AN ANALYSIS OF TREE NICHE WIDTHS IN A MID-MISSOURI FOREST

by

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INTRODUCTION

This study was designed to test several hypotheses concerning the functional specialization of species in relation to ecological, life history and morphological characteristics. Functional specialization of a species is a measure of its specialization with respect to its functions in a community and with respect to the array of communities in which it may successfully persist. Since niche is often defined to include such intra- and intercommunity relationships, the purpose of this study is to test several hypotheses on species niche widths.

The Niche

The concept of niche was first formalized early in this century by Grinnell (1917) who first proposed the niche as a species place in an association of species. He later expanded this concept (1928) to mean the ultimate distributional unit that bounds each species, structurally and functionally. This concept of the niche is one that involves both habitat components (where the species actually lives) and intercommunity relationship and intracommunity relationships (how the species relates to other species and the environment).

Hutchinson (1958) defined niche in a more formal way as an n dimensional hypervolume, where each dimension of the hypervolume represented some environmental variable affecting the species. The species' tolerance of conditions along this dimension would determine the point along the axis that would fall within that species' hypervolume. If temperature was a dimension, for example, the temperatures tolerated by the species would fall inside its hypervolume and temperatures that were either too cold or too hot would fall outside the hypervolume. Similar sets of points would represent the species' tolerance to other environmental variables in other dimensions, such as moisture or light conditions. The hypervolume represented by all possible favorable points was called by Hutchinson the fundamental niche. He distinguished the fundamental niche from the realized niche, a hypervolume that was usually a subset of the fundamental niche due to competition or competitive exclusion with respect to other species.

Odum (1971) defined the ecological niche as composed of three components, a spatial niche, a trophic niche, and a multidimensional or hypervolume niche. The hypervolume component is the equivalent of Hutchinson's fundamental niche, the spatial niche component to be equivalent of habitat (e.g., the habitat of white oak in Kansas is moist bottoms) and the tropic niche component refers to the species place in the energy relations of a community (e.g., a white oak is a primary producer). Whittaker, Levin, and Root (1971) consider the fundamental niche of Hutchinson to be equivalent to the ecological niche of Odum if the fundamental niche hypervolume includes both physical and biological variables.

Whittaker, et al., suggest that the word niche be used exclusively for the species intracommunity relationships and the niche plus habitat concept be called ecotope. The term niche used here will be the approximate equivalent of ecotope.

The breadth of resources utilized, or range of habitats and communities occupied may then be used as a measure of niche width, with wider niches belonging to species that have a wider range of resource utilization. Niche widths can then be compared to other characteristics of species in an attempt to determine if indeed there are biological characteristics which endow species with wide or narrow niches. Several different methods of estimating niche widths have been proposed (Levins, 1968; Pielou, 1972; Findley, 1973). In addition three new ones are presented here.

Hypotheses on Species Properties Correlated with Niche Width

While discussing species abundance and variance, Darwin (1859) observed that species in polytypic genera were generally more abundant than species in monotypic genera or genera with only a few species. He also noted that more abundant species tended to be more variable. While the concept of niche and niche width had not yet been formulated, one may conclude that Darwin was suggesting that what is now termed niche width increased with increasing variation. In more recent times other correlations between various physical and biological properties and niche widths have been proposed or at least alluded to, but

usually these have been presented without empirical or experimental support. These hypothetical relationships have instead been derived from theoretical consideration or mathematical relationships. Levins (1968) proposed that organisms that are uniformly distributed over their environment have wider niches than those that are clustered in one or a few environments, though care must be taken to assert that clustering is not due to poor dispersal of the young. He states that wide dispersal implies a wide range of tolerance for environmental variables which would be characteristic of a large fundamental niche. Van Valen (1965) states that species that display a wide variance in phenological or morphological characteristics have a wider niche than species that have narrow variation. He concludes that a wide variance allows utilization of a wider spectrum of resources. Margalef (1968) states that diversity increases with succession and the increase in diversity is caused by an increase in the number of niches. Odum (1969) concludes that the developmental stages (early succession) species tend to have wide niches and mature stage (climax) species have narrow niches. Hairston (1964) proposed that species which occur in polytypic genera will have wider niches than those which occur in monotypic genera.

Many of the different relationships between niche widths and other characteristics had their origin with Darwin. Darwin (1859) alluded to relationships that have been stated more formally recently, for example, Darwin made observations similar to those proposed by Hairston (1964).

Hypotheses have been formulated relating variability and community structure to species niche width. Estimates of niche width will now be compared to measures of variation, community structure, and other species properties to see if they are in fact correlated.

