A multivariate analysis of the niches of plant populations in raised bogs.

II. Niche width and overlap

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Received July 19, 1976


The results of a principal components analysis are used to define the ecological niches of the plant populations in raised bogs. This paper examines the niche parameters of width and overlap. Dominance is positively related to niche width and inversely related to the number of species (richness). Richness is shown to be positively related to increased environmental complexity and predictability. Dominants appear to decrease in environments that are more complex and predictable because as a class these organisms are less opportunistic. Niche differentiation measured as overlap is greater in the richer, more environmentally complex and predictable parts of raised bogs.


Introduction

In part I of this pair of papers, principal components analysis was used to elaborate the ecological niches of plant populations in 90 sample plots in raised bogs in Maine. The niche parameter of dimension was related to two environmental factors: 'salinity and snow cover' and 'ombrotrophy-mesotrophy.' This paper will be devoted to examination of niche width and overlap. Niche width or tolerance of a particular population can be measured separately on each niche dimension or combined for all dimensions. Niche width measures a population's position in the niche hypervolume and also its population size at that position. Simply it gives an indication of how wide a range on an environmental factor(s) a population can exist and where a population's optimal response is located. Niche overlap indicates the degree of ecological similarity and therefore also differences in the use of the same factor(s) by different populations.

Questions about collecting procedures and specifics on the principal components analysis are referred to part I.

Niche Parameter: Width

Niche width is the measure of the position and degree of performance of a species population along its niche dimensions. It is usually measured by a variance equation. Several different ways of measuring niche width have been proposed (Simpson 1949; Moisita 1959; Levins 1968; McNaughton and Wolf 1970; Colwell and Futuyma 1971). The most widely used width measure has been the Shannon–Wiener information equation (Shannon and Weaver 1949). For our purpose the width equation (B) of McNaughton and Wolf (1970) is preferred because besides measuring variance along the dimension it weights the positions.

Data were prepared for calculation of B in the following manner. Components were each

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divided into eight equally spaced intervals numbered from 1 at the far positive end to 8 at the far negative end. Since the intervals contained different numbers of sample plots, the frequencies in each interval were summed and divided by the number of sample plots in that interval. These values were then used to calculate $B$. Components based on species variables involve a linear assumption that is known from the transformation analysis not to be completely met. This is recognized as a limitation to some kinds of interpretation of niche width. Furthermore, width is based on frequency as a measure of species population behavior, which also limits its interpretation.

**Abundance and Niche Width**

The conventional definition of dominance is confusing (Greig-Smith 1964) but generally dominance implies a situation where a few species are able to usurp more of the resources of the environment and have greater influence on other species (cf. Oosting 1959).

Niche width allows us to test the first part of the dominance definition. If dominance is interpreted as having a positive relation to niche width, then there should also be a positive relation between niche width ($B$) and maximum (modal) abundance ($A_{max}$). The results of this determination are shown in Figs. 1 and 2. The fitted equations of these graphs are as follows:

**component 1**, $B = 2.48 + 1.84A_{max}^{**}$, $r = 0.92^{**}$.

**component 2**, $B = 3.24 + 1.88A_{max}^{**}$, $r = 0.81^{**}$.

It would seem from these results that species with the largest niche width do in fact have the largest maximum abundance.

Other studies of niche width and maximum abundance have given similar results in tropical birds (Klopf 1960), in fruit flies (Pico et al. 1965), and in several different types of vegetation (McNaughton and Wolf 1970).

**Species Richness**

Since dominance and the number of species are intricately related (Whittaker 1965), the changes in the numbers of species is best discussed now. The number of species per sample

$\text{plot will be called areal species density, or for short, richness. Other more elaborate measures of species number density have been suggested but are at best confusing (Hurlbert 1971) or are in fact measures of dominance (Whittaker 1965, 1972).}$

Richness ($R$) increases toward the positive end of the first component ($C_1$) (Fig. 3), as described by the equation $R = 13.21 + 0.002C, r = 0.62^{**}$. By height class the fitted equations are as follows:

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$^2$Convention: *, significant at 5%; **, significant at 1%.
shrubs, $R = 6.03 + 0.004C_1$, $r = 0.29$;
herbs, $R = 3.46 + 0.001C_1$, $r = 0.63$;
mosses, $R = 3.53 + 0.001C_1$, $r = 0.46$.

The richest sample plots are the ones with high positive values on the salinity–snow-cover factor. Inspection of the equations reveals that the herb and moss height classes account for the increase in richness since the shrub height class is fairly constant.

Richness ($R$) on component 2 ($C_2$) increases towards the positive end then decreases slightly (Fig. 4). The linear equation is $R = 13.21 + 0.001C_2$, $r = 0.29$. The richest sample plots are in the medium-dry moisture segment of the gradient.

