Ecological Pattern in the Moss Species Ensembles of a Hemlock-Hardwood Forest Mosaic

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ABSTRACT: A simple method using incidence (presence) data, the Jaccard index of similarity and the nonparametric Wilcoxon T statistic is shown to produce an ecologically interpretable ordination of moss species ensembles in 13 forest stands of the Huyck Preserve near Rensselaerville, New York. The method is also applied to the tree species ensembles of these forests and there is only a little conformity of the moss and tree patterns. There is actually little overall pattern, though considerable heterogeneity, to the tree communities.

The new method is compared with principal components ordination and appears to yield a richer, more interpretable set of results, as well as allowing statistical inference about the distinctiveness of pairs of individual species ensembles. The new method may be generally useful in the search for community patterns in space or time when only incidence data are available and considerable species sharing among communities is present.

In comparison with one another, many of the moss species ensembles appear to be random subsets of the whole species pool. Ordination of all ensembles together, however, reveals two major and divergent tendencies which divide the ensembles. The division arises from the interplay of species diversity and random versus non-random assembly of species ensembles. Hence, the new Jaccard-Wilcoxon ordination takes place against a backdrop of familiar ecological concepts. The ordination of the moss ensembles also makes sense given their microgeographical positions within the Huyck Preserve.

The data set developed here provides an extensive floristic description of the mosses of a hemlock-hardwood forest mosaic which has developed over the past 50 years following extensive distrubance by humans.

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Introduction

The first step in the study of the composition of natural communities, or species assemblages, is the extraction of meaningful patterns. Such patterns provide a foundation for conclusions about the similarity and dissimilarity of communities spread out in space and time. Patterns in space may reflect underlying climatic, edaphic, dispersal or species-interactive effects, and they may represent synchronous or asynchronous successional change. Patterns strictly arranged in time, as in the paleontological record, may represent the cumulative effects of many biogeographical, ecological and adaptive events. Behind this search for pattern there always lurks the null hypothesis that observed differences in species representation are due to chance occurrences of colonization and extinction, or chance effects of sampling.

Over the years many attempts have been made to extract patterns from data for community composition (Dice, 1945; Cole, 1946; Preston, 1948; 1962; Bray and Curtis, 1957; Fager, 1957; Curtis, 1959; Morisita, 1959, Hairston, 1964;

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Williams, 1964; Lambert and Dale, 1964; MacArthur, 1965; Williams and Lambert, 1959, 1966; Cairns and Kaesler, 1969; Roback et al., 1969; Langford and Buell, 1969; Williams et al., 1969; Goodall, 1970; Andersen, 1971; Botkin et al., 1972; Whittaker, 1973; Williamson, 1978). For the most part these papers inquire about: mechanisms or factors which influence the bringing together of species into assemblages; trajectories of succession; mechanisms controlling patterns of relative abundance among species; or how we can best recognize when species ensembles at different sites are distinct. This last question is a major concern of this paper.

Early methods often introduced an unwelcome arbitrariness or circularity by assigning each species an importance value which reflected preconceptions (possibly often correct) about the composition of typical or climax communities. Later approaches have usually attempted to overcome this circularity with unweighted multivariate analyses, but these suffer from difficulty of interpretation. It is difficult or impossible to ascertain what properties of the data the various axes or factors of a multivariate solution are most responsive to in a biological or ecological sense. Some multivariate procedures, particularly principal components analysis (PCA), do "line up" the sites or stations quite well (Williamson, 1978). However the critical problem of the degree of distinctiveness between seemingly quite similar ensembles has eluded most methods of analysis. Fager (1957), almost alone among the early authors, directly tackled the problem of statistically distinguishing the species ensembles at different locations.

Many of the methods proposed for the ordination and classification of communities use measures of abundance as well as species lists, but increasingly attention has focused on the use of incidence data (Fager, 1957; Lambert and Dale, 1964; Goodall, 1970; several of the papers in Whittaker, 1973; and Williamson, 1978). Incidence data have a number of practical advantages over abundance data: they are more easily and quickly collected; they are the typical data of most early floristic and faunistic studies, many of which are irreplaceable; they are probably the only generally reliable data for fossil assemblages; and for most colonial animals and vegetatively propagating plants they are often the only data one can reasonably collect. Even when we could conceivably record the cover or mass for every species the task of identifying every scrap of material may be insurmountable. This is certainly the case with mosses, although an indication of relative species abundance can be gotten from frequencies of encounter during sampling, as in the various columns of our main data set given in Appendix, Table 1.

In this paper we explore patterns among the moss species ensembles of 13 neighboring locations, or stands, in the forest tract of the Edmund Niles Huyck Preserve, Rensselaerville (just South of Albany), New York. We also examine the tree species ensembles for 11 of the same stands using data collected by Russell (1955) close to the time the moss samples were taken (1956). The sampling of mosses and subsequent taxonomic determinations were done by B. B. Coleman.

A new method of analysis using the Jaccard index of similarity (Jaccard, 1902, 1912; Southwood, 1968; Orloci, 1973; Williamson, 1978) and the Wilcoxon T statistic (Wilcoxon, 1945; Siegel, 1956) was developed to produce an ordination of the moss or tree species ensembles of the Huyck Preserve. This procedure was devised by C. A. Istock. A single computer program, written in BASIC, was used to carry out these calculations, with a species by stand matrix of incidence data as input (Appendix, Table 1 for the mosses, and Table 1 for the trees). While the method is essentially a multivariate technique, it reduces to two kinds of two-dimensional plot which are readily interpretable in relation to the species richness and the species sharing patterns (patterns of similarity) of the ensembles singly and collectively. When the method is explained more carefully below it will be seen that its rationale involves recognition of the joint influences of species diversity and random versus non-random assembly of species into ensembles. Hence, unlike multivariate ordination procedures such as PCA, we know beforehand the conceptual content of each calculation and its numerical result. This type of ordination not only clusters or lines up the locations, it does so against a palpable backdrop involving the commonality and richness of species ensembles.