METHODS

Data

The data for the estimation of niche width was furnished by John Rochow (Rochow, 1972) from the Ashland wildlife area in Boone County, Missouri. The Ashland wildlife area is an 890 hectares (2200 acres) tract in southeast Boone

County (38° 45' N 92° 12' W). The average annual temperature is 12.77° C (55° F.), the average temperature for the hottest month is 25.94° C (78.7° F.) and the average temperature for the coldest month is -.94° C (30.3° F.). The area has an average annual rainfall of 939.8 mm. (37 inches). The soils are generally loessial derived silt loam overlying Mississippian and Ordovician limestone. The area has been owned by the state of Missouri since 1936 and is currently operated by the University of Missouri as a natural area for research and wildlife preservation.

Circular plots of .081 Ha. (0.2 acres) were the sampling units used and basal area of all woody plant species over 8.89 cm. (3.5 inches) in diameter at 137 cm. (4.5 feet) above the ground was recorded for each individual of each species. A total of seventy five plots were sampled and permanently marked, and a total of thirty five living tree species were present in one or more of the study plots. For a complete species list see Appendix A.

The data were arranged in two matrices, each matrix seventy five plots by thirty five species. One matrix contained the basal area values, where any one element represented the total basal area of the species in a given plot. The other matrix was constructed similarly except that the elements consisted of total number of individuals rather than total basal area. Both number of individuals and basal area were used in the analysis since they are two different measures of the importance of a species in a plot. Basal area is a measure of the size of a tree and hence the biomass of the species in that community. The number of individuals measures the importance of a species in a different way unless all individuals are of the same size. That these two quantities measure different aspects of a species role in a community means that they will give rise to different niche width values for the same species. The basal area niche width weights for importance in the biomass accumulated by species, whereas the numbers niche width weights for the proportion of individuals irrespective of their biomass. The former represents an energy and nutrient resource

view of the niche, while the latter represents more a habitat and successional view.

The raw data in each matrix was converted into relative frequency data for calculating all niche widths except that of Pielou (1972) which requires raw data for calculation. Relative frequency was figured such that the sum of all the species values in any plot totaled one.

(1) $$p_{ij} = \frac{\chi_{ij}}{\sum_{j=1}^{n} \chi_{ij}}$$

where; p_{ij} = relative frequency of jth species in the ith plot

χ_{ij} = species value (basal area or number) of the jth species in the ith plot

n = number of species in the plot

Niche Width Estimates

The first method of calculating niche widths is that of Levins (1968) and will hereafter be called Levins' 1. It is calculated as follows:

(2) $$B_j = 1 / \sum_{i=1}^{n} p_{ij}^2$$

where; B_j = niche width of the jth species

p_{ij} = the proportion of the jth species in the ith plot

n = number of plots

The second method of calculating niche width is also from Levins (1968) and will be called Levins 2. It is calculated by the following formula:

(3) $$B_j = e^{-\sum_{i=1}^{n} p_{ij} \ln p_{ij}}$$

where; B_j = niche width of the jth species

p_{ij} = the proportion of the jth species in the ith plot

n = number of plots

The third method of calculating niche width was adapted from Findley (1973) and hereafter so refered to as Findley. Findley niche widths are calculated from the data by the following method. Each of the seventy five plots is considered a point in a thirty five dimensional space, where each dimension represents the frequency of a species. The arrangement of these points is called a hypercloud since the points are in a space of more than three dimensions. From the resulting hypercloud of seventy five points, the points that

represent plots in which a given species occurs form a hypercloud which is used to calculate the niche width of that species. A center for this hypercloud of points is found, and the niche width for the species is calculated as follows:

$$(4)\quad d_{ij} = \sum_{i=1}^{n} (p_i - p_c)^2$$

where; d_{ij} = niche width of the jth species

p_i = the points representing plots where the jth species is present

p_c = the center of the hypercloud of p_i points

n = the number of points in the hypercloud

The fourth method of calculating niche width is from Pielou (1972) and will hereafter be refered to as Pielou. It is the only method that used the raw data rather than the relative frequency data, and Pielou niche widths are calculated as follows:

$$(5)\quad N_j = \left(1 \Big/ \sum_{i=1}^{n}\sum_{j=1}^{m} p_{ij}\right)\left[\ln\left(\left(\sum_{i=1}^{n} p_{ij}\right)!\right) - \sum_{i=1}^{n} \left(\ln\left(p_{ij}!\right)\right)\right]$$

where; N_j = niche width of the jth species

p_{ij} = the actual numerical values of the jth species in the ith plot

n = number of plots

m = number of species

The fifth method of calculating niche widths is original with this study. Since this method was based on factor analysis it is referred to as Factor. To calculate Factor niche width, the relative frequency frequency data was arcsin transformed and a seventy five by seventy five correlation matrix between plots was calculated by a computer correlation program BMDO2D (Dixon, 1967). This correlation matrix was used as input into a factor analysis program BMDO3M (Dixon, 1967) and a rotated nine by seventy five matrix was the output. Nine factors were chosen since that number was sufficient to explain 90-95% of the variance of the eigenvalues. The rotated factor matrix was then used as a set of seventy five points in nine dimensional space. The niche

width for a particular species was determined by selecting the points that corresponded to plots where that particular species occurred. This set of points was then treated as a nine dimensional hypercloud and a central point of the hypercloud was calculated. The average distance from the center of the hypercloud to the points in the hypercloud was calculated by the geometric methods used in the Findley method and this value was called the niche width for the species represented by the hypercloud.

