

VEGETATION: A MOSAIC OF DISCRETE COMMUNITIES, OR A CONTINUUM?

Summary: A simulation model, using the often observed log-linear relationship between the relative abundance and rank of species, shows that vegetation will tend to form a series of communities of constant composition along an environmental gradient even if the constituent species are initially responding independently to those environmental changes. The discreteness of these communities increases with increasing conformity to the log-linear relationship. An index quantifying this conformity (range 0 -1.0) is defined and a method for estimating it from field vegetation data devised. In three vegetation data sets tested the conformity index was 0.0, 0.32 and 0.37.

Keywords: Vegetation; phytosociology; abundance of species; environmental gradients.

Introduction

In the development of ecology, like other sciences, there is the interplay between observation and their abstraction into concepts and models. For plant ecologists concerned with vegetation description (phytosociologists) there has been abstraction into a number of difference concepts. At one extreme, some view a plant community as an organic unit of higher organisation, above the individual species of which it is composed (e.g., Braun-Blanquet, 1932). This synthetic or holistic view uses concepts like association, coenosis, synusia, and ecosystems with an implication that each community is a discrete whole with an implied constant composition and ecological relationships, and distinctly separate in space and time from other such communities, apart from some transitional regions. However, other concepts of vegetation see each species as having an individualistic relationship with the various environmental factors, with the vegetation or community at any site just being the sum of the species of which it is composed - any constancy in composition being related to either co-occurrence of response to environmental factors, or one or more of the species being the principal determinant of environment for other species (e.g., Hanson, 1958; Whittaker, 1956). Terms like continuum, modal community, and gradient analysis are used in such an approach.

These concepts of the plant community have been a controversial topic for the whole of this century, and are still a matter of debate (Kent and Ballard, 1988). That the debate continues suggests that at least field observational data on actual vegetation composition along environmental

gradients have more clumping or grouping than would be consistent with the continuum concept, and more variation than would be consistent with the holistic concept. The concept of an ecotone, to identify areas where the vegetation is clearly changing, can be seen as one attempt to accommodate both views.

More recently it is the concept of gradient analysis which is being debated, as it relates to the response of individual species, in isolation, to changes in environmental factors, as compared to their response when they are part of a vegetation. This has been high-lighted by the different response observed in field studies as compared to monoculture field, glasshouse and laboratory studies. The manner in which abundances of particular species vary in relation to environmental gradients, in the absence of interference from other species, has created concepts and terms like physiological response function (Ellenberg, 1953; Austin and Austin, 1980), fundamental environmental niche (Austin, 1985), or relative physiological performance (Austin, 1982). The corresponding terms for observed response in the presence of other species are ecological response function, realised environmental niche, or normalised ecological performance.

However, it is a third group of concepts, relating to the relative abundance of species, which is focused on in this paper. While these have been recognised in the description of vegetation data, I do not believe they have been sufficiently taken into account in explaining the other concepts in phytosociology. The paper identifies the concepts and explores the relationship between them using simple mathematical models of variation of species abundance along an environmental gradient.

Relative abundance of species

There have been many studies in plant and animal ecology on the relationship between the number of species in an area (species diversity) and the number or mass of each species (abundance), (reviews by Preston, 1948; Whittaker, 1972; Pielou, 1975; May, 1981; Southwood, 1978; Wilson, 1991). When species' data from a sample are arranged from the most to least abundant, the most notable feature has been the near linear relationship between the logarithm of abundance of each species and the rank order. Fig. 1 shows this for five data sets available to me, and is comparable to many other published records. The slope of the line is a measure of the diversity of species within a particular vegetation.