The Study Area and Previous Studies There

The Huyck Preserve includes 1200 acres in the watershed of Ten Mile Creek, a tributary of Catskill Creek which flows to the Hudson River. One dam in Ten Mile Creek created Lincoln Pond, another dam downstream created Lake Myosotis. These two water bodies along with Pond Creek create wetter habitats with pondside and streamside vegetation (Figure 1). The Preserve lies on the Helderberg Plateau with elevations ranging from 425-525 m. The vegetation has been largely undisturbed since 1931 when the Preserve was established. Prior to this time the tract had a complex history of cutting, plowing and planting.

Odum (1943) recognized 26 distinct forest communities on the Preserve based on his study of tree species composition. He outlined a complicated pattern of successional trajectories and concluded that these forests belonged to the Hemlock-White Pine-Northern Hardwoods Region (Nichols, 1935; Braun, 1950). With the exception of red and white spruce and red and jack pine, the other tree species expected for this forest region were found.

Russell (1955) took exception with Odum's view of successional change on the Preserve. He recognized only 11 forest types (Table 1). He asserted that "in spite of closely similar land use histories, physiographic situations, and local climates, each of eleven forests is seen to be distinct from the others. In the absence of long range studies of plant succession, it is concluded that ... arrangement of the 11 forests into any sort of successional scheme is presently inadvisable."

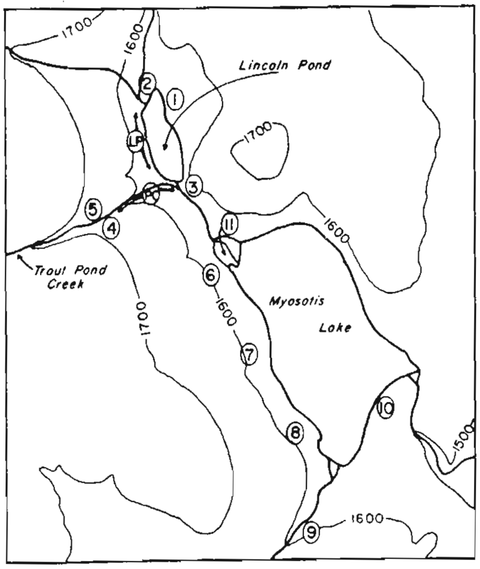

Figure 1. Geographical positions of the sampling locations (= forest stands) within the Huyck Preserve. North is exactly to the top of the map. The elevations are shown in feet.

Table 1. Russell's (1955, his table 12) listing of species in 11 stands of the Huyck Preserve Forest. An * means the species was present.

	Stand no.										
Species	1	2	3	4	5	6	7	8	9	10	11
Tsuga canadensis	*	*		*		*	*	*	*	*	
Acer saccharum			*	*	*	*	*	*	*	*	*
Fagus grandifolia	*	*	*	*	*	*	*	*	*	*	
Fraxinus americana			*	*	*	*	*	*	*	*	*
Quercus rubra			*			*	*	*		*	
Tilia americana			*	*	*	*	*	*		*	*
Ostrya virginiana			*	*	*	*	*	*		*	*
Ulmus americana					*		*				*
Betula lutea	*			*		*	*	*			
Pinus strobis									*		
Acer pensylvanicum				*	*				*	*	
Juglans cinerea								*			*
Acer rubrum										*	
Betula papyrifera				*					*	*	
Carpinus caroliniana									*		*
Prunus serotina	*										*
Populus grandidentata				*					*		
Prunus virginiana											*
Carya ovata						*					
Salix sp.							*				

Russell returned to the Preserve in 1964 and studied his original 11 areas. His results are on file at the Preserve. In six of Russell's stands hemlock is one of the dominants, in 3 of them beech is one of the dominants and in 4 others sugar maple is one of the dominants. Judging from his results for 1964 it appears that the general successional trend could be toward the dominance of hemlock and several hardwoods, with white pine locally dominant in one area, and with other stands representing varied seral types. The validity of this conclusion is of interest to us, but not critical to our subsequent analyses and conclusions concerning the moss species groupings of the Preserve.

In this paper we use moss-species data from Russell's 11 stands, and add two wetter sites (PC and LP, figure 1) to encompass a wider representation of moss habitats. While our concern is principally with the structure of moss communities we will ask, quite tentatively, about the conformity of moss and tree community patterns and about the issue of succession raised by Odum and Russell.

Materials and Methods

Table 2 lists the number of m^2 quadrat samples taken along line transects within each of Russell's 11 stands plus the 2 wetter sites to create the moss species data set of Appendix, Table 1. The locations of the samples within the Huyck Preserve are shown on figure 1.

Table 2. General characteristics of the moss data set: number of samples and species per stand; sharing of species between stands.

Stand	No. of quadrats	Total no. of spp. ( )	No. of stands with which spp. were shared	Av. no. of spp. shared ± (Std. Dev.) for adjusted data
1	20	34	12	13.75 (4.01)
2	20	31	12	12.92 (3.63)
3	20	26	12	8.08 (1.44)
4	27*	38 (38)	12	13.83 (3.90)
5	40*	53 (40)	12	12.08 (2.61)
6	20	26	12	10.92 (2.84)
7	20	25	12	11.83 (3.24)
8	20	38	12	15.91 (3.09)
9	20	37	12	15.33 (4.36)
10	20	36	12	14.08 (4.01)
11	16	29	12	10.83 (2.29)
PC	46*	37 (28)	12	9.33 (2.57)
LP	75*	80 (48)	12	13.08 (3.65)

*Adjusted to 20 randomly selected quadrats for the "adjusted data set", to equalize sampling.
( ) No. of species remaining after adjustment of the sampling.

* * *

Mosses on a lake shore

Beginning at the east end of the dam and a meter from the shore of Lincoln Pond (LP), 75 m^2 quadrats were located around the pond to the west side of the dam at 10 m intervals. In each quadrat mosses were removed from soil, rock, dead wood, living tree bases (including exposed roots), and living trees.

