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A pragmatic approach to functional ecology

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Introduction

As ecology matures and as the world's environmental problems continue to multiply, the need for general predictive models also grows. However, it is one thing to assert that such models are needed, and quite another to produce them. I would like to draw attention to two recent parallel developments in ecology. When combined, they may produce general models, with immediate potential for use in solving both theoretical and applied problems. They also illustrate what we might think of as the basic tools of functional ecology (and *Functional Ecology*).

After introducing these recent developments, or research tools, I will illustrate some aspects of their application using research on wetlands. These examples were selected because we have been trying explicitly to combine these tools for the last 5 years, and they illustrate some of the strengths and weaknesses of this approach. Although the examples emphasize my background in plant ecology, it should be obvious that identical approaches apply to animal ecology as well.

In the early issues of *Functional Ecology*, the question arose as to what functional ecology is (Bradshaw 1987a; Calow 1987; Grime 1987). I suggest that functional ecology has three basic components: (1) constructing trait matrices through screening; (2) exploring empirical relationships among these traits; and (3) determining the relationships between traits and environments. Ideally, functional ecology deals with traits measured on large numbers of species, since measurement of traits on very few species has two problems. First, it does not provide sufficiently large sample sizes to test whether correlations among traits, or between traits and environments, are statistically significant. Second, it does not tell us whether the observed patterns are general patterns in nature, or simply peculiarities of the autecology of the few species examined.

The two tools for this research strategy in functional ecology already exist. One tool is screening such as we find in Grime & Hunt (1975) and Grime *et al.* (1981). The other tool is empirical ecology such as we find in Peters (1980) and Rigler (1982). Let us consider these tools in turn.

Screening

Screening as a tool has been developed by Grime's team at the University of Sheffield. Although comparative ecology is by itself not a new discipline (Grime 1965; Rorison *et al.* 1987), the use of screening for comparison is. In its most general sense, the screening involves measuring one trait on a large number of species simultaneously. This could include traits such as size, reproductive output, morphology, clutch size, metabolic rate, etc. This approach of compiling life-history traits, in itself, is also not new. But the novel angle which Grime and his team have pioneered is the design of bioassays for a trait measured simultaneously on a large number of species — screening. That is to say, they have developed bioassays for the measurement of ecological traits which are not obvious on inspection, but can only be measured under experimental conditions by creating one or more environments and measuring the response of large numbers of species to them (e.g. Grime & Hunt 1975; Grime *et al.* 1981). The classical example of this is the work done by Grime & Hunt (1975) to measure maximum relative growth rate in 132 members of the British flora simultaneously. Here a standardized resource-rich environment was created and then all species were grown in it, with their relative growth rates being measured and compiled. Table 1 gives some other examples of screening in the recent literature. The list is by no means exhaustive or complete.

There are two possible weaknesses in such an approach. Let us illustrate them by returning to the Grime and Hunt example. First, it is not necessarily true, or even likely, that all species will achieve maximum growth rates under exactly the same environmental conditions. We may therefore ask whether we are measuring something useful. Fortunately, in many cases there are large differences in relative growth rate among species. Therefore other sources of variation, such as the precise environment used for screening or within-species variation, are residuals that fail to obscure general trends. That is to say, for some traits the signal is so large that the problems arising from the bioassay can be relegated to noise. The challenge in using this approach is to screen for traits in such a way that the noise-to-signal ratio is as high as possible.

Another weakness in this approach as it appears in the literature is the analysis of the data generated. In student seminars where I have introduced the Grime and Hunt paper, a criticism frequently made by students is that the analysis of the data fails to make full use of the rich data set which is presented. The

Table 1. Some recent examples of traits which reflect plant function and for which screening has been conducted

Trait	Examples
Germination	Grime *et al.* 1981
	Shipley *et al.* 1989
Relative growth rate	Grime & Hunt 1975
	Sheldon 1987
	Shipley *et al.* 1989
	Shipley & Peters 1990
Nutrient foraging	Crick & Grime 1987
	Grime 1993
Shoot extension rates	C. Boutin & P. A. Keddy, unpublished observations
Evergreenness	Givnish 1987
	Wisheu & Keddy 1989
Competitive ability	Gaudet & Keddy 1988
Stress tolerance	Shipley & Keddy 1988
Biomass partitioning	Shipley & Peters 1990
Drought tolerance	Raynal, Grime & Boot 1985
	Boot, Raynal & Grime 1986*
Palatability	Sheldon 1987
	Southwood, Brown & Reader 1986
	McCanny *et al.* 1990
Canopy form	Givnish 1987
	Shipley *et al.* 1989
Genomic form	Bennett 1987
Sensitivity to acid rain	Percy 1986
Flood tolerance	Justin & Armstrong 1987