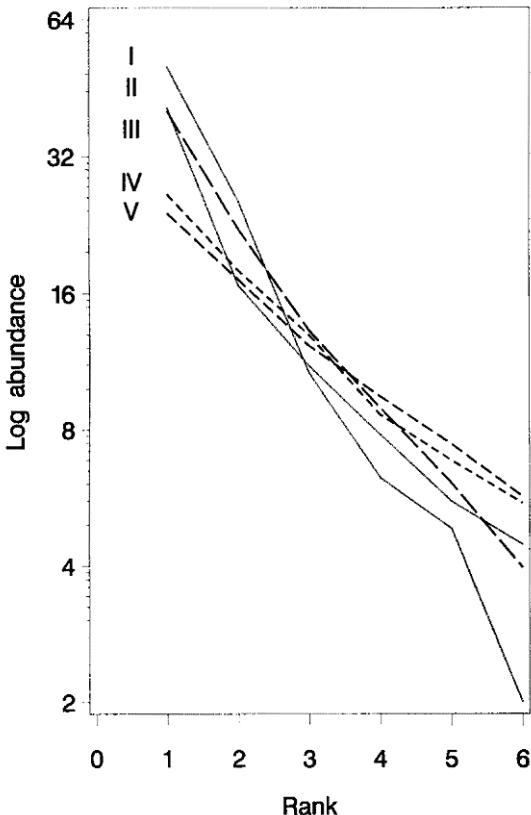


Figure 1: *Relative abundance of species in five vegetations. Note logarithmic scale. I = Tall tussock standing crop (Evans, 1980). II = Alpine tundra standing crop (Scott and Billings, 1964). III = Tall and short tussock point intercepts (Scott et al., 1986). IV = Tussock, scrub and herbfield relative height frequency (Scott, 1965, 1977). V = Tall tussock point intercept (J. Holgate, pers. comm.).*

A number of explicit mathematical models (geometric, logarithmic and broken stick series) and statistical models (log normal, truncated log normal, random, random pre-emptive) have been used to describe this relationship (see reviews above). The simplest and often best fitting is the geometric series, where the percentage contribution of species (P_R), of rank R , is related to a diversity coefficient K indicating both the diversity in the community and the proportional reduction between successive ranked species

$$P_R = 100 (1-K)K^{R-1} \quad (1)$$

The values of the diversity coefficient K may range from 0.8 or more and give a low slope of the abundance/rank graph in species rich vegetation, to 0.2 or less in a species poor vegetation and consequent steep slope.

A review of 702 sets of pasture data of species composition and rank indicated modal values of the diversity coefficient K between 0.43 and 0.70 and a correlation coefficient of fit greater than 0.94 (Scott, 1993). In another example, the geometric series closely predicted the coefficients of the dry-weight rank method of pasture analysis using a value of $K = 0.32$ († Marnette and Haydock, 1963; Haydock and Shaw, 1975; Jones and Hargreaves, 1979; Barnes, Odendal and Beukes, 1982; Scott, 1986; Mazaika and Krausman, 1991).

The implication is that the log-linear relationship between abundance and rank may be one of the few quantitative empirical relationships in ecology. If it can be accepted as an empirical trend of high repeatability, then it should be taken into account in any consideration of species composition within vegetation.

Conformity index

A new index is needed to describe the closeness of the observed vegetation data to the log-linear relationship. The correlation coefficient between rank and abundance is not suitable for this purpose as it will always be high and negative for ranked species data.

In developing a conformity index using the concepts reviewed above, the observed proportion of a species in a vegetation is seen as a combination of the proportion determined by its physiological suitability relative to other species, modified by the extent to which that proportion has to adjust if the combined species' proportions conform exactly to the log-linear relationship at that point on an environmental gradient. This fractional change will

be assumed to be the same for all species. Stated more formally the ecological (ECOL) or observed proportions of a species (i) at a point (j) on an environmental gradient, is its relative physiological (PHY) proportion at the same point, less the product of the conformity index constant (C), multiplied by the difference between the proportion if determined by relative physiological suitability and the proportion if the exact log-linear (LOGL) relationship between species contributions existed.

$$ECOL_{i,j} = PHY_{i,j} - C * (PHY_{i,j} - LOGL_{i,j}) \quad (2)$$

The conformity index has a range from zero (no constraint by the log-linear relationship) to one (for exact conformity to the log-linear relationship). For simulation studies the index could vary in relation to the environmental conditions. However, as discussed later, for estimation from field vegetation data, it will have to be assumed to be constant across at least a proportion of an environmental gradient.