The sixth method of measuring niche widths is also original and will be referred to as Sherwood. Sherwood niche widths are calculated as follows:

(6) $R_j = \sum_{i=1}^{n} ((\ln S_i)\, p_{ij})$ where; R_j = niche width of the jth species

S_i = the number of species in the ith plot

p_{ij} = the proportion of the jth species in the ith plot

n = number of plots

Two niche width estimates for each method of calculating niche width were computed, one using the basal area data and the other individual numbers data. The abbreviation BA will be used after all niche widths calculated from basal area data and the abbreviation I after all niche widths calculated from the individual numbers data.

The six different methods of calculating niche widths weight for different factors. Levins 1 weights for rare species in the absence of any plots with common species, but the common species when present are the major factors in determining niche width. Levins 2 weights for abundant species. Pielou weights for abundant species and also for numerous species. Sherwood weights for species in plots that have many different species and for species that are abundant in plots. Findley weights for species that occur in different types of plots (i.e. in plots where there is wide variance in the other species and other species frequencies present). Factor weights similarly to Findley.

The mean plot diversity ($\bar{H}'$) for plots in which a species occurs was originally considered an independent variable. Species which occur in higher diversity communities are predicted to have narrow niche widths. The method for calculating mean plot diversity and niche width are not independent and the relationship between them is trivially true. As such, mean plot diversity may be considered simply another measure of niche width.

To calculate $\bar{H}'$ first the diversity for each plot was calculated by the Shannon-Wiener function (Shannon and Weaver, 1949) as follows:

$$(7)\quad H_i' = -\sum_{i=1}^{m} p_{ij} \ln p_{ij}$$

where; H_i' = diversity of the ith plot

p_{ij} = the proportion of the jth species in the ith plot

m = number of species in plot i

This produces seventy five plot diversity values and the diversities of the plots where a species was present were summed and divided by the number of plots in which the species was present as follows:

$$(8)\quad \bar{H}'_j = \sum_{i=1}^{n} H'_i/n$$

where; $\bar{H}'_j$ = average plot diversity for the jth species

$\Sigma H'_i$ = the sum of plot diversities where species j was present

n = the number of plots with species j present

Independent Variables

Eighteen independent variables were selected for the examination of their relation to niche width. They fall into three general categories. The first category consists of four taxonomic variables, the second category, consists of six variables dealing with distributional characteristics and the third category consists of eight variables that deal with morphological and life history relationships.

These data were taken from the following references; Brockman (1968), Fageri and Pijl (1966), Fowells (1965), Grimm (1962), Harlow (1957), Harrar and Harrar (1962), Hough (1907), Little (1971), Petrides (1972), Platt (1952),

Preston (1961), Stephens (1969), Stephens (1973), Standley (1923), Stefferud (1949), and Willis (1966).

The first set of four variables were chosen to test the hypothesis of Hairston (1964) on niche widths. While Hairston refers specifically only to the species per genus relationships, other taxonomic relationships were also examined. The four taxonomic variables are species per genus, eastern United States species per genus, genera per family, and species per family.

The six distributional variables are used to test Van Valen's (1965) and Levins' (1968) theories about distribution and abundance of species in relation to niche widths. These are size of distributional range, position in species range of the research area, northern limit, southern limit, eastern limit, and western limit. The latter four of these variables are also measurements of climatic tolerances. Size of range was a measure of the total amount of area occupied by the species range, and was divided into five relative size classes. Position in range was scored as central, intermediate, marginal or isolated.

The morphological and life history characteristics are successional stage, flower type, pollination vector, and dispersal. The four size variables were to test the importance of biomass and light gathering ability in niche widths. The relationship between successional stage and niche width was suggested by Odum (1969), and Margalef (1968). This variable was scored by dividing succession into nine categories. A species occupying the very earliest stage of succession received a successional stage value of one, and species normally found only in the climax community received a value of nine. Relationships between niche width and flower type, pollination methods, and seed dispersal methods may be postulated. These variables all relate to variability and distribution. The variable, flower type, was measured on a scale of one to eight, running from perfect flowered species to dioecious species. The variable, pollination type, was assigned a value of one if the flower was

wind pollinated or two if the flower was insect pollinated. Sufficient information was lacking to divide the insect pollination class any further. The variable seed dispersal type was divided into five classes, wind, water, scatter hoarding, transported through a mammalian digestive tract, and being transported through an avian digestive tract. This variable could not be ordered in a logical way so testing with niche width was done by analysis of variance as opposed to regression analysis.

