

D. Raup:

Stephens

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"Large acreages which had formerly been in pasture or cultivation had reverted to nearly pure stands of white pine, etc."

I am afraid the word "reverted" will be interpreted as meaning something that has gone back to its original condition or ancestral form, which certainly isn't true. Therefore, could you express it in another way:

"Large acreages which had formerly been in pasture or cultivation had been replaced by
been succeeded by
had relinquished their status to
etc"

Only a suggestion, otherwise I think it is very good.

Carl

7
Comments on: Stout & Dill.

Comments on the Continuum

BM
Mark Swan

1. Seems to suffer from the problem of all methodological discourses. The reader isn't really told why he is being led through this plan. It would have helped to know that the authors thought the Gleason view was good but undocumented. Hence, they are describing a study that tried to present evidence for the concept graphically. (i.e. for easy communication). That's possibly why quantification is useful - not because Plato thinks little is left if you don't do it.

2. I don't think a reader would understand this ^{description} as it is without having first struggled through Curtis & McIntosh (1951) and Bray and Curtis (1957). Actually the description seems to be a very complex and long-winded way of saying species have overlapping tolerances & no two are alike. After reading this I wondered if I had missed something because I knew the bit about overlapping ranges already.

3. The conclusion: "Can we in good conscience disdain the use of the most sophisticated tools available to describe our environment and the interactions of the population and the environment?" draws 2 responses from me:

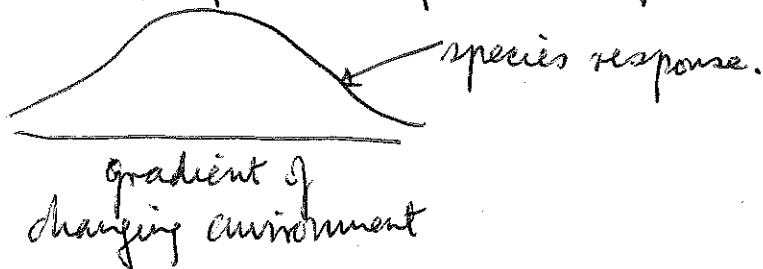
- (a) If there is a simpler way of doing things, shouldn't we use it. and
- (b) What sophisticated tools? Present ordination techniques may be

mathematically sophisticated ~~by~~ but they are not very sound biologically.

4. The "Foot" outlined here is not sophisticated. As I understand Curtis and McIntosh it is a way of expressing an intuitive arrangement of vegetation samples ~~in a way~~ so ~~that~~ it can be acted out by others. - a rationalization.

5. I am not sure what Curtis' contribution has been here but I think it may be true that he was the first to demonstrate that plots could be juggled around ^{in space} so that adjacent ones are similar in composition, while distant ones are not. He did this juggling without tying plot positions down to environmental ~~positions~~ characteristics and then found that ~~the~~ ~~environment~~ some things, like moisture, changed in parallel with his ordering of vegetation samples.

6. Lotka's models and species response surfaces I take to mean:



This is very theoretical and while a mental impression of species gradually changing in abundance or frequency from one place to another may be tenable, I see no reason to try to formulate this mathematically. For one thing, a species present in a place one year may not be there the next because of disturbances.

possibly. Also the invasion of a species into a freshly disturbed habitat may be due to things like a good seed year. Also, competition is hard to evaluate from patterns in the field. So I ask, how predictable is a "response surface" and do we know enough to give it a mathematical formulation?

7. I think there is ~~value~~ ^{it} in Curtis' work here. But, ~~not~~ because of any new concept he has developed. The "continuum idea" is another way of saying what the taxonomist already knows about variability in species and the fact that some factors of the environment - such as moisture - may relate to the distribution of many species, but each responding differently. If we are talking about a "continuum of communities" as Ben implies in the 1st para., then we're into the realm of Bull, I think! Curtis' work demonstrated the overlapping tolerances of species ~~along~~ ~~in~~ relation to moisture for Wisconsin, and I like that. But you can question his "Importance Values" and "Climax adaptation values". It could have been expressed more simply. I suppose Clausen, Keck and Heisey really demonstrated the "continuum" idea too. Perhaps Turesson was the first. Curtis made it sophisticated with a name.

H.M. Raup

Comments on the Continuum

B.B. Stout and Norman Dill

"The entire series of communities whose floristic composition gradually changes along an environmental gradient has been termed a 'vegetational continuum' (Curtis and McIntosh, 1951), to emphasize the fact that no discrete divisions, entities, or other natural discontinuities are present." (Curtis, 1959, p.52). The admonition of Plato, "If arithmetic, mensuration and weighing be taken away from any art, that which remains will not be much," is sufficient to suggest to one who views vegetation as a continuum that quantification must be used to elucidate the concept.