Mosses of a stream gully

Beginning at the junction of Trout Pond Creek with Ten Mile Creek, 37 quadrats (PC samples) were set out upstream to the area where the stream flows through an open field on land outside of the preserve. Quadrats were located every 20 meters according to the following system. At the junction of the streams a quadrat fell on the right side of the tributary, approximately one meter from the middle of the stream bed. Twenty meters upstream a quadrat fell in midstream, the next quadrat fell on the left bank, and so on. The compass direction was west. Any tree nearest to either the right or left bank quadrats was sampled if there was no tree within the quadrat.

Mosses of Russell's 11 stands

Samples were taken in stands delineated by Russell as follows. In Stand 1 a north-south compass line was followed beginning at the Pond Hill Road and a 1 m^2 quadrat was sampled at every 10 meters. Compensation NE had to be made from time to time to avoid by 20 m the shore of Lincoln Pond which was sampled separately. When no trees were present in a quadrat, the nearest tree was sampled. All stands except 5 and 11 were sampled similarly. Stand 5 was sampled in 2 parts: for 5a 20 quadrats came from a drier spruce planting; for 5b 20 quadrats came from a more mesic hardwood forest on the north side of Trout Pond Creek, these samples were pooled for the analysis given here. The area of the Ten Mile Creek flood plain forest at Stand 11 was much smaller in area than the other stands and only 16 quadrats and trees were sampled.

All samples were pressed and dried. Standard manuals (Grout, 1928, 1933, 1936, 1965; Welch, 1958; and Darlington, 1963) were used to determine genera and species.

Adjustment of Sample Sizes

For purposes of analysis the number of quadrat samples per stand was adjusted back to 20 for the four stands where more than 20 were originally taken. This was done by selecting 20 samples at random from the original 27, 40, 46, and 75 samples for stands 4, 5a and b pooled, PC, and LP respectively. The resulting drop in species number for these four stands is shown in table 2 and the individual species which dropped out at a given stand are shown with an asterisk in Appendix, Table 1. Stand 11 had to be left with only 16 samples.

Principal Components Analyses

PCA calculations were performed by the BMDP factor analysis program P4M (Dixon and Brown, 1977) with ROTATE = NONE. The moss or tree data sets used as input were matrices of joint occurrences. The calculated correlation matrix was factored about the origin as recommended by Williamson (1978).

The Jaccard-Wilcoxon Analysis (JWA): Procedure and Rationale

Procedure

The data set required is a matrix of incidence (presence) data, i.e., a matrix of species by locations as in Appendix, Table 1 for mosses or table 1 for trees. The subsequent calculations are:

1. Compute the Jaccard indeces (S) of similarity for all possible comparisons between locations (= ensembles). The matrix of joint occurrences is also obtained as part of the calculations (numerators for the Jaccard indexes), and the average Jaccard values ($\overline{S}$) are also obtained for each location.
2. Calculate the Wilcoxon T statistic for all possible pairs of locations. Each pair of locations provides two columns of (n-2) paired Jaccard values, where n is the total number of locations. Also calculate the average of T, i.e., $\overline{T}$.

The Jaccard index is $S = c/(a+b-c)$ where c is the number of species in common between two locations, while a and b are the numbers of species for each of the locations separately. S is not likely to be symmetrically, or normally, distributed. Figure 2 shows the asymmetrical distribution of S for the moss ensembles. A half-matrix of S values is given above the diagonal in table 3. The full matrix is, of course, symmetrical. Statistical comparison of the S values for any two locations requires a nonparametric test, hence the choice of the Wilcoxon T.

It is important to recognize that the list of S values for any given location describes the <u>species sharing behavior</u> (species matching) of that location with respect to each of the other locations. When the lists for any two locations are compared for the remaining n-2 paired values of S we are exploring the degree to which the two locations have similar species sharing behavior. The nonparametric Wilcoxon T makes this comparison by forming the signed difference between each of the n-2 values and ranking the differences without regard for sign. The sign of each difference is then carried over with the rank and positive and negative ranks are summed separately. T is the smaller of these two sums. Tables giving the probability of a given T for a given sample size are available (Siegel, 1956; also see Siegel for procedure to break ties). Thus we have a direct test of whether any two locations differ significantly in S within the context of all the species and locations of the whole data set. Values of T for the moss data set are given below the diagonal in table 3 with asterisks to indicate significant departures from random species sharing behavior.

The distribution of T values for the moss data set is shown in figure 3. The maximum value T can assume with a sample size of 11 (= 13-2) is 33 (= 1/2 the sum of 1 to 11). T = 33 comes with equal division of the ranks 1 to 11 between positive and negative differences. When all the ranks are of one sign, T=0. The theoretical distribution of T is approximately normal (Siegel, 1956). Despite our small sample size, the non-normality of T in figure 3 is a first clue that there is pattern in the data. We have far too many low and high values, suggesting that both strong similarity and sharp dissimilarity exist among the ensembles.

The use of the Wilcoxon T here is more than a means of statistical inference, T serves also as a measure of distance between ensembles. In this sense we have a multivariate description, i.e., a mapping in a hyperspace where the ensembles label the axes and T is the mapping variable. Rough graphical realizations of this property of the method are employed later (figures 7, 8 and 9).

A two dimensional plot of the ensembles with $\bar{T}$ and $\bar{S}$ as axes yields an ordination which is readily interpreted using the ecological logic behind the method. Such a plot appears in figure 4 for the mosses and in figure 10 for the trees of the Huyck Preserve. An atypically high $\bar{S}$ combined with a low $\bar{T}$ exposes an unusually rich ensemble which contains the most complete subset of the more common species (location 8 is an example in both figures 4 and 10), an ensemble which has many of the rarer species and fewer of the common ones will have both low $\bar{S}$ and low $\bar{T}$, such as stand 3 in figure 4, or stand 11 in figure 10. A depauperate ensemble with common species will fall low in $\bar{S}$ but have a more typical value for $\bar{T}$, such as 1 and 2 in figure 10. Less and less deviant ensembles with typical values for both S and T will be toward the "center" of the plot nearer to $\bar{S}$, $\bar{T}$; shown as an * in the figures.