We will now examine component 1 in more detail to see if the reasons for the increase in richness can be ascertained. Increased richness can result from two possibilities. (1) It is possible that the areas studied are not all in equilibrium as far as species number, i.e., invasion is still occurring. (2) The environment could be changing in such a way along the gradient that more species can use certain parts of it.

An invasion effect seems unlikely on the basis of geological evidence. Most of the richer sample plots are closer to the coast which has only recently been exposed (Milliman and Emery 1968; Grant 1968) by the receding sea as a result of postglacial rebound of the coast. Poorer sample plots are inland in areas not covered by the sea. However, it could be argued from ignorance of the ages of origin of these raised bogs that coastal bogs are actually older than inland bogs. Thus an ecological test of a possible invasion effect would be appropriate.

Preston (1962) has proposed a resemblance equation based on the distribution of abundance among species and its relation to area. The equation is as follows:

$$\left(\frac{N_1}{N_{1+2}}\right)^{1/2} + \left(\frac{N_2}{N_{1+2}}\right)^{1/2} = 1.$$

$N_1$ and $N_2$ are the numbers of species in two areas 1 and 2, $N_{1+2}$ is the numbers of species in common between the two areas 1 and 2. $Z$ equals the resemblance of two areas. The equation is solved for $Z$, which can range from 0 to 1.0. Preston defines equilibrium to mean a steady state in which species are freely exchanged between two areas. That is, the species in one area have had a chance to colonize the other area. A zero $Z$ means that the two areas are not only identical but are subsamples of the same area. These two areas are in equilibrium by definition. If two areas are isolated but still able to exchange species so that their species numbers are still in equilibrium, the $Z$ value is theoretically determined to be 0.27 (Preston 1962). If the two areas have no species in common and thus are in complete disequilibrium, the $Z$ is equal to 1.0. Geographically
related changes in Z can thus give a good indication of immigration.

Z values for all combinations of 19 raised bogs were calculated using an algorithm incorporating the suggestions of Preston (1962, p. 418). The mean Z value is 0.37, standard deviation is ±0.10, and the range is from 0.11 to 0.59. The high mean compared with the expected Z of 0.27 would seem to indicate areas fairly isolated from each other. Although this may be true it should be remembered that the assumption that the species abundance is distributed lognormally is being violated since abundance is distributed more in a geometric series (Johnson 1972, unpublished results). The important point is that the Z values show no consistent relation to an invasion gradient relative to the coast.

The second possible means of increasing richness along the component seems to be more promising. If in fact the environment is changing, the capacity of the environment along the component to 'carry' more species should be increasing with increasing species number.

Carrying capacity has been defined by McNaughton and Wolf (1970) as the sum of the niche widths in an interval along the component. By comparing this sum of niche widths (K) with richness (R) a very good linear relation is described by the equation \( K = -7.86 + 2.26R^{**}, \ r = 0.97^{**}, \) and Fig. 5. Although richness was used as the independent variable in the above equation, we do not really know which variable, richness or carrying capacity, is forcing the other. They are both probably dependent on an environmental change.

MacArthur and MacArthur (1961) and MacArthur (1957, 1965) were the first to point out that in fairly similar environments new species are added by increasing the structure of the environment. By structure is meant the arrangement in patterns of the variables of the environment. To measure changes in structure Brillouin's formula was used (Pielou 1966). This equation describes the total information content of an interval:

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H_i = \ln \frac{N!}{N_1!, N_2!, N_3!, \ldots N_E!}.
\]

\( H \) was calculated for interval \( i \) on component 1, \( N \) was the total values of 14 environmental (peat) measures in interval \( i \), and \( N_E \) was the value of a particular environmental measure E.

All environmental measures were means of all the values from the sample plots in a particular interval. The standard error of the means of intervals 1 and 2 are larger than the rest because of fewer sample plots. All means were standardized to a 0-10 scale since the different measures are on different scales. This standardization was done by setting the maximum mean at 10.

Since the number of environmental measures remains constant in each interval, we are actually measuring what is called evenness or equitability (Lloyd and Chelardi 1964). Evenness is usually calculated by the formula \( J = \frac{H}{\ln E}, \ E \) being the number of measures in the interval. The \( H \) and \( J \) values here are perfectly related, \( r = 1.0. \)

The graph of the environmental complexity \( H \) against richness (Fig. 6) indicates a positive relation of increasing environmental complexity and increasing species number density (richness). Values for intervals 1 and 2 deviate markedly from the rest of the points. This is expected from the large standard error associated with the environmental measures for these intervals.