To accomplish this elucidation and to place assemblages of plants in perspective relative to other assemblages, the following procedure is used. The procedure is in bare outline and may have added refinements for a particular area. We use for discussion purposes here the presentation in Curtis and McIntosh (1951) on the forest dominated by sugar maple (Acer saccharum).

For a particular stand a Continuum Index is determined for each species by taking it as the product of the Importance Value of a species times the species Adaptation Number. The Importance Value is the summation of relative frequency, relative density, and relative dominance. The Adaptation Number is an assigned value; in the cited case the values range from 1 to 10. The higher the number the greater the ability of a species to survive in a forest dominated by sugar maple. The Compositional Index for a stand is the summation of all the species Continuum Indices for that stand.

Inspection of Compositional Indices for many stands will usually show considerable variation. Furthermore if an environmental moisture gradient is established from dry to mesic it can be seen that the Compositional Indices are perhaps a function of this gradient. Therefore, if the Compositional Indices are equated with the environmental gradient and plotted on the abscissa and the Importance Values of the individual species are plotted on the ordinate a pattern should emerge showing the distribution of the species along the environmental gradient.

Once the patterns are established they may be used to draw inferences regarding the relationships that exist between the species and the gradient on the abscissa. Moisture has been used in this example. Bray and Curtis (1957) used, as we shall see, 16 factors along the abscissa.

We have attempted to present in the above the essential features of the method that has been developed by Curtis and his co-workers to quantify the study of vegetation. It is proposed that since this is a quantifying effort that it be examined in equation form. Changing from a verbal to a equational form should not alter meaning; it may make for greater clarity of the method and allow closer scrutiny.

For each species in a stand a Continuum Index (Y_I) is determined:

$$Y_I = (X_{AN}) (X_{IV}) \tag{1}$$

where:

X_{AN} = Adaptation Number, assigned values, in the cited case, of from 1 to 10 based on the ability species to survive in a forest dominated by sugar maple (Curtis, 1959, p.94).

X_{IV} = Importance Value, the summation of relative frequency, relative density and relative dominance. Therefore: $0 \leq X_{IV} \leq 300$.

Having arrived at the Continuum Index for each species, a Compositional Index (Y_C) for a stand is arrived at by summing all Y_{Ii} for the stand, thus:

$$Y_C = \sum_{i=1}^n Y_{Ii} \quad (2)$$

where:

n = number of species in the stand. For example, if an assemblage of plants is all one species with an Adaptation Number of 1,

$$Y_C = 300; \text{ or } 3000, \text{ if } X_{AN} = 10.$$

Empirically it is then suggested that

$$Y_C = f(\text{Habitat}) \quad (3)$$

where:

$Y_C = 300$ in a dry habitat and 3000 in a mesic situation.

It was noted above that

$$Y_C = \sum_{i=1}^n Y_{Ii} \quad (2)$$

The next step is to say that

$$X_{IV} = f(Y_I), \text{ for a given species.} \quad (4)$$

Using this equation and by plotting the data, bell shaped areas or segments thereof are formed (Fig.1)

However, due to the initial assumption,

$$Y_I = (X_{AN}) (X_{IV}) \quad (1)$$

and the fact that X_{AN} was arbitrarily given values from 1 to 10, in effect dry sites were valued at 1 and mesic sites as 10. But the X_{AN} was originally defined as being an expression of the adaptability of a species in relation to, in the Wisconsin case, (Curtis and McIntosh, 1951), sugar maple. So to this point what has been said is that sugar maple tends to dominate mesic sites in the area of study in Wisconsin.

By plotting $X_{IV} = f(Y_I)$ for a given species all or a part of a bell shaped curve, a Gaussian distribution function, or probability density function, which is defined by:

$$f(X) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(X-\mu)^2}{2\sigma^2}} \quad (5)$$

is obtained. Therefore by scaling the adaptation number (which is in effect μ in the probability density function) from 1 to 10 the position of the curve for a given species is set by the initial scaling decision.

The mean values of the Y_I falling under the curve can be determined for discrete units of Y_C . With these means at hand, curves for individual species can be constructed. They are similar to Figure 1 without the individual points plotted.

It was pointed out by the originators that no identical curves were found (Curtis and McIntosh, 1951). In addition to the fact that different species react differently to a similar environment, there is also the fact that the position of the distribution, μ , was set when the tree was assigned its Adaptation Number.

In the example the composition index Y_C was equated with habitat. In a like manner it can be equated with any number of factors, either singly or in combination; for example, light conditions and measures of soil characteristics. Bray and Curtis (1957) used three axes:

$$X_1 = f(\text{Depth of } A_1, \text{ Organic Matter, pH, Ca, P, and } (\frac{.1 \text{ Ca}}{K}))$$

$$X_2 = f(\text{Drainage, Soil air, Water retaining capacity, and } NH_4)$$

$$X_3 = f(\text{Disturbance, Gap phase replacement, K, } (\frac{.1 \text{ Ca}}{K}), \text{ Organic Matter})$$

Then by saying that $Y_C = f(X_1, X_2, X_3)$ the positions of the individual stands can be located in 3 dimensional space. When this is done no two stands occupy identical positions in that space--the spectrum is continuous, and it can be called a vegetational continuum.