Each ensemble falling in or near the central cluster is akin to a set of random draws from the entire species list, where the species in the list have frequencies roughly equivalent to those reflected in column 3 (no. of samples) of Appendix, Table 1. Simple comparisons between any two central ensembles may occasionally be significant, a few examples can be found in tables 3 and 4. Much more frequently two ensembles which plot close together have a T approaching the maximum T indicating that they behave as similar subsets of the whole species set in their capacity to share (or match) species.

Williamson (1978) has pointed out the "horseshoe effect" which arises when zeros exist in the matrix of joint occurrences among locations and PCA is used as the method of ordination. With such zeros the resulting plot from PCA has a horseshoe shape which gives the mistaken impression that ensembles which share few or no species are more similar to each other than to ensembles with which they share more species. He developed a "step-across" method to estimate more accurately the distances between the ensembles not sharing species. His technique is very effective in a hypothetical case and moderately effective with a real and more complex data set.

Zero joint occurrences also cause a horseshoe-like result in applications

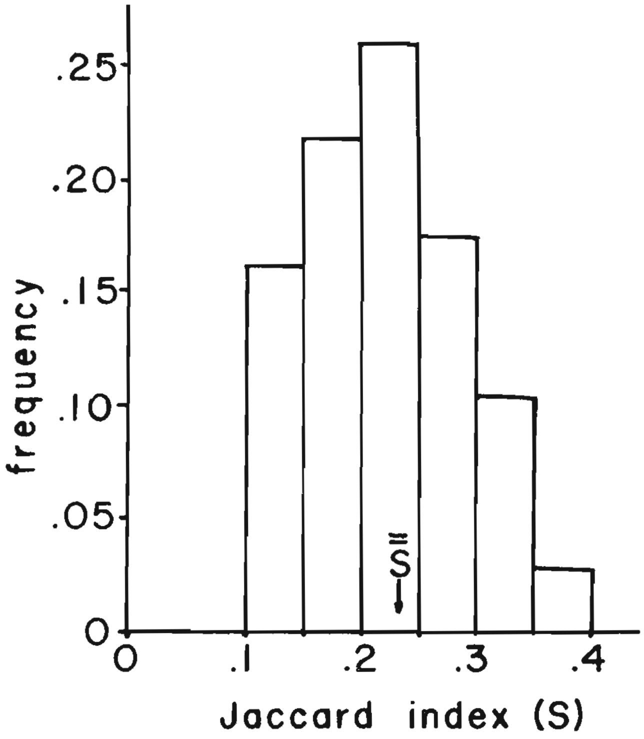

Figure 2. Frequency distribution for Jaccard indeces of similarity calculated from the adjusted moss data set and listed in table 3. $\bar{S}$ is the grand mean.

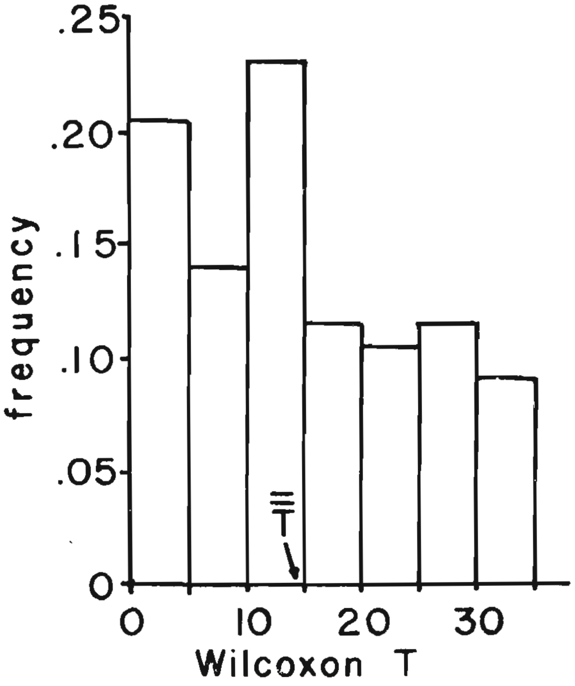

Figure 3. Frequency distribution for the comparisons between all pairs of moss ensembles. The T values appear in table 3. $\bar{\bar{T}}$ is the grand mean.

Figure 4. JWA ordination of the moss species ensembles using the $\bar{S}$, $\bar{T}$ plot and the adjusted data set. The asterisk indicates the grand means for S, T. See text for discussion of this graph.

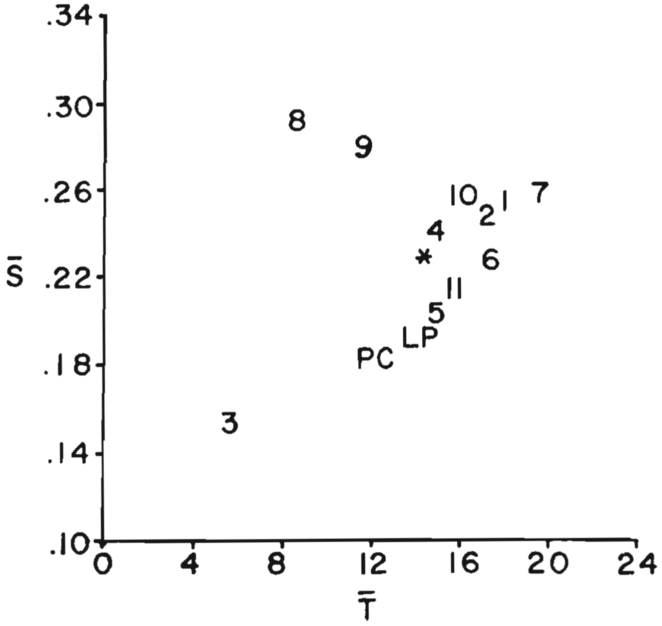

Table 3. Jaccard indices of similarity between stands for moss species (above diagonal), and associated values of T (below diagonal), using the adjusted data set. Grand means are in the lower right-hand corner.