The log-linear proportions would have to be determined from equation 1 using estimation of the diversity coefficient from the relative proportions of species at each point. Depending on the context this would be either from the observed ecological or physiological proportions, and the resulting log-linear estimates of proportions will differ in detail. Also in relation to the applicability to actual vegetation data, where errors are likely to be similar for estimates of proportions of different species, I consider it better to do direct iterative least squares fitting to equation 1, rather than to use logarithmic transformations and regression analysis. Also in relation to actual data, estimates may be confined to the more common species; in the examples that follow, analyses were limited to samples with at least four, and no more than nine species making a contribution of greater than 0.5% each to the total vegetation.

Simulation

The simulation used an artificial data set for seven species along an environmental gradient. It further assumed that the relative contributions of the species to the vegetation at each point would be proportional to their relative physiological responses (Fig. 2A). In subsequent simulations the proportions of each species at points along the gradient were investigated for successively higher values of the conformity index. The resulting distribution of the observed ecological proportions of species for two of the values is given (Fig. 2B, C).

The feature of the results is the tendency for the values along the environmental gradients to segregate into sections where the relative proportions of different species were near constant

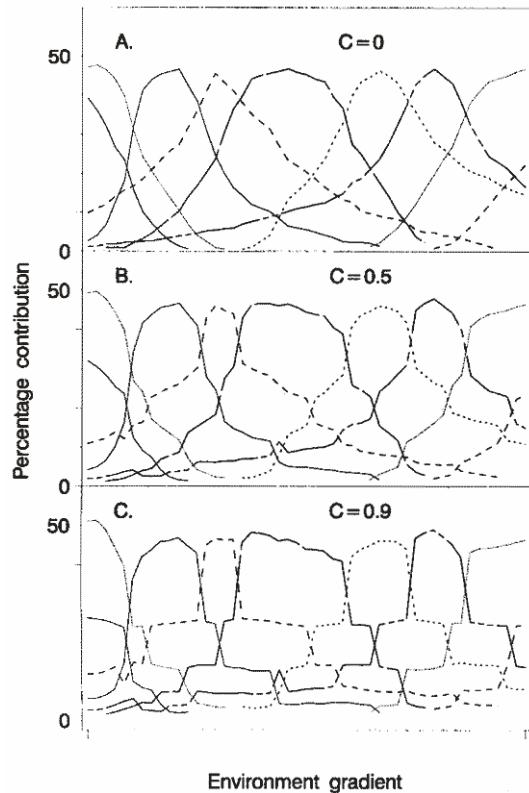


Figure 2: Variation in percentage contribution of seven species along an environmental gradient. Scaled to sum to 100% at each point. **A:** Assumed relative physiological response. Equivalent to a conformity index of $C=0$. **B:** Top graph adjusted to a conformity index of $C=0.5$ to a log-linear relationship between abundance and rank at each sampling point. **C:** Top graph adjusted to a conformity index of $C=0.9$.

and could be interpreted as vegetation associations or communities. While this is most obvious for the high value of the conformity index (Fig. 2C), the trend can be detected at intermediate values of the conformity index (Fig. 2B). The data in Fig. 2C could be interpreted as fourteen communities of near constant composition of major and minor species, distributed along the environmental gradients, with short sections of transition zones between them. The same simulations show that the differences between the relative physiological and ecological responses were greatest near the transition or ecotone regions of changing dominance between species.

This simulation used a somewhat similar distribution of physiological response for all of the species. Other simulations not presented used variable different distribution for different species

and also showed the same trends of aggregating into sections of near constant species composition along the environment gradient as the value of the conformity index was raised.

Determination of conformity index

While the potential usefulness of the conformity index can be illustrated by simulation studies where two or three of the parameters in equation 2 can be assumed, the need is to be able to determine the conformity index in real vegetation data where the observed ecological response of species proportions is what is measured, but the physiological response is not known. This situation is not solvable by conventional curve fitting methods.

However, it is estimable from a second feature of the simulation apparent in Fig. 2, if the conformity index can be assumed to be constant over a section of the environmental gradient. It will be noted that an effect of imposing the conformity index on the physiological response was that the ecological response, represented by the percentage contribution of each species, measured at intervals along the environment gradient, became progressively more stepped for successively higher values of the conformity index; i.e., there were increasing differences between the gradients in successive sections of the distribution curve. This contrasts with the relatively smooth (minor) changes in gradient between successive portions in the physiological response curves. Thus the criterion of minimum cumulative sum of squares of differences between gradients of successive portions of the response curve for all species becomes a measure of the average smoothness of curves.