From these results it is apparent that species are added to the system's environmental factor 'salinity – snow cover' by increasing the carrying capacity (the structural complexity) of the environment. A similar result was found for component 2 'ombrotrophy–mesotrophy.' These results could have been surmised from what we already knew about these factors from the niche dimension section. Conclusions similar to this
have been arrived at in other studies by Whitaker (1960, 1965) and MacArthur (1965).

**Dominance and Richness**

Theoretical discussions of ecological systems have often led to the belief that richness and dominance are inversely related (Margalef 1963). To test this, an abundance definition of dominance of McNaughton (1967) was adopted:

$$D_{1i} = 100\frac{Y_{1+2}}{Y_i}.$$  

$D_{1i}$ is calculated for the $i$th interval on component 1, $Y_{1+2}$ is the sum of the two most abundant species in the $i$th interval, and $Y_i$ is the total abundance in the $i$th interval.

The suggested inverse relation of richness and dominance is demonstrated in Fig. 7. It should be remembered that richness is defined here so that it is logically independent of dominance.

The implication of decreasing dominance with increasing richness is that the dominant species are losing abundance as richness increases and the total niche width is distributed among more species.

Table 1 shows this implication not to be true since the percentage of very rare species (i.e., less than 1.0 frequency) increases as the number of species decreases and the frequency of the dominants remains similar. It appears that the $D_{1i}$ values are being influenced not by a decrease in the numerator of the $D_{1i}$ formula, as is often implied, but by a faster increase in the denominator than the numerator.

**Environmental Predictability**

Dominant organisms do not decrease in abundance. They simply are not able to increase in abundance as fast as some of the smaller-niched species. This implies that dominants are less opportunistic in not being able to expand as a group as the carrying capacity of the environment increases. Further, the class of species which increases is the narrow-niched group which was very rare when the carrying capacity was lower. In fact, at the lower carrying capacity, these species had very low population sizes and probably suffered a corresponding high extinction rate. As the carrying capacity increased, these species as a group showed a tendency to be able to occupy this increasing carrying capacity (i.e., to be opportunistic).
(Skellam 1951; Hutchinson 1953, 1957; MacArthur and Levins 1964, 1967) that along an environmental gradient the ability of an organism to occupy particular parts of that gradient is in direct relation to its predictability (i.e., the change from one segment of the gradient to the next). To measure the change in predictability along the first component, the rates of change of both the environmental structure and the biologically determined carrying capacity were determined.

The changes in slope between intervals of the environmental structure (\(H_e\)) and biologically determined carrying capacity (\(K\)) were determined (Fig. 8). The predictability in environmental structure and in carrying capacity as shown in Fig. 8 are relatively similar.

Thus the gradient on the component runs from a more predictable environment to a less predictable environment. Levins (1968) has suggested on theoretical grounds that wide-niched species are better adapted to uncertain environments. This he explains on the basis that species of more generalized tolerance are needed in an environment which has low predictability. Also he shows that in less predictable environments there should be fewer numbers of small-niched species and these would be subject to high turnover rates. Slobodkin and Sanders (1969) have suggested a similar explanation. They contend that low predictability determines the properties of an organism that occupies that kind of environment. They believe that low predictability leads to organisms with high extinction rates and selection for wide tolerance. Wide tolerance allows the organism to better cope with unpredictable changes by being able to adjust to a wide set of conditions.

The results presented here seem to support these ideas. In a less predictable environment the wide-niched species (dominants) are more important and there is a large number of very small-niched species which have presumed high turnover rates. These results suggest that a plant on a gradient which is less predictable would find it more advantageous to adjust to a larger part of the gradient than to a smaller part. Hence, in the terminology of MacArthur and Levins (1964), the plant would respond to the gradient as if it were 'fine-grained,' that is, as if the positions along the gradient were so finely divided that the plant would not respond to them differentially.

**Niche Parameter: Overlap**

Niche overlap is a measure of that part of a species niche width which is simultaneously occupied by other species. This does not necessarily imply simultaneous use of the same resource in a competitive relationship. No distinction is made between types of interaction in this parameter.

Several measures of niche overlap have been suggested (Moisita 1959; Horn 1966; Levins 1968). All of these measures have in common that they are forms of interspecific association and community resemblance. Niche overlap will be calculated by interval using the formula suggested by Horn (1966). From the discussion of niche width, wide-niched species are not as efficient at increasing in abundance in a pre-
dictable environment as narrow-niched species. Ecologically this implies that wide-niched species are not as efficient in interactions in these environments. If in fact these interpretations of niche width are reasonable, then the total overlap per interval should be lower in the predictable environments and higher in the unpredictable environments. Whittaker (1960) has pointed out that more overlap would mean more complete intermixing of the flora and less niche differentiation. Figure 9 demonstrates these ideas to be acceptable.