Methods of Analysis

The fourteen dependent variables were each regressed on the seventeen independent variables using a stepwise multiple linear regression BMD02R (Dixon, 1967). A correlation matrix for all thirty two dependent and independent variables was also computed to assess relationships between the various types of niche width estimates and between the independent variables.

RESULTS AND DISCUSSION

Different methods gave very differing values for niche widths of species. (Complete niche width values for all 35 species are given in Appendix A). The maximum and minimum values and the species assigned these values are found in Table I.

Six of the methods (Levins 2 BA, Levins 2 I, Sherwood BA, Sherwood I, Pielou BA, Pielou I) have Quercus alba L. (white oak) as the species with the maximum value. White oak occurred in the most plots; in 64 of the 75 plots studied, and was also usually found with high frequency in the plots where it was present. In general, the more plots in which a species occurred the higher was its average frequency within these plots. The correlation coefficient beoccurrence in plots and frequency within plots was .738 for the basal area data and .746 for the individual numbers data; both of these are significant at the 0.1% level. These six measures of niche width all weight for frequent occurrence.

Table I

Maximum and Minimum Values of Niche Width Estimates

Niche Width				
$\bar{H}'$ BA	Quercus marilandica Muenchh.	2.202	Quercus velutina Lam.	0.878
$\bar{H}'$ I	Gledirsia tricanthos L.	2.443	Quercus velutina Lam.	0.915
Pielou BA	Quercus alba L.	1.690	Quercus marilandica Muenchh.	0.0
Pielou I	Quercus alba L.	1.655	Quercus marilandica Muenchh.	0.0
Levins 1 BA	Cercis canadensis L.	4.210×10^{4}	Quercus alba L.	4.498×10^{-2}
Levins 1 I	Gymnocladus dioicus (L.) K. Koch.	2.116×10^{3}	Quercus alba L.	4.495×10^{-2}
Levins 2 BA	Quercus alba L.	4.742×10^{6}	Cercis canadensis L.	1.040
Levins 2 I	Quercus alba L.	2.855×10^{6}	Gymnocladus dioicus (L.) K. Koch.	1.087
Sherwood BA	Quercus alba L.	5.150×10^{1}	Cercis canadensis L.	1.758×10^{-2}
Sherwood I	Quercus alba L.	5.048×10^{1}	Gymnocladus dioicus (L.) K. Koch.	5.402×10^{-2}
Factor BA	Quercus rubra L.	0.6736	Liquidambar styraciflua L.	0.3334
Factor I	Cercis canadensis L.	0.7834	Acer saccharum Marsh.	6.232×10^{-3}
Findley BA	Quercus velutina Lam.	0.6783	Quercus marilandica Muenchh.	0.0
Findley I	Quercus velutina Lam.	0.6892	Quercus marilandica Muenchh.	0.0

Two of the variables (Findley BA, Findley I) have Quercus velutina Lam. (black oak) as the species with the maximum value. Black oak was the seventh most abundant species, but it occupies a variety of habitats, one of the conditions necessary to have high values when computed by the Findley method. Factor BA had Quercus rubra L. (red oak) for the species with the maximum value. Red oak was the second most abundant species in the research area. The five remaining methods ($\bar{H}'$BA, $\bar{H}'$I, Levins 1 BA, Levins 1 I, Factor I) had maximums that were represented by species that were found in one plot, Quercus marilandica Muenchh. (blackjack oak), Gleditsia tricanthos L. (honey locust) and Gymnocladus dioicus (L.) K. Koch. (Kentucky coffeebean), or found in two plots, Cercis canadensis L. (redbud). That these rare species should have maximum values is related to the fact that they occur in communities with many species. These measures have higher values for species in communities with many species. The exception is redbud which is found in two widely different plots and therefore has a high value as measured by Findley which weights for community heterogeneity. Minimum values for the other measures of niche width were found in these same species plus Liquidambar styraciflua L. (sweetgum). The Findley and Pielou methods are calculated in such a way that any species that occurs in only one plot receives a value of zero. There are therefore, four species with values of zero for each of these methods, they are blackjack oak, sweetgum, honey locust, and Kentucky coffeebean.

