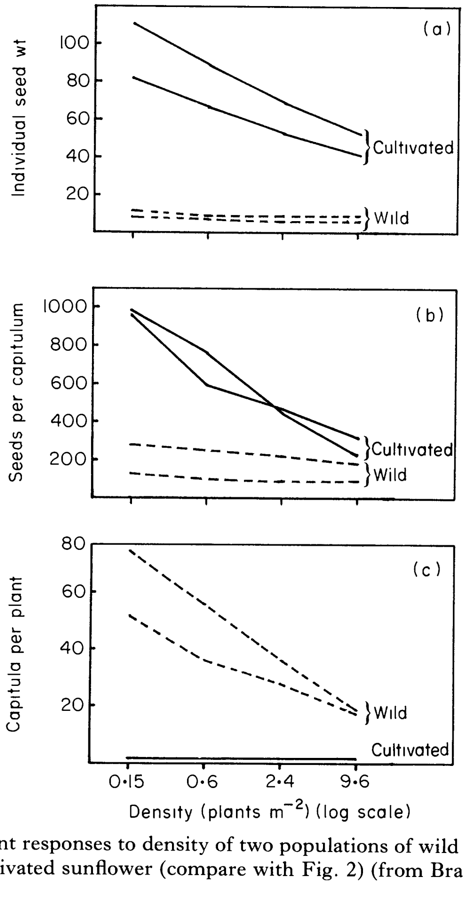

Fig. 11. The different responses to density of two populations of wild sunflower and two varieties of cultivated sunflower (compare with Fig. 2) (from Bradshaw, 1974).

no plant genotype produces only one phenotype; its phenotype, and therefore its ecological behaviour, can be altered by environment (Bradshaw, 1965). It is therefore important that, wherever possible, phenotypic response must be measured. It can give most interesting insights into differences in adaptation of different species, such as between the bryophytes *Thuidium tamariscinum* and *Lophocolea bidentata*, in response to shade (Rincon & Grime, 1985). It can also be found that the behaviour previously ascribed to a species (Fig. 2) is not typical of all of that species. In this particular case, wild sunflowers have the stability of seed size which is normal in wild plants; this is in complete contrast to cultivated material (Fig. 11). All this again means further work but, without it, the ecology of species will be improperly understood.

ON LEVELS AND TYPES OF COMPARISON

All the previous comments arise from the argument that the products of evolution are diverse and that the comparisons from which we can understand this diversity and relate it to the environment are important. This does not mean that we should not look for the generalizations that are so well argued for by Grime & Hodgson (1987). But it does mean that deviations from these laws are as important as the laws themselves and we should try to understand them.

This apparent contradiction within comparative plant ecology can indeed be understood if we bear in mind the nature of evolution. There are basically two trends which are possible: evolution which leads to divergence and evolution which leads to convergence. If we are looking for divergence, we must look for

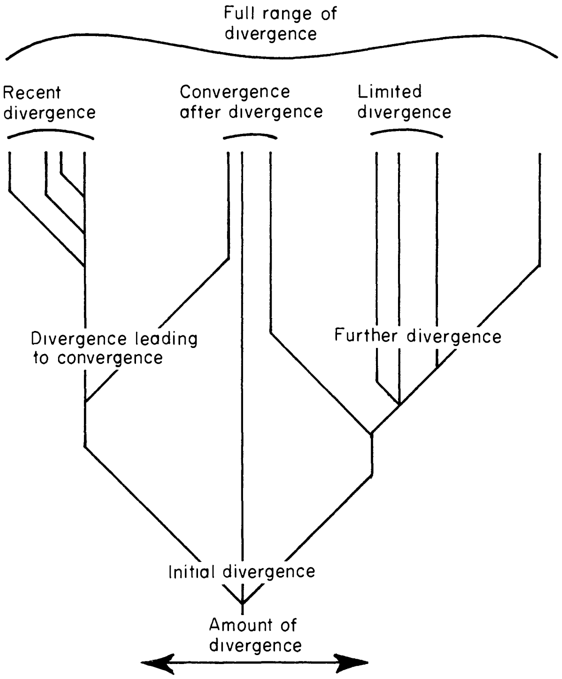

Fig. 12. Origins of the subject materials for comparative ecology: the processes of evolutionary change leading to divergence and convergence.

differences. Convergence should lead to similarities, which we may be able to recognize as general laws. Clearly, divergence is the primary step in evolution, so differences should be the primary material for study. But similarities can be equally important, not only because they are material from a second step in evolutionary adaptation, but also because parallelism in different material may well provide the replication which is needed to establish patterns in the products of primary divergence (Fig. 12).

At the same time, the occurrence either of similarities or of differences will provide primary evidence of what happens in particular situations. When two species occupy the same habitat, do we expect them to be more similar than when they do not? Is coexistence associated with convergence or with divergence? The matter is still a major problem in ecology (Begon, Harper & Townsend, 1986) and evidence is needed. The work of Fitter (1987) shows what fascinating things are to be found.

Of course, important comparisons can also be made at other quite different levels in ecology, notably at the level of community and ecosystem. Indeed, some of these urgently require attention. But these represent a different type of study which requires a separate justification.

SOME FINAL COMMENTS

In essence, the comparative ecology which I am supporting, and which is the subject of this symposium, is a reductionist and experimental autecology. As such, if it is well planned, it ought to be immune from sloppiness of evidence and argument. However, there are still further pitfalls, of which we must beware.

The first is the problem of ancestral characters. To Jacob (1977) we owe the reminder that evolution is a process of tinkering, in which the new is made out of the old. Much of what we see and examine has been evolved in the long past. At the same time, almost everything else has, inevitably, been evolved in the nearer past. Almost nothing can be said to be directly a product of the present. Harper (1982) therefore argues that we should talk about *abaptation*, rather than *adaptation*, evolution from, rather than evolution towards.

Even if we do not go to this extreme and accept that evolution *towards* existing conditions must certainly be occurring, we must remember that such evolution does not mean that the species has already arrived at a state of perfect adaptation; rather, it may simply have made some progress. We must also remember that these species must be made up mostly of ancestral characters from the past. As such, they will be only partly related to present-day conditions and the characteristics of a group of species may be determined by ancestry, as elegantly shown by Hodgson (1986) and further elaborated by Grime & Hodgson (1987). This argument has been used to question the possibility of evaluating the occurrence of adaptation at all (Gould & Lewontin, 1979).

At the same time, some non-adaptive characters may have evolved in parallel with adaptive characters by pleiotropy, or some other process leading to correlated response. All this leads to the conclusion that, if we are to assess the adaptive value of any character, we should do so by its effects rather than by its apparent causes (Clutton-Brock & Harvey, 1979), forgetting any expectation of perfection and seeking only comparative superiority. All of this is profound argument for the experimental, reductionist approaches which are so evident in this series of papers.

We must, therefore, go carefully to find out what is really adaptive – what really counts for survival and provides the *why* in ecology. However, it is only by comparison that any progress is possible. So let us make sure we employ, and analyze, comparisons properly.

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