* Only two species were 'screened', but these are included because it is an idea that merits further work.

paper therefore has less of an impact on the reader. While screening can generate systematic data on traits which have never been measured before, generating data is not an end in itself. There must be a method of analysing the data which maximizes the amount we can learn from it.

Empiricism

Here is where the second tool, or conceptual approach, must be introduced. This approach was explicitly introduced in Rob Peters' (1980) classic paper, 'From natural history to ecology' and expanded upon in his latest book *A Critique for Ecology* (Peters 1991). He argues in both that there are important differences between natural history and ecology. Natural history involves the patient accumulation of detail, often involving the appreciation of detail for its own sake. The objective is rarely to develop general predictive theories and the data collected can rarely be assembled in such a way as to develop general models. In fact, participants in this research approach sometimes argue that the diversity of evolutionary outcomes is of primary interest, and therefore attempts at generalization could be both naive and/or misleading (e.g. Bradshaw 1987b; Aarssen & Epp 1990). I have argued elsewhere (Keddy 1989) that many of the unresolved issues in the study of competition arise out of this approach and philosophy. In contrast, Peters argues, ecology requires generalizations in order to make progress. Both he and Rigler (1982) propose a greater emphasis on 'empiricism', the search for quantitative relationships between measurable dependent and independent variables. In the context of screening, these relationships could be correlations among pairs of traits (e.g. relative growth rate and competitive ability) or traits and environments (e.g. relative growth rate and soil fertility).

One of the inherent limitations of empiricism is that one can only look for relationships among traits and/or environments which are measured. Traditional traits which are easy to measure without screening (e.g. seed weight, body size, weight, clutch size, etc.) by themselves offer a very small window into the rich landscape of traits which organisms actually possess. Combining screening with empiricism uses the strengths of each approach and yields general empirical relationships among traits.

The merit of traits

An important feature of the foregoing combination is that it produces quantitative models using traits, not species. With the large number of species on this planet, models based on species taxonomy have limited generality (see also Rigler 1982; Wimsatt 1982; Keddy 1990a). For example, a model based on species names for managing wetlands in UK could not be easily transferred to a different flora in

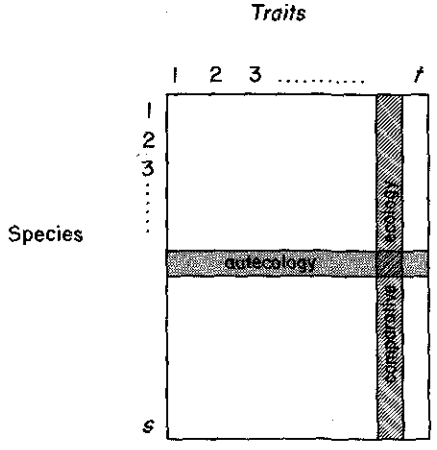

Fig. 1. Trait matrix of *s* species by *t* traits. Few such matrices currently exist, in part because ecologists have emphasized studying species autecology (rows) rather than comparing traits (columns). These matrices are an essential first step to exploring the inter-relations of traits and the distributions of traits along environmental gradients.

south-east Asia. If, however, that model were based upon traits such as aerenchyma diameter, plant height and germination requirements, then it would be much easier to develop a general model which could be calibrated for a particular region of the planet by simply noting which local species had the traits with which the model dealt. There is a growing literature which emphasizes the importance of traits (*e.g. Grime 1977, 1979; Noble & Slatyer 1980;* Givnish 1982, 1987; Menges & Waller 1983; Tilman 1988; Grace 1989; Keddy 1989, 1990b; Shipley *et al.* 1989).