Relationships between Niche Width Measures

The correlations between the dependent variables (niche width measures) are found in Table II. The methods fall into groups on the basis of similarity as measured by correlation. Because the methods of computing niche width are not independent it is not possible to use standard tests of significance on the correlation coefficients. The first is a group of six measures composed of Levins 2 BA, Levins 2 I, Pielou BA, Pielou I, Sherwood BA, and Sherwood I. The correlations between the Sherwood and Pielou methods ($r = .989$ and .988 for I

Table II

Correlations Between Estimates of Niche Width

	$\bar{H}'$	Levins 1	Levins 2	Pielou	Sherwood	Findley	Factor
$\bar{H}'$	.933	.400	-.246	-.321	-.333	-.775	.301
Levins 1	.316	.428	-.071	-.131	-.178	-.546	.103
Levins 2	-.243	-.046	1.000	.969	.924	.182	-.018
Pielou	-.328	-.131	.956	.987	.988	.234	-.053
Sherwood	-.347	-.115	.909	.989	.982	.241	-.077
Findley	-.841	-.139	.173	.232	.247	+.990	-.072
Factor	-.044	-.182	-.185	-.074	-.033	+.199	-.051

Lower left triangle - correlations between basal area niche width estimates

Upper right triangle - correlations between individual numbers niche width estimates

Diagonal values - correlation between basal area and individual numbers for each dependent variable

and BA respectively) are so high as to suggest that the more easily computed Sherwood method is a good approximation of the Pielou method. These methods, as stated earlier, weight for the same factors and are observed to have high correlation between them.

A second group of four measures $\bar{H}'$ BA, $\bar{H}'$ I, Levins 1 BA, and Levins 1 I show high correlation amongst them and lower correlations with the other measures of niche width. The basal area and number data for the Findley method give similar results to one another, but the order of species is essentially the reverse of the previous group. Factor BA and Factor I show low correlation with all other measures including themselves. The two measures that weight for differences between communities in which a species occurs do not give very similar estimates of niche width. The Factor method removes the effect of correlation between species and this may account for the difference between Findley and Factor results.

Regression Results

The independent variables that proved to be significant at the five percent level are summarized in Table III. Average plot diversity BA had a significant partial regression on genera per family. Genera per family is one of the four taxonomic variables included to test the Hairston hypothesis. Mean plot diversity I had two significant partial regression variables, genera per family and Eastern United States species per genus. These are both taxonomic variables and are not correlated for the species that were included in the study.

Levins 1 BA had one significant partial regression variable, genera per family and Levins 1 I had two significant partial regression variables, genera per family and flower type. Flower type had a positive partial regression coefficient, suggesting that increasing dioeciousness is found in trees as Levins 1 I niche widths increases.

Four dependent variables, Pielou BA, Pielou I, Sherwood BA, and Sherwood I all show significant regression on species per genus. The basal area and

Table III

Independent Variables Showing Significant

Partial Regression Coefficients

Dependent Variable	Independent Variables with Partial Regression Coefficients of $p < .05$
$\bar{H}'$ BA	+ genera/family
$\bar{H}'$ I	+ genera/family; - Eastern U.S. species/genus
Pielou BA	+ species/genus
Pielou I	+ species/genus
Levins 1 BA	+ genera/family
Levins 1 I	+ genera/family ; + flower type
Levins 2 BA	none
Levins 2 I	none
Sherwood BA	+ species/genus
Sherwood I	+ species/genus
Findley BA	- genera/family
Findley I	- genera/family
Factor BA	- East
Factor I	none

+ indicates positive correlation - indicates negative correlation

numbers of individual niche widths computed by Levins 2 had no significant regression coefficients with any of the independent variables.

Findley BA and Findley I numbers had negative significant partial regression coefficients with one independent variable, genera per family. This is more evidence that these two methods measure niche width much differently than the others.

The variable Factor BA had a significant negative partial regression coefficient on the independent variable East. This is either a spurious relation (since it is unique) or it reflects the fact that Factor reflects spatial distributional characteristics of the niche.

Findley and Factor methods measure the spatial niche of Odum giving maximum values of niche width to species which occur in the most widely different communities. These two measures do not fit the trend of increasing niche width with increasing taxonomic diversity. A related result was observed by Johnson (1966) where genetic variability was not correlated with the range of habitats successfully occupied by buttercup populations. Perhaps the habitat component of the niche is not related to genetic variability.

The five independent variables that have significant partial regression coefficients with one or more of the dependent variables were species per genus, eastern U. S. species per genus, genera per family, flower type, and maximum eastern extension. The first three of these are all taxonomic in nature and were significant in ten of the fourteen analyses. The last two all occurred only once among the fourteen regression analyses. These independent variables show no significant correlations among themselves except for species per genus and Eastern United States species per genus (Table IV).

The significantly regressed independent variables showed about the same groupings in relation to the dependent variables as the correlation coefficients among the dependent variables. The exception is that the two Levins' 2 measures did not have any significant partial regression on any of the seventeen

Table IV

Independent Variable Correlations

		B.	C.	D.	E.
A.	Species/Genus	.930	-.239	.071	-.143
B.	Eastern U.S. Sp./Gen.		-.273	.090	-.057
C.	Gen./Fam.			.012	.190
D.	Flower type				-.280
E.	East				-

$p < .05$ for $r > .339$

independent variables.