	1	2	3	4	5	6	7	8	9	10	11	PC	LP	$\overline{S}$
1	-	.383	.154	.385	.233	.250	.255	.309	.291	.250	.189	.127	.281	.257
2	25	-	.140	.278	.164	.267	.333	.327	.283	.241	.224	.135	.254	.252
3	3**	3**	-	.143	.158	.156	.133	.208	.167	.127	.146	.173	.156	.155
4	25	20	1**	-	.238	.208	.212	.310	.339	.254	.175	.158	.229	.242
5	8*	11*	11*	14	-	.245	.203	.200	.283	.226	.150	.172	.128	.200
6	26	22	5**	27	27	-	.378	.333	.212	.216	.196	.125	.138	.227
7	28	30	4**	33	17	14	-	.340	.292	.356	.286	.152	.141	.257
8	14	12	0**	5*	0**	4**	19	-	.415	.345	.264	.222	.229	.292
9	24	26	0**	9*	4**	9*	22	19	-	.431	.222	.182	.250	.281
10	30	26	0**	19	11	18	31	13	18	-	.226	.185	.235	.258
11	15	12	4**	19	32	20	14	10*	2**	5**	-	.357	.132	.214
PC	11*	13	20	3**	21	8*	11*	5**	7*	11*	12	-	.169	.180
LP	6*	8*	17	4*	22	31	13	0**	0**	12	33	25	-	.195
$\overline{T}$	17.9	17.3	5.7	14.9	14.8	17.6	19.7	8.4	11.7	16.2	14.8	12.3	14.3	.231
														14.3

*T $\leq$ 11, $p \leq .05$

**T $\leq$ 5, $p \leq .01$

Table 4. Jaccard indices of similarity between stands for tree species (above diagonal), and associated values of T (below diagonal). Grand means are in the lower right-hand corner.

	1	2	3	4	5	6	7	8	9	10	11	$\overline{S}$
1	-	.500	.111	.272	.100	.300	.272	.300	.182	.182	.083	.230
2	13	-	.143	.200	.125	.222	.200	.222	.222	.222	0	.206
3	7	6*	-	.455	.625	.667	.600	.667	.250	.500	.364	.438
4	6*	1**	17	-	.545	.583	.538	.583	.583	.583	.267	.461
5	2**	8	21	10	-	.455	.545	.455	.333	.455	.455	.409
6	4*	3*	5*	20	12	-	.727	.800	.286	.500	.286	.483
7	6*	3*	13	9	19	17	-	.727	.267	.462	.357	.470
8	3*	3*	2**	18	11	0**	9	-	.286	.500	.385	.492
9	16	2**	8	1**	13	0**	8	0**	-	.500	.200	.311
10	6*	7	17	4*	22	5*	13	5*	0**	-	.200	.410
11	13	13	0**	0**	0**	0**	0**	0**	16	0**	-	.260
$\overline{T}$	7.6	5.9	9.6	8.6	11.8	6.6	9.7	5.1	6.4	7.9	4.2	.379
												7.58

*$T \leq 6$, $p \leq .05$

**$T \leq 2$, $p \leq .01$

of the JWA, but with the horseshoe turned on its side in the $\bar{S}$, $\bar{T}$ plot. The horseshoe effect is most marked when many zeros occur. The moss data set used here contains no zero joint occurrences and the tree data set contains only 1 case where no species are shared between a pair of ensembles. While the horseshoe effect appears not to be a problem with our data sets, it will be necessary to incorporate Williamson's step-across technique or some other correction when many zero joint occurrences are encountered. Ordination across gradients of community change in space or the fossil record will often encounter this problem.

The above weakness of the JWA emphasizes that the primary purpose of the method is to explore patterns of community relatedness when the issue is confused by a complicated sharing of species, not to explore pattern or relatedness in communities strung out over some clear gradient of species replacement.

Results and Conclusions

Moss communities

All 13 stands sampled in the Huyck Forest shared moss species with the other 12 stands. Between 6 and 22 species were shared over all pairwise comparisons with a total of 137 species appearing in the entire adjusted data set (147 species in the unadjusted set). The average number of species shared by each stand ranged from 8.08 for stand 3 to 15.91 for stand 8 (Table 2).

Most species were rare. No species occurred in every stand. Eight species were nearly ubiquitous, occurring in 10, 11, or 12 of the stands: *B. salebrosum*, *D. viride*, *H. adnatum*, *M. cuspidatum*, *P. denticulatum*, *P. repens*, *R. serrulatum*, and *T. delicatulum* (generic names given in Appendix, Table 1). Only a few species such as *B. recurvans*, *D. montanum*, *H. haldanianum*, and *P. nutans* were moderately common and locally dominant. Very few species such as *C. cordifolium* and *P. wahlenbergii* were rare generally, but locally abundant.

The moss species ensembles were definitely interconnected by species sharing, but in a loosely knit fashion which defies easy interpretation by inspection alone. Dominance of the 13 species ensembles, either individually or collectively, by a few species is strikingly absent. Heterogeneity is much more apparent.

The Jaccard-Wilcoxon Analysis (JWA) applied to the adjusted data set produced the $\bar{S}$, $\bar{T}$ plot of figure 4. Stand 8 is statistically distinct from stands 3, 4, 5, 6, 11, PC and LP in its species sharing behavior. Stand 8 shows moderate affinity with stands 7 and 9 ($T = 19$, table 3), though 9 plots closer to 8. Stand 8 holds its special position in figure 4 because it has the best subset of the commonly shared species, hence stand 8 has a run of higher than typical S values. Stand 8 does not have particularly many species, six other stands have about the same or more species. At the time the data were taken stand 8 was a young, open, drier forest dominated by oak (*Quercus rubra*), but with sugar maple (*Acer saccharum*) increasing as oak declined (Russell 1955, and unpublished notes of 1964).