A good example of the importance of traits (and screening) in developing general predictive models is van der Valk's (1981) model dealing with vegetation dynamics in wetlands. The wetlands where he worked, prairie potholes, show dramatic differences in water level from 1 year to the next, and given the importance of these potholes for wildlife, it is important to be able to predict vegetation types under different water level management regimes. He argues that a key trait is simply whether or not a species can germinate under flooded conditions. Those species which cannot germinate under flooded conditions can regenerate only when water levels are lowered. Wetland plant species which reproduce only during low water periods, can be found in wetlands around the world, making it possible to generalize from prairie potholes to other vegetation types such as lakeshore wetlands (e.g. Keddy & Reznicek 1982, 1986). If van der Valk had written instead about the autecology of several plant species of prairie potholes, his model would not have had the generality and impact which it currently has. Instead he wrote about traits, and the importance of low water periods in wetland vegetation management is now accepted and used around the world.

Traits and trait matrices

Screening for traits is a specific research strategy well differentiated from others. Consider the trait matrix in Fig. 1. Plant population ecology (e.g. Harper 1977), considered by some to be synonymous with plant ecology, deals with the rows in the matrix. That is, in a typical population study there are relatively few species considered, but usually many population traits are measured. The functional or comparative approach is literally (as well as conceptually) orthogonal to the population approach. Here the emphasis is upon columns rather than rows. We might postulate that general models will emerge most rapidly from examining columns and that emphasis upon rows often leads to natural history (*sensu* Peters 1980, 1991).

Which traits shall we measure for a matrix? Here there is considerable room for exciting innovation. One might begin arguing from first principles by asking which are the basic functions organisms perform, and which traits most efficiently measure those functions. We might begin with three functions: resource acquisition, the ability to tolerate environmental extremes, and the ability to compete with neighbours. One might then look for traits which measure these functions, or one might try for a direct bioassay of them. An example of the former is the use of relative growth rate as a measure of rates of resource acquisition (Grime & Hunt 1975). An example of the latter is screening for relative competitive ability by using one or more standard phytometer species (Gaudet & Keddy 1988). There are limitations on this approach because we may not know in advance which functions (and therefore which traits) to start with — perhaps antiherbivore defences deserve a higher priority than traits correlated with competitive ability, for example. Alternatively, one may be able to screen for a trait, and show that it differs among species, but be hard-pressed to explain its linkage to a specific function. And of course one always faces phylogenetic constraints. But a pragmatic approach (*sensu* James 1975) is to measure large numbers of traits on large numbers of species and then see what the patterns are. In the absence of such data we can argue interminably about where to start and what to do. Once we have some measurements, we can begin to explore the patterns in them, propose new traits which we might add, and suggest refined approaches to measurement for those already reported. Such matrices could be constructed with the same enthusiasm which underlies efforts to map the human genome, and could become common intellectual property kept in a central data repository.

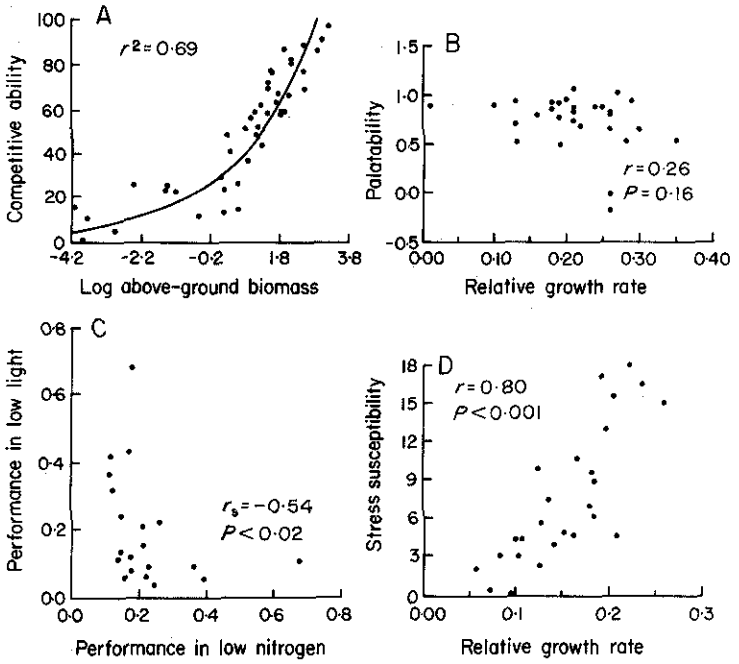

Fig. 2. Once ecological traits have been measured in large numbers of species, it is possible to look for relationships among them. These examples all come from wetland plants. (A) Competitive ability plotted against plant biomass (Gaudet & Keddy 1988); (B) palatability plotted against relative growth rate (McCanny *et al.* 1990); (C) performance in low light plotted against performance in low nitrogen (P. Fricker & P. A. Keddy, unpublished data); (D) stress susceptibility plotted against relative growth rate (Shipley & Keddy 1988).

