# Functional diversity in vegetation – the role of the individual

## Results from a Co-ordinated Programme in Vegetation Dynamics

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Debate in the 1990s among SEERAD-funded ecologists identified the need for a robust set of concepts and methods to link scientific theory and practice in vegetation management. The first step was to form a co-ordinated research programme among the organisations so as to combine their skills, infrastructure and experience. The second step was to petition SEERAD to fund a central project that would raise and integrate the organisations' capability in important generic topics such as advanced statistics, nitrogen dynamics, genetic fingerprinting and mathematical modelling. The project concentrated on a 'model' system - species-rich grassland, a widespread form of vegetation that supports sheep and cattle, holds a rich source of biodiversity and contributes notably to the landscape.

The main scientific aim of the project was to make progress on the question of 'the individual' in 'the system'. The physiological processes of individual plants determine their survival and fecundity, which in turn govern the continuous selective and adaptive changes in vegetation. However, the vegetation is measured, defined and managed by system-scale variables that include biomass, nutrient retention, and the abundance and distribution of species. Uncertainties in grassland management arise from knowing too little about the link between the individual-scale and system-scale properties of grassland. If the proportions of individuals change, or if some die out – how is the system affected? If the community is managed in a specific way – which individuals coexist within it? Such questions have been considered at the relatively crude level of the species or assemblage (e.g. suppress these species, conserve those). Yet great variation might exist among individuals of a species and contribute to ecosystem function. The aim of the project was to measure variation among the individuals of species and assess the importance of such variation to habitat functioning.

A particularly formative step was the construction of a community dynamics model, which when populated with individuals made up from the measured traits, produced emergent, system-scale, properties (such as species abundance curves) that reproduced structures normally found at much larger scales among species in habitats. As among species, the reason why many genetic types coexist in a small area of land seems to depend on optimisation of tasks. Plants can never do all tasks, such as intercepting resource, reproducing, dispersing, to the maximum. Here, stable modelled communities were composed of individuals having trade-offs between traits. Also, by producing emergent properties from the traits of one species, the modelling showed that within-species variation, at least of the major species, should be considered when assessing the diversity of swards. Two swards of similar species complement could be functionally very dif-

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ferent if their main species have different levels of variability but the more detailed analysis is still under way. Some results from the project, including initial descriptions of the model, have now been published (see Bibliography). However, much of the detailed analysis is still in progress. Here we report on a statistical approach to biodiversity that is complementary to the spatial dynamics modelling and which can use measured data to define diversity at the scale of the individual.

**Trait-space** In studying ecosystem structure and function the predominant approach is to adopt a taxonomic classification of organisms and to describe the mean behaviour of the resulting groups. Yet in many instances there may be no mechanistic relationship linking the ecological process under consideration to the taxonomic classification of the organisms involved. When ecosystems are composed of variable populations the failure of taxonomic classification in this way sets a limit on our understanding. In response to this problem we take an approach that is both functional and individual based in which we define individuals with respect to a set of key functional traits (phenotype) and recognise the individual as the fundamental unit of diversity.

Individual organisms are considered to exist within a multidimensional space, the 'trait-space', the dimensions of which represent the key functional traits. At any one time an individual is represented as a point in trait-space and a group of individuals or a population can be envisaged as a 'cloud' of points. The distribution of individuals in trait-space provides insight into the structure of a population or community in functional rather than taxonomic terms and may be used to address issues such as the recognition of functional types and the quantification of functional diversity.

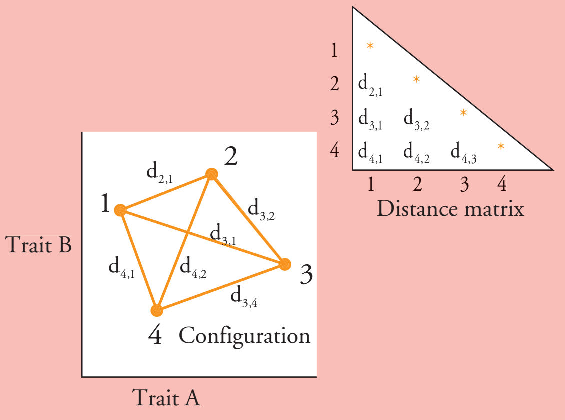

**Figure 1** A diagrammatic representation of a bivariate trait-space demonstrating a configuration of 4 points, the inter-point distances and the corresponding distance matrix.

### Trajectories reveal more than population mean

The growth and reproduction of Rumex acetosa are dictated by the uptake and use of nitrogen within periods defined by grazing events and the length of the growing season.

The mean values of 20 accessions (genotypes) measured ex situ and sampled on 7 dates over one year showed changes in biomass and nitrogen in different plant parts that were characteristic of perennial life-history processes (figure 1).