Figure 4 identifies stand 3 as the converse of stand 8, low species matching with other stands, but not a particularly low total number of species. By not possessing commonly shared species stand 3 acquires distinctiveness and a string of low S values. Stand 3 is statistically distinct from all other stands in its species matching, except for PC and LP (table 3). This affinity with the two wetter sites is surprising because stand 3 lies on a steep southwest facing slope, is well drained, and at the time of sampling was dominated by red oak with sugar maple increasing and white ash (*Fraxinus americana*) and beech (*Fagus grandifolia*) beginning to establish themselves at the site (Russell, 1955, and his notes of 1964). The geographical proximity of 3, LP, and PC may play a role.

The rest of the species ensembles trace out a fairly simple pattern in figure 4. The absence of tight bunching of the stands is a graphical rendering of the looseness with which the mosses are organized into communities. There is no clear subclustering, something one would expect if there were recurrent groups of species in the sense of Fager (1957).

The JWA may not be too sensitive to unequal sampling. Figure 5 shows an $\bar{S}$, $\bar{T}$ plot for the unadjusted data set. The more intense sampling of stands PC, LP, and S understandably pulled them farther into the central cluster, apparently also causing stand 11 to be pushed outward.

The clearest JWA ordination of the moss communities results when LP and PC are dropped as in figure 6. This plot was created for comparison with the ordination of tree communities, but it also shows the effect of eliminating the wetter sites and makes the relation of stand 11 to stands 3 and 5 clearer. Stand 11 is unusual. It lies on the flood plain of Lake Myosotis and its forests were dominated by white ash and American elm (*Ulmus americana*) (Russell, 1955).

The configuration inside the hypervolume of a JWA ordination can be glimpsed by using any two stands as axes and plotting all stands according to the T values found for comparison with the stands labeling the axes. A stand is assumed to have $T = 33$, the maximum T, with itself. Figures 7, 8, and 9 are useful examples of such graphs. With them we can explore interstand affinities in more detail than was possible with the $\bar{S}$, $\bar{T}$ plot. Figure 7 uses the extreme stands 3 and 8 as axes, the figure also includes dashed lines at $T = 11$ indicating a statistical difference from the appropriate reference stand, at $p \leq 0.05$, for any stand falling inside the line. From figure 7 the affinity of stands 8, 9, and 7 and of stands 3, PC, LP and 5 is clear. Stands 4, 6 and 11 are significantly different from both reference stands. When stands 6 and 4 are used as reference axes the plot in figure 8 results. Now the more extreme species matching tendencies of stands 3 and PC, and of stands 8 and 9 appear as significantly different from the reference stands, the affinities of LP and 5 with 3 and PC appear less strong. In figure 9 the reference stands are 9 and PC and rather familiar clusterings reappear 9, 8, 7, 1 and 2 as opposed to PC, 5, LP, and 3, while stands 4 and 6 fall into the square of significance and the affinity of stand 11 with the 3-PC cluster appears clarified.

A graph such as figures 7, 8, or 9 is a sort of selective ordination and is particularly valuable in exploring the strength of affinities and clusterings that are difficult to read from the numerical values of table 3 or from the $\bar{S}$, $\bar{T}$ plot.

The JWA has exposed two different tendencies in the moss communities of the Huyck Preserve. The moss species groups of stands 8, 9, 10, 1 and 2 are generally richer in common species, they have greater species matching capacity both with themselves and with the remaining stands. The species ensembles at stands 3, PC, LP, 5 and 11, while not particularly depauperate, tend toward greater uniqueness in species composition and hence possess less species matching capacity. Stands 6 and 4 are intermediate.

The way the JWA ordination of the stands fits the arrangement of the stands on the landscape of the Preserve (figure 1) is not likely to be coincidence.

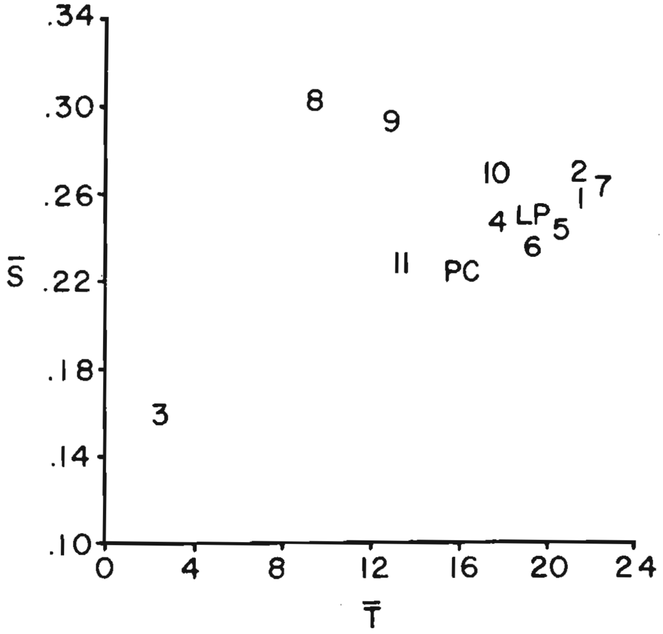

Figure 5. JWA ordination of the moss species ensembles using the $\bar{S}$, $\bar{T}$ plot and the unadjusted data set.