The analysis of variance of niche widths between classes based on mode of seed dispersal showed species with scatter-hoarding by mammals to have considerably higher niche widths than the other forms of seed dispersal (significant at the 1% level). An examination of these data reveals that this results from the fact that seed dispersal is generally the same for taxonomic groups. The oaks, a diverse group with wide niches, are dispersed by scatter hoarding. It is therefore unlikely that scatter hoarding per se endows species with greater niche widths.

It was not the purpose of this study to compare the methods of computing niche widths as to their relative value, however some comment on that is appropriate here. The methods fall into three classes based on what aspect of the niche is being emphasized. Factor and Findley measure the intercommunity aspects of niche width but the two methods give rather different results. The reasons for this are not clear. Levins 1 and $\bar{H}'$ measure intracommunity relationships and assign high niche width values to species that occur in communities with many other species. Pielou, Levins 2, and Sherwood measure both intra- and intercommunity relationships and produce about the same distribution of niche width values. These three are the preferable methods for that reason. Sherwood is the easiest to compute, Pielou is the most elegant, and Levins 2 maximizes the range of niche width values, but all three appear equally suitable for computing niche widths and all three were highly correlated in this study.

CONCLUSIONS

The following conclusions are drawn from this study:

1. In general, niche width is defined in both formal mathematical or word definitions in terms of species diversity. The means that as they are defined, niche width is related by definition to species diversity rather than the relationship being an interesting biological one. Diversity may then be considered a measure of niche width.

2. A new method of measuring niche width ($R = \sum_{i=1}^{n} (\ln S_i)p_{ij}$)) is highly correlated with one given by Pielou (1971) and is an approximation of it for this data.

3. The hypothesis that niche width increases with increasing genetic variability is supported by significant correlations between niche width and measures of genetic variability.

4. Methods of measuring niche widths which weight for similar factors give similar values for niche width.

5. Niche width values based on community structure are not similar to those based on the range of habitats occupied by a species.

6. The methods Pielou, Levins 2, and Sherwood are considered the best overall measures of niche width.

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APPENDIX A

Species Number	Species	Common Name	$\bar{H}'BA$	$\bar{H}'I$
1	Juniperus virginiana L.	eastern red cedar	1.539	1.623
2	Juglans nigra L.	black walnut	1.422	1.548
3	J. cinerea L.	butternut	1.689	1.936
4	Carya ovata K. Koch.	shagbark hickory	1.393	1.593
5	C. laciniosa Load.	shellbark hickory	1.718	1.906
6	C. tomentosa Nutt.	mockernut hickory	1.107	1.246
7	C. texana Schn.	black hickory	1.100	1.173
8	C. cordiformis K. Koch.	bitternut hickory	1.672	1.183
9	Ostrya virginiana K. Koch.	hophornbeam	1.515	1.800
10	Quercus alba L.	white oak	1.134	1.243
11	Q. macrocarpa Michx.	bur oak	1.735	1.959
12	Q. stella Wang.	post oak	1.025	1.065
13	Q. muhlenbergii Engelm.	chinquapin oak	1.568	1.736
14	Q. rubra L.	red oak	1.221	1.346
15	Q. shumardii Buchl.	shumard oak	1.444	1.577
16	Q. velutina Lam.	black oak	8.776×10^{-1}	9.154×10^{-1}
17	Q. marilandica Muenchh.	blackjack oak	2.202	1.962
18	Ulmus america L.	white elm	1.705	1.914
19	U. rubra Muhl.	red elm	1.520	1.704
20	Celtis occidentalis L.	hackberry	1.789	1.963
21	Morus rubra L.	red mulberry	1.613	1.826
22	Liquidambar styraciflua L.	sweet gum	1.932	1.914
23	Platanus occidentalis L.	sycamore	1.639	1.822
24	Gymnocladus dioicus (L.) K. Koch.	Kentucky coffeebean	1.932	1.914
25	Gleditsia tricanthos L.	honey locust	1.953	2.443
26	Cercis canadensis L.	redbud	1.961	2.315
27	Acer saccharum Marsh.	sugar maple	1.365	1.494
28	Acer nigrum Michx. f.	black maple	1.830	2.035
29	Aesculus glabra Willd.	buckeye	1.643	1.948
30	Tilia america L.	basswood	1.927	2.064
31	Cornus florida L.	flowering dogwood	1.370	1.615
32	Bumelia lanuginosa (Michx.) Pers.	gum bumelia	1.520	1.755
33	Fraxinus america L.	white ash	1.242	1.368
34.	F. pennsylvania Marsh.	green ash	1.393	1.606
35	F. quadrangulata Michx.	blue ash	1.507	1.649
	Mean niche width for species 1 - 35 ($\bar{x}$)		1.549	1.710
	Variance of niche width for species 1 - 35 (s^2)		0.3029	0.3350