Examples of this approach

We have been explicitly attempting to work with these two tools simultaneously, using wetland plants as a model system. Figure 2 shows some representative results. These results illustrate correlation between pairs of traits across many species. In Gaudet & Keddy (1988) we developed a bioassay for competitive ability and tested which plant traits were the best predictor of competitive ability. We found size-related traits were most important, with biomass being the best predictor across 44 species of wetland plants (Fig. 2a). In Shipley & Keddy (1988) we tried to extend Grime & Hunt (1975) by simultaneously measuring relative growth rates under fertile and infertile conditions, thereby deriving both a measure of maximum relative growth rate and a measure of relative stress susceptibility. We showed that these were positively correlated across 28 species of wetland plants (Fig. 2d). There may well be better ways to screen for these attributes, and there are undoubtedly many additional attributes for which one could develop screening techniques — deciding what traits to screen for and the most realistic and economical ways of screening for them is an area begging for more attention (Keddy 1990b).

The potential of these techniques for hypothesis testing must also be emphasized. If we want to test for general answers to general predictions, this is the obvious combination of tools to use. Again, consider some recent examples. In the study of plant–herbivore interactions, one general prediction is that plants in resource-poor environments will increase allocation to antiherbivore defences (Coley, Bryant & Chapin 1985). By screening 29 wetland plant species for palatability and by measuring the soil nutrient levels associated with the occurrence of each species McCanny *et al.* (1990) were unable to find evidence to support this prediction or for correlation between the traits of palatability and relative growth rate (Fig. 2b). Tilman (1982, 1988) has made some important general predictions about plant competition and plant traits. One prediction is that plants should show a negative correlation between ability to tolerate low light levels and low nitrogen levels: that is to say, there should be a negative correlation between above- and below-ground foraging ability. By growing 20 wetland plant species under both shaded conditions, and nitrogen-limited conditions, and comparing performance to growth under control conditions, we found some evidence for this trade-off (Fig. 2c). Another important generalization in Tilman's work is the predicted relationship between growth rate and allocation to above- and below-ground structures. Shipley & Peters (1990) screened for these traits in 68 wetland plant species and concluded that they had falsified this aspect of Tilman's model, although rebuttals and counter-rebuttals have appeared.

Trait–environment relationships

Tests for correlations among traits provide important material for the understanding of plant evolution and comparative plant ecology. The linkage to community ecology arises when we can specify which traits (and, therefore, of course, which sets of species) occur under specified sets of environmental conditions. In plant ecology there has been a long history of describing plant traits and environments — a vast literature embraces everything from descriptions of world vegetation types to the descriptions of plant zonation along small shoreline gradients. But in most cases the actual quantitative linkages between the environment and the trait are missing. Therefore, the next logical step is to provide such quantitative linkages. To draw an analogy with physics, it would be useful to be able to predict specific environmental conditions where the botanical equivalent of 'phase changes' will occur. For example, which soil variables will predict the transition from deciduous to evergreen tree species? Which water level variables will predict the transition from woody plants to herbaceous plants? These sorts of relationships between traits and environments will enable us to specify which subsets of species will be selected from a given species pool in a landscape. I have argued elsewhere (Keddy 1992) that the ability to make such predictions lies at the heart of the elusive search for 'assembly rules', and that success may be nearer than expected. There are already some surprisingly convincing examples at both the local (e.g. van der Valk 1981) and global (e.g. Box 1981) scale.

In conclusion, screening and empiricism offer two important tools for advances in ecological theory. I suggest this combination of tools should be the foundation of what we currently call functional ecology (and *Functional Ecology*). This combination of tools, and the distinction between rows and columns of trait matrices, may also help differentiate between ecology and natural history. Each of these points is obviously open to discussion and debate, but if we are looking for future avenues of research in ecology, it appears investment in the systematic study of traits and trait matrices will yield significant returns. Among the challenges remaining is the selection of traits and the development of techniques to screen for them. At present there is a great deal of room for innovation and experimentation.

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