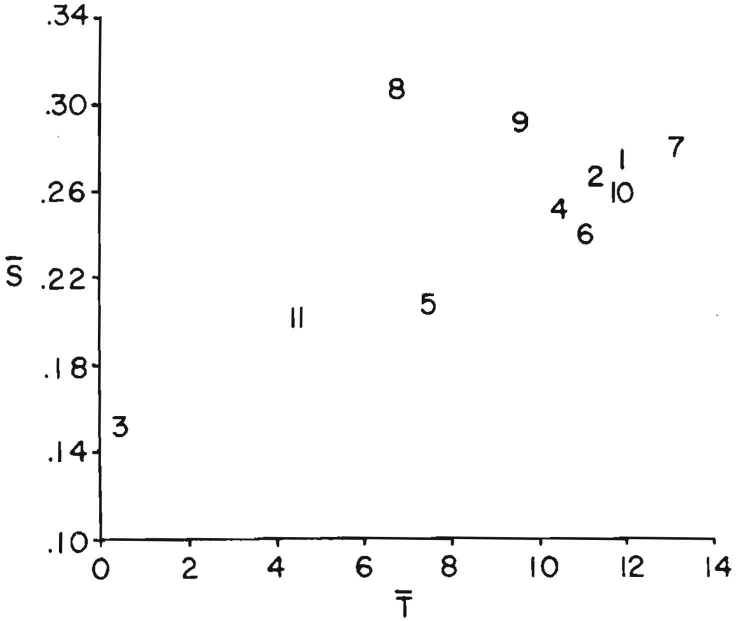

Figure 6. JWA ordination of the moss species ensembles with only stands 1-11 included (PC and LP dropped); for comparison with JWA ordination of tree species ensembles in figure 10.

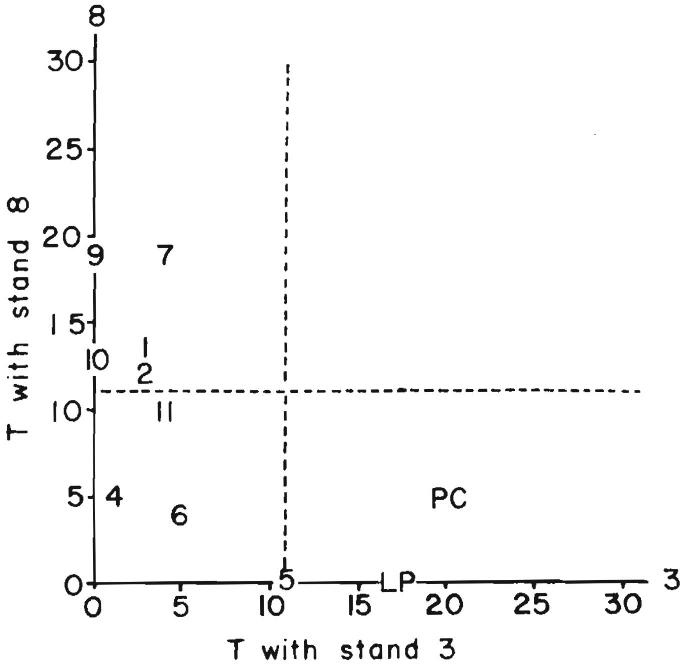

Figure 7. Affinities among the moss species ensembles indicated by the values of T for each stand compared to reference stands 8 and 3. See text for interpretation and discussion of this plot.

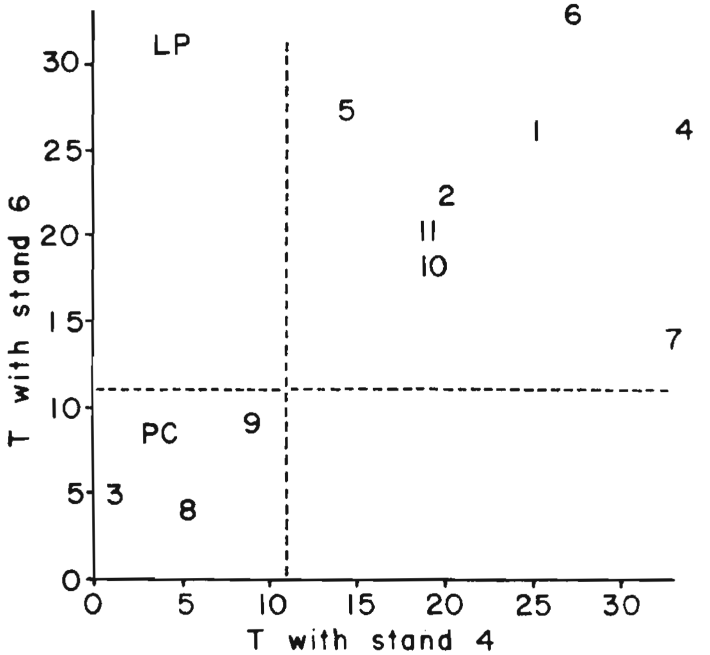

Figure 8. Affinities among the moss species ensembles with stands 6 and 4 used as reference stands. See discussion of this figure in text.

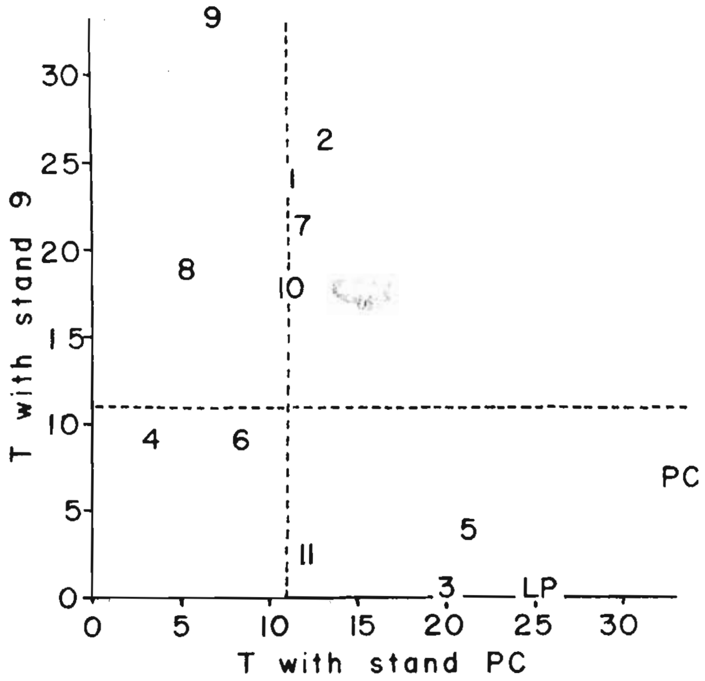

Figure 9. Affinities among the moss species ensembles with stands 9 and PC serving as reference stands. See discussion of this figure in the text.