	Sherwood BA	Sherwood I	Factor BA	Factor I	Findley BA	Findley I
1	6.138×10^{-1}	9.132×10^{-1}	.5468	.3985	.4635	.4780
2	4.416	3.428	.4157	.5762	.3832	.3753
3	2.020×10^{-1}	4.447×10^{-1}	.4977	.5552	.3675	.3376
4	2.502	3.824	.4151	.4633	.4148	.3889
5	1.892	2.533	.4217	.4266	.3041	.2826
6	1.603×10^{-1}	4.942×10^{-1}	.4270	.3328	.5163	.5258
7	4.637×10^{-1}	7.609×10^{-1}	.4282	.2755	.5830	.5700
8	3.700	4.477	.5832	.5762	.3388	.3023
9	1.225×10^{-1}	7.922×10^{-1}	.5647	.1261	.4464	.3744
10	5.150×10^{1}	5.048×10^{1}	.3788	.4426	.5438	.5320
11	6.039×10^{-1}	5.471×10^{-1}	.4538	.4765	.3958	.3810
12	2.160	1.673	.3497	.5006	.6105	.6371
13	1.171×10^{1}	1.413×10^{1}	.4480	.5097	.3565	.3391
14	1.945×10^{1}	1.201×10^{1}	.6736	.5515	.5100	.4949
15	7.630	5.260	.5513	.5551	.4025	.3888
16	5.920	4.352	.3727	.4208	.6783	.6892
17	1.651×10^{-1}	1.434×10^{-1}	.5020	.4435	0	0
18	1.606	2.821	.4562	.4474	.3407	.3106
19	1.881	2.811	.5361	.4787	.3499	.3246
20	2.881×10^{-1}	5.968×10^{-1}	.5442	.5396	.3899	.3503
21	1.077×10^{-1}	4.267×10^{-1}	.5001	.5017	.3656	.3371
22	6.770×10^{-1}	1.026	.3334	.3883	0	0
23	3.026	1.438	.4424	.4360	.4552	.4076
24	3.312×10^{-2}	5.402×10^{-2}	.4227	.3303	0	0
25	2.613×10^{-2}	6.601×10^{-2}	.3419	.6031	0	0
26	1.758×10^{-2}	1.345×10^{-1}	.4157	.7834	.3975	.3437
27	7.929	1.210×10^{1}	.5524	.6232	.4310	.4159
28	4.002	2.996	.4097	.4278	.3359	.2944
29	3.664×10^{-1}	1.632	.3848	.4636	.4072	.3585
30	2.594	1.781	.5340	.4148	.3099	.3043
31	1.663×10^{-1}	7.098×10^{-1}	.6409	.5186	.5198	.4539
32	1.520×10^{-1}	2.080×10^{-1}	.5099	.5763	.4685	.4232
33	1.834	2.644	.5513	.5017	.5035	.4874
34	1.405×10^{-1}	1.013×10^{-1}	.4855	.4105	.4693	.4388
35	8.783×10^{-1}	1.120	.4300	.4672	.3924	.3880
$\bar{x}$	3.970	3.970	.4720	.4550	.3843	.3639
s^2	9.178	8.804	.0832	.1342	.0269	.0265