However, in so doing, Bray and Curtis (1957), for example crowd onto 3 axes 16 different factors, almost anyone of which may interact with or be a function of several other factors.

In essence the concept of the continuum is that

$$Y_F = f(X_1, X_2, \dots, X_n; E_1, E_2, \dots, E_j) \quad (6)$$

where:

Y_F = Flora of a given unit area.

X_i = Characteristics of the species that make up the vegetation

E_j = Factors of the environment.

In so presenting vegetation in this light, history may well look upon Curtis and his co-workers as having made a major contribution to the understanding of vegetation.

This does not alter the fact, however, that in the method Importance Value (X_{IV}) is used as an independent variable to predict Continuum Index (Y_I), the dependent variable, in the early stages of the calculations and later Y_I is used as an independent variable to predict X_{IV} , now the dependent variable. Once this is done, the argument has gone full circle.

The consistent part of the scheme is the Adaptation Number (X_{AN}). It was pointed out that after all the manipulations the peaks of the curves fell in an orderly array along the abscissa. Perhaps what this means is that the Adaptation Number is really a good description of the species, at least so far as our knowledge of the species--environment interactions are concerned.

Beyond this, due to the circularity, it may be hazardous to tread. Discussions of succession, ordination or environmental scalars must hang on the validity of the values assigned to the Adaptation Number. If these are valid, no matter whether subjectively or objectively assigned, then the conclusions drawn may be valid. Not because of the method, no matter how complex, but because the Adaptation Number values were put in reasonably good order originally.

The admonition of Plato was quoted earlier. A comment on classification by a 20th Century commentator may point the way for a next step. Whitehead (1956) says, "Classification is a halfway house between the immediate concreteness of the individual thing and the complete abstraction of mathematical notions. The species take account of the specific character, and the genera of the generic character. But in the procedure of relating mathematical notions to the facts of nature, by counting, by measurement, and by geometrical relations, and by types of order, the rational contemplation is lifted from the incomplete abstractions involved in definite species and genera, to the complete abstractions of mathematics. Classification is necessary. But unless you can progress from classification to mathematics, your reasoning will not take you very far."

What are the mathematical abstractions to which he refers? From whence do they come?

Fortunately for students of ecology the abstractions are presently extant. Lotka (1956, p 44) gives a model that may be used to describe an assemblage of plants. He views it as a dynamic system. This is suggested by each derivative being taken with respect to time. Time may be in units long enough so that the ecologist could view this "n-dimensional" system as a surface. This idea has been suggested by Hutchinson (1957) and by Waterman (1962). Figure 2 is a response surface in three dimensions. In Lotka's model it would be the representation of an instantaneous condition for one species Y_1 with respect to two independent variables, X_1 and X_2 . For an assemblage plants on a particular spot on the earth's surface there would be an equation (and surface) for each species. The level each species attained would be a function of the environmental variables and the influence of the interactions between the several species.

Viewed in this light the flora for the particular location would be the list of all species (Y_i) whose response surface was exposed. Exposed is used in the sense that if a single plant of a species is living on an area some part of that specie's response surface is sufficiently elevated above that of other species to permit its survival. The vegetation would be that pattern of species whose surfaces were sufficiently exposed (as determined subjectively) to consider that the landscape was dominated by them.

This latter view, that is the delineation of a certain group of exposed surfaces as a vegetation, is essentially what has constituted classification in ecology. Because the response surface of a species cover a region may now be exposed, now covered, this has led to the extensive vocabulary of ecology. For a species whose surface is barely projecting above another species' surface a very slight shift in any one of the X_i variables could produce a quite different assemblage of plants.

We do not know what the n-dimensional response surfaces look like; we can, however, conceive a three dimensional one as resembling a relief map. There would be a map for each species. The altitudes on the map could suggest degree of, say, dominance for the species. The east-west and north-south axes could represent levels of two variables. Moving to a contour line and following along it we would be at points of equal response. However, with each step we would move to a new combination of east-west and north-south variables. Or, in another and earlier sense, each location on the map is individualistic, yet many locations give rise to equal degrees of dominance. Viewed in this light Gleason and Lotka have given us the conceptual framework and tools to use in a study of vegetation. As Whitehead suggested, we needed classification so that we could move to the mathematical abstraction.