However, the means masked considerable variation between the accessions (figure 2).

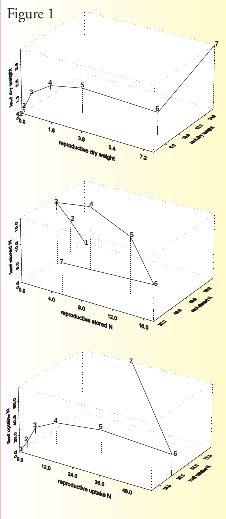
Figure 1

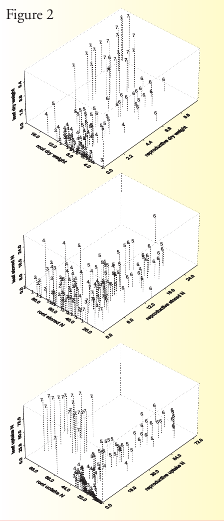
Figure 2

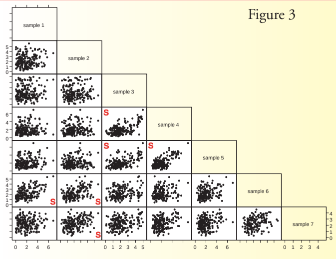
Figure 3

Scatterplot matrix of distances separating individual accessions in 'dry weight' trait space. [S indicates a significant correlation (p<0.01)]

Significant positive correlation occurred between distances during peak reproduction (Sample 3-5) and in a comparison of trait positions before and after reproduction. Further examination of the data suggests that these were due to individual differences in the timing of reproduction and the storage capacity of the roots (figure 3).

**Box 1.** As an example the non-parametric statistical method for the detection of individual differences in trait-space trajectories has been applied to a study of the life-cycle of the perennial grassland species Rumex acetosa.

To infer structure from data or to simulate communities with known structural properties requires the distribution of individuals in trait-space to be modelled. At its simplest, the distribution of individuals may be modelled as a single multivariate probability density function. However, more complicated probability models such as mixture or a hierarchical models may be necessary to provide a realistic characterisation of community structure.

To this point we have taken a static view of trait-space, yet in many cases the trait values characteristic of an individual change over time so that an individual follows a trajectory through trait-space. In general terms a trajectory may be modelled as $y_t = f(x, \theta_t)$. Here, the vector of trait values for an individual at time $t$, $y_t$, is determined by $f(\cdot)$ a function of the variables $x$ with the parameters $\theta_t$. Variation in parameter values is representative of variation between individual trajectories. Therefore, assuming that the form taken by $f(\cdot)$ is the same for all individuals, the distribution of the parameter values reflects the distribution of the dynamic attributes of a community. By treating the parameters themselves as continuous random variables their distribution may be modelled using the same approach applied to the distribution of to the trait-values in the static case.

Modelling the distribution of individual points and trajectories in trait-space in this way provides a novel viewpoint from which to consider key issues such as the quantification of diversity, the identification of functional groups, and the importance of variation between individuals. It is in relation to the latter point that the modelling described has been used as a basis for developing a non-parametric statistical method to identify differences in the trait-space trajectories of individuals. To illustrate we return to the geometric representation of trait-space. The distance matrix, i.e. the set of distances between each pair of points defines the configuration of points in trait-space at that time (fig.1). The similarity between configurations at two times can be measured by the correlation between their distance matrices. It can be shown that this correlation is dependent on the values taken by the parameters of the function $f(\cdot)$ and consequently it is possible to use the correlation between the distance matrices to provide a measure of the extent to which trajectories vary among individuals. This method has been successfully applied to the analysis of plant life-history data (Box 1). Notably, the analysis showed that individual plants moved towards a seasonal end-point (e.g. an amount of nitrogen stored in a tap root) but did so in different ways that would not have been detected by taking a series of population averages. Knowing how individuals 'behaved' differently enabled better prediction of how the community might change in response to external forcers such as grazing intensity and the first frost at the onset of winter

Next steps This project was among the first of the SEER-AD co-ordinated research programmes, bringing together a diverse range of skills in ecophysiology, modelling, molecular ecology, statistics and habitat management. Scientific progress was possible that could not have been made by any partner alone. From commissioning to completion, the project was designed and executed to explore basic scientific problems in vegetation. For practical benefit to be realised, further coordinated effort is required to test the importance of within-species diversity to the resilience of vegetation. The partners have at their disposal a range of unique field sites and facilities in which to carry out these studies. The results will be of significance to agri-ecological regions throughout northern Europe and beyond. The concepts outlined here, and the theoretical work in collaboration with the University of Abertay Dundee, are being extended to a other vegetation types, notably the habitats of arable and early successional vegetation.

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