	Pielou BA	Pielou I	Levins 1 BA	Levins 1 I	Levins 2 BA	Levins 2 I
1	4.665×10^{-3}	1.036×10^{-2}	5.328×10^{1}	2.371×10^{1}	2.315	3.0014
2	9.036×10^{-2}	7.025×10^{-2}	4.170	9.640	1.744×10^{2}	1.173×10^{2}
3	2.125×10^{-3}	2.818×10^{-3}	5.860×10^{2}	9.696×10^{1}	1.422	1.818
4	4.523×10^{-3}	6.961×10^{-2}	9.721	5.411	2.706×10^{1}	1.091×10^{2}
5	2.283×10^{-2}	2.823×10^{-2}	9.384	7.149	6.085	1.095×10^{1}
6	1.901×10^{-3}	5.929×10^{-3}	9.389×10^{2}	9.351×10^{1}	1.445	2.411
7	4.540×10^{-3}	8.151×10^{-3}	6.494×10^{1}	2.527×10^{1}	2.097	2.812
8	6.300×10^{-2}	5.874×10^{-2}	4.131	3.501	3.543×10^{1}	6.243×10^{1}
9	1.625×10^{-3}	6.321×10^{-3}	1.605×10^{3}	2.442×10^{1}	1.329	2.856
10	1.690	1.655	4.498×10^{-2}	4.495×10^{-2}	4.742×10^{6}	2.855×10^{6}
11	3.426×10^{-3}	4.023×10^{-3}	4.240×10^{1}	6.607×10^{1}	1.812	1.837
12	2.404×10^{-2}	2.471×10^{-2}	4.250	9.002	7.715	7.434
13	2.093×10^{-1}	2.857×10^{-1}	6.009×10^{-1}	4.784×10^{-1}	3.245×10^{3}	1.190×10^{4}
14	4.475×10^{-1}	2.404×10^{-1}	2.984×10^{-1}	7.900×10^{-1}	1.142×10^{5}	3.814×10^{4}
15	1.300×10^{-1}	1.053×10^{-1}	1.120	2.496	4.724×10^{2}	2.188×10^{2}
16	1.413×10^{-1}	1.209×10^{-1}	1.084	1.181	4.607×10^{2}	1.928×10^{2}
17	0	0	2.264×10^{2}	3.004×10^{2}	1.197	1.179
18	1.821×10^{-2}	3.201×10^{-2}	1.028×10^{1}	3.230	4.616	7.992
19	3.141×10^{-2}	4.755×10^{-2}	1.579×10^{1}	1.038×10^{1}	1.088×10^{1}	3.280×10^{1}
20	3.080×10^{-3}	5.051×10^{-3}	1.540×10^{2}	4.240×10^{1}	1.552	2.801
21	1.205×10^{-3}	4.236×10^{-3}	1.994×10^{3}	1.785×10^{2}	1.266	1.989
22	0	0	1.347×10^{1}	5.862	1.425	1.441
23	2.932×10^{-2}	1.164×10^{-2}	1.640	6.953	3.847	3.070
24	0	0	5.631×10^{3}	2.116×10^{3}	1.059	1.087

	Pielou BA	Pielou I	Levins 1 BA	Levins 1 I	Levins 2 BA	Levins 2 I
25	0	0	1.126×10^{4}	1.764×10^{3}	1.045	1.093
26	8.096×10^{-5}	4.315×10^{-4}	4.210×10^{4}	7.230×10^{2}	1.040	1.210
27	1.582×10^{-1}	2.412×10^{-1}	1.380	7.362×10^{-1}	1.759×10^{3}	2.126×10^{4}
28	6.418×10^{-2}	3.190×10^{-2}	2.865	5.027	3.039×10^{1}	1.473×10^{1}
29	2.726×10^{-3}	9.683×10^{-3}	8.225×10^{1}	5.177	1.551	2.877
30	3.025×10^{-2}	1.901×10^{-2}	3.905	1.524×10^{1}	7.844	6.849
31	1.403×10^{-3}	5.156×10^{-3}	8.395×10^{2}	4.653×10^{1}	1.372	2.506
32	3.461×10^{-4}	7.015×10^{-4}	3.752×10^{2}	2.296×10^{2}	1.258	1.331
33	3.099×10^{-2}	5.048×10^{-2}	1.512×10^{1}	8.238	1.401×10^{1}	3.255×10^{1}
34	6.011×10^{-4}	4.315×10^{-4}	4.146×10^{2}	8.190×10^{2}	1.251	1.196
35	9.462×10^{-3}	1.203×10^{-2}	3.548×10^{1}	1.948×10^{1}	3.417	4.002
$\bar{x}$	9.410×10^{-2}	9.05×10^{-2}	1.900×10^{3}	1.906×10^{2}	1.389×10^{5}	8.364×10^{4}
s^2	0.2923	0.2817	7.302×10^{3}	4.764×10^{2}	8.012×10^{5}	4.823×10^{5}

AN ANALYSIS OF TREE NICHE WIDTHS IN A MID-MISSOURI FOREST

by

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AN ABSTRACT OF A MASTER'S THESIS

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The relationship between niche width and ecological, morphological, and life history characteristics was examined for thirty-five eastern deciduous forest tree species. These tree species occurred in one or more of seventy-five 0.20 acre plots in the University of Missouri's Ashland Research Area in Boone County, Missouri. Niche widths were calculated by seven different methods from relative frequency of basal area values and relative frequency of individuals in these plots. Four of these methods were taken from the literature and the other three are new to this study. Ecological, morphological, and life history characteristics were compiled for each tree species and these characteristics were selected to test various hypothesis that there are properties which endow species with greater niche widths. These characteristics include species position in succession, distribution of the species, size of the species, flower type, seed dispersal methods, etc. Each niche width measure was used as a dependent variable and multiple regression preformed with the ecological, morphological, and life history characteristics as independent variables. Only the proposed relationship between niche width and genetic variability was significant in more than one case. Ten of the fourteen niche width measures had significant correlations with one of two measures of taxonomic diversity; species per genus or genera per family.