The approach is illustrated by treating the output data set from the middle and lower examples in Fig. 2 as 'new' data sets of observed vegetation data and attempting to estimate the conformity index from which they were derived. The diversity coefficient at each point was estimated using the observed ecological proportions, and then iterative fitting using a series of assumed conformity indices to

estimate the smoothed physiological response with minimum cumulative gradient changes. Back estimates of the conformity index were obtained (Table 1). These are lower than the original values used in the generation of the data. At least one source of the difference between the two relates to the estimation of the diversity coefficient, which was based on the physiological responses in the forward simulations, and on the ecological observed responses in the back estimation.

The estimation of the conformity index is given for three examples of actual vegetation data (Table 1). All are for pooled vegetation data from many sites. In two of these, field sampling had been deliberately in sites of contrasting species composition and environmental conditions (Scott and Billings, 1964; Scott, 1977). The third example was from seven sites of more similar vegetation (Scott, Dick and Hunter, 1988). For the present purposes a single environmental gradient for each data set was defined as the first principal component of factor analysis using measurements of major species, major environmental factors and estimates of total vegetation cover or biomass. The conformity indices of the species' proportions along this gradient were then determined by the method above. The two estimates from New Zealand tussock grassland sites were in the range of 0.3-0.4, while the value was close to zero for the alpine tundra site.

Discussion

The observation on which this paper builds, is that any assemblage of plant species forming a vegetation, shows a relatively fixed relationship in proportions of different species. This log-linear relationship in proportions is apparent in the reviews cited and further supported by the examples given in Fig. 1. Such a strong empirical relationships should be accepted, even if it cannot be explained. It has two important implications in vegetation analysis.

Firstly, as shown by the simulations in this paper, the log-linear relationship does provide a link

Table 1: *Estimated conformity and diversity index in five vegetation data sets.*

Data set	Sample size (n)	Conformity Index (C)	Diversity Coefficient (K)
Back estimation from C=0.5 (from Fig. 2)	49	.37	.53
Back estimation from C=0.9 (from Fig. 2)	49	.51	.52
Tussock grassland - Tongariro (Scott, 1977)	12	.32	.73
Tussock grassland - Waimakariri (Scott <i>et al.</i> , 1988)	191	.37	.61
Alpine tundra - Medicine Bow (Scott and Billings, 1964)	50	0	.62

between two divergent views of plant communities. Both views can be correct. Each species may react to the environment in its own individualistic manner, according to its relative physiological performance, and it may interact with those of other species. However, there may also be overall community interactions, at presently ill defined, such that species' proportions tend to conform to the log-linear relationship and consequently that certain species' proportions are more stable than others. Depending on the relative importance of the different effects, the consequence is that the landscape may appear as a mosaic of communities of relatively fixed proportions with different ranking of species prevailing over different segments of an environmental gradient.

The second implication is that, when unravelling the environmental relationships of individual species, the measured abundance of a particular species within a vegetation is a combination of both an environmental suitability and a community effect; i.e., one is measuring the ecological response function rather than the physiological response function. It will be necessary to decode the field measurements of abundance for both the community diversity and conformity indices to get at the true physiological response function for individual species. The last section showed how this could be done and provides an avenue for linking field studies involving many species, and laboratory/glasshouse studies on physiological traits of particular species. It is probable that all these interactions vary with environmental conditions and that they need to be separated in seeking understanding of particular situations.

The concepts and analysis methods need further development. There is need to check the suggestions on a greater range of actual field data. The three examples used in estimating the conformity index (Table 1) were from pooled data from many sites giving a consequent high diversity index, and also assumed a single environmental gradient. There is a need, also, to explore further the application of the concepts to original sample data and from different environmental gradients. The simulation studies indicate that the interactions of the various concepts discussed are most marked in ecotone zones where there were major changes in species composition, and that these would be a fruitful source of data to further develop and test the concepts.

It is hoped that this paper will prompt further discussion on the concepts of phytosociology and give another dimension to the analysis of vegetation data and determination of species/environmental relationships.

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