In effect the accomplished ecologist has integrated the things we have called response surfaces in his mind as he moved over the landscape. He knows that one factor can be substituted for another in some instances and not in another; that certain plants can exist over a wide range (a high smooth response surface) and that others exist in only specific and restricted habitats (a response surface of low relief with a few high, sharp peaks). This integration is the product of long years in the field. That it can be done is manifested in remarks such as, "Who needs all these numbers? I can see what is going on in a forest just by walking through!" It is true that this can be done. The question we raise is: Can we in good conscience disdain the use of the most sophisticated tools available to describe our environment and the interactions of the population and the environment?

Summary

The concept of the continuum is valuable. Because of a circularity in the methods of studying the continuum devised by Curtis and his co-workers we argue that the concept of the response surface is a logical continuation of Gleason's ideas and that this can be accomplished by using the basic form of Lotka's model.

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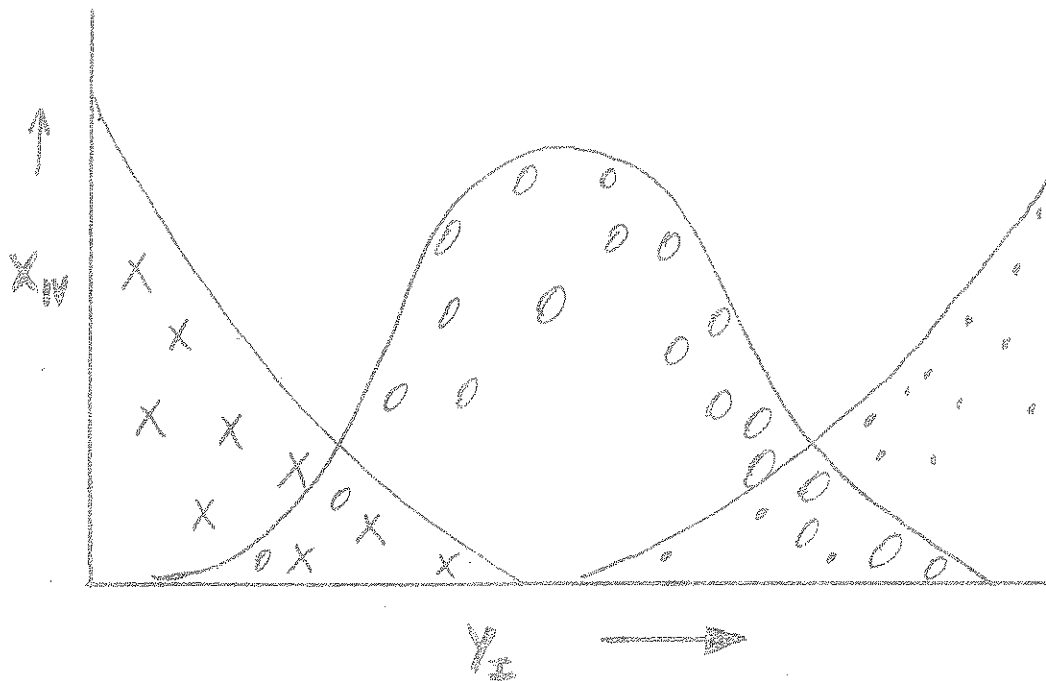


Figure 1. Schematic representation of three species - x, 0, · - using Equation 4.

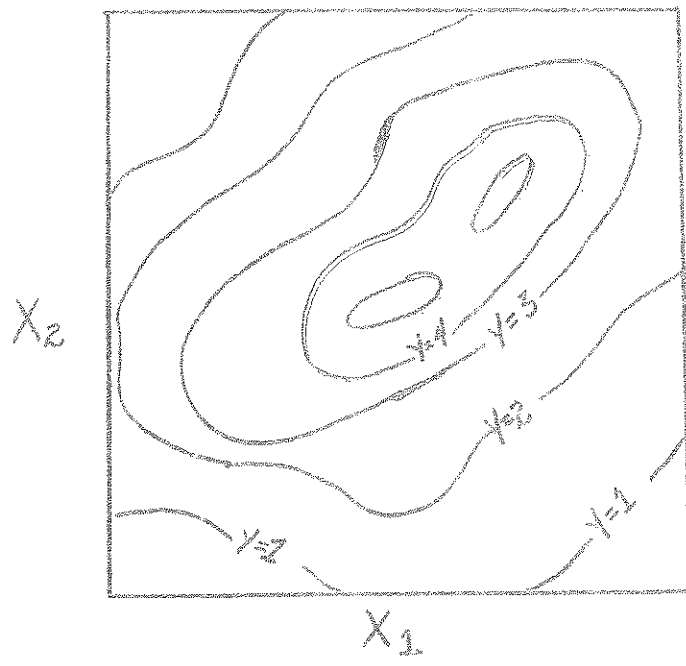


Figure 2. Contour expression of response Y to varying levels of X_1 and X_2 . Schematic.