**Conclusion**

Most of the raised bogs in Washington County, Maine, are located in a narrow band along the coast; they are never found more than 40 to 48 km inland. Most of the raised bogs studied are located in sandy outwash. These bogs probably developed from shallow marshes or by paludification resulting from the formation of an iron pan in flat outwash areas (McKeague et al. 1968).

Raised bogs are characteristically considered a ‘severe’ ecological system. The tree height class is all but eliminated. The severity is not caused by fire or other destructive influences. Raised bogs can be viewed as ecological systems which ‘leak’ nutrients. Raised bogs are supplied mineral ions mainly from atmospheric sources. This supply is very scanty and in addition is ‘leaked’ from the system owing to the nearly inoperable detritus cycle (Danman 1971), which normally would recycle this supply.

The sensitivity of the system to very low mineral ions is reflected by a general lack of trees and the higher abundance of shrubs and mosses (but not herbs) adapted to low mineral-ion budgets, e.g., Ericaceae and *Sphagnum*. It is generally believed (see Whittaker 1954; Woodwell 1970) that reduction in number of strata in vegetation is due to the disadvantage of large height in severe systems. This is because the greater respiratory demands of the live parts of these stems cannot be met by the limited efficiency of photosynthesis.

Niche analysis has shown that the two most important environmental factors are related to mineral-ion concentration: (1) atmospheric input differences owing to proximity to the ocean, and (2) a mineral-soil groundwater influence.

It has been further shown that these two environmental factors represent two important gradients in the surface water quality in the state of Maine. Comparison of the structure of the physical environment and the vegetation within the raised bogs has demonstrated their similar but non-linear relationship.

Thus the plant composition in raised bogs seems to be primarily queued to the mineral-ion budget not only for its existence as a system but for the variation and organization within that system.

The concept of dominance has a long and controversial history in ecology. Most recently, McNaughton and Wolf (1970) have attempted to show the importance of dominance in ecological systems. Adopting an abundance definition of dominance they hypothesize that it arises out of unequal efficiencies at the interactions of the inter- and intra-population level. Their hypothesis is not violated by any conclusions here. However, the concept of dominance becomes excess baggage. If niche width and dominance (high abundance) are positively correlated, and if niche width is determined by environmental complexity and predictability, then dominance is a logical outcome of a wider niche. It would seem more informative to speak of niche width than of dominance.

From niche analysis it was learned that a wide-niched species has a higher abundance and should thus interact more with other individuals of its population than with individuals of another species. This interaction between individuals of the same population will cause ‘internal’ (i.e. within the population) divergence of the *individual’s* niches. This divergence between in-
individuals will cause a widening of the population's niche. Thus the individuals of the population act as if they could, teleologically speaking, distinguish parts of the environment, that is, as if the environment were coarse grained. On the other hand, the population would appear to be unable to differentiate parts of the environment. The population thus reacts to the environment as if it were fine grained.

In the more complex and predictable parts of the system, there are more narrow-niched species and consequently more species. Narrow-niched species have smaller populations and thus individuals will have a greater chance of interacting with individuals of different species populations. Niche differentiation will then occur in response to other populations and niche width will not increase. Narrow-niched populations appear to react to the environment as if it were able to differentiate parts, that is, as if it were coarse grained. The individual in these populations on the other hand will appear to be reacting to the environment with indifference or as if the environment were fine grained.

Acknowledgments

I thank S. J. B. Johnson and W. D. Valentine for their help in collecting the data in the field and R. B. Pike and the late S. T. Pike for their generous hospitality in Lubec. I thank A. R. Hodgdon for checking my plant identification.

I also thank P. H. Allen, B. F. Chabot, A. R. Hodgdon, S. J. B. Johnson, Y. T. Kiang, W. B. Leak, J. W. Sheard, and W. D. Valentine for their valuable critical suggestions on the project and manuscript.

A grant from the Computer Center of the University of New Hampshire made the necessary computer time available. E. A. Joslin provided valuable help and advice on programming.

I acknowledge the facilities provided by the Marine Biological Laboratory of Woods Hole, MA, during the analysis of the data.

A grant from the National Cancer Institute of Canada to V. S. Gupta aided in the preparation of the manuscript.


LLOYD, M., and R. MACARTHUR. 1961. The advanced
KLOPFER, P. H., and R. H. LAMBERT, LEVINS, GREIG-SMITH, HEINSELMAN, M. L. 1963. Forest sites, bog processes and
HORN, H. S. 1966. Measurement of "overlap" in compara-
HURLBERT, S. H. 1971. The nonconcept of species diver-
HUTCHINSON, G. E. 1953. The concept of pattern in ecol-
IVIMEY-COOK, R. B., and M. C. F. PROCTOR. 1967. Factor
SLOBODKIN, L. B., and H. L. SANDERS. 1969. On the