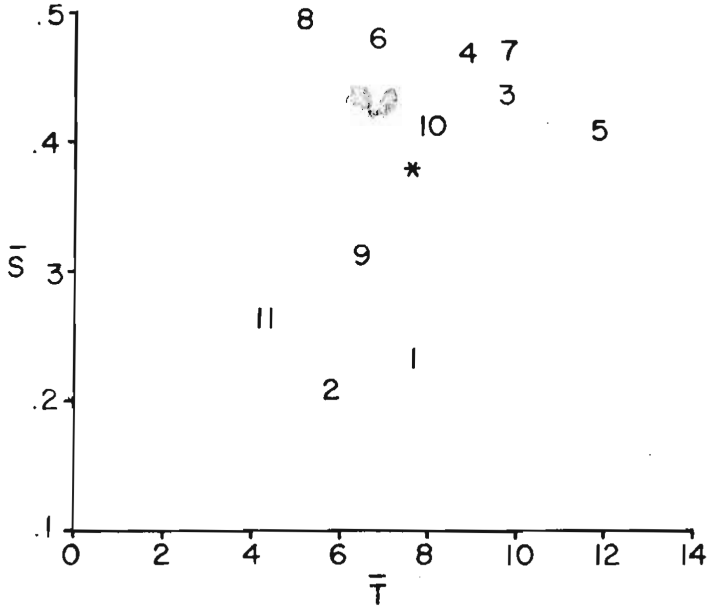

Figure 10. JWA ordination of the eleven tree species ensembles (table 1) using the $\bar{S}$, $\bar{T}$ plot. Compare this pattern with that of figure 6, further discussion in the text.

Ensembles which clustered together tend to be geographically close. Even the two outlying stands, 1 and 2 (see figure 1), appear to tie in through stands 6 and 4 (figure 8). Species contagion and microenvironmental similarity among neighboring stands may account for some of the observed congruence between the ordination pattern and the microgeography of the stands.

Results from two PCA ordinations of the moss ensembles are given in Appendix, Table 2. More than 85% of the variance is explained by factor 1 in both cases, this lines up the stands well along factor 1. The PCA ordination agrees well with the JWA ordination on several counts. The placing of stands 8, 9, and 10 at one extreme and stands 3, PC and 11 at the other extreme are clear points of agreement. The positions of stands 6 and 7 however are in sharp disagreement. When PC and LP are dropped from the PCA, case (2) of Appendix, Table 2, the only change from case (1) involves the positions of 6 and 11. The reason for dropping PC and LP was to create a PCA ordination comparable in its 11 stands to the ordination of tree data by PCA, case (3), to be discussed later. Apparently PCA and JWA similarly resolve the more extreme species ensembles but respond differently to the central cluster of more typical ensembles.

Tree communities

Figure 10 and table 4 present the JWA for Russell's tree data (Russell, 1955; and our table 1). The plot in figure 10 shows some agreement with the figures 4, 5 and 6 for the mosses. Stand 8 has its usual extreme position and its relation to stands 6, 7, 4 and 10 is vaguely reminiscent of the moss ordination. Stand 3 is however in a very different position, now appearing as a typical ensemble, while stands 11 and 2 tend toward uniqueness. Stand 9 is also in a very different position as are stands 1 and 5. In short, there is relatively little congruence between the JWA ordinations for mosses and trees beyond the role of stand 8.

The same lack of congruence is shown by PCA ordination. Cases 2 and 3 of Appendix Table 2 show this poor agreement. The PCA ordination of tree species ensembles does not even pull out stand 8 to head the list.

The broad scatter of stands in figure 10, and the many significant differences among pairs of stands in table 4 argue that the tree species ensembles of the Huyck Preserve are extremely heterogeneous and, as Russell asserted, attempts to draw conclusions about successional trajectories are almost certainly premature.

Discussion

The disturbance of the vegetation of the Huyck Preserve prior to 1930 has probably had a less lasting or telling effect on the moss communities of the Preserve, than it has had on the tree communities. The much greater number of moss species also probably confers greater "resolving power" on this stratum of the vegetation when an ordination is performed.

The JWA produced a relatively clear ordination for the mosses. It identified a group of geographically contiguous communities (3, PC, LP, 11, and possibly 5) which are slightly less species-rich, and perhaps typical of lower and wetter parts of the terrain (but not 3 or 5). These same communities tend more toward uniqueness in their species composition relative to the "typical" species ensembles of higher elevations. The species group at stand 3 is particularly extreme, being statistically distinct from all other stands except

LP and PC (table 3). The moss ensemble of the young, open forest at stand 8 ran up the next most sizeable string of statistical differences, but did so principally because of its frequent high similarity to other stands. The moss ensembles at stands 10, 9, 7, 1, and 2 are all closely allied with stand 8, in fact stand 8 is not statistically different from any of these, while it is statistically different from 3, PC, LP, 11, 5, 4, and 6 (table 3). Stand 8 and all of its allied stands are on well-drained uplands or slopes. The moss ensembles of stands 6 and 4 serve as a bridge between the stand 8 group and the stand 3 group. These rather clear results from the JWA ordination would not have been possible without the statistical inference conferred by use of the Wilcoxon T, and the opportunity to visually rotate the hyperspace of the ordination as in figures 7, 8, and 9. These two features of the method allow considerable and detailed secondary exploration of the JWA ordination. PCA ordination did not give enough information to support, refute, or even allow such deductions.

With Russell's caveat (quoted earlier) in mind, we tentatively conclude that the moss species ensembles sort out into at least two major and different moss vegetation types and that these are likely to be long maintained. Whether they presage similar trends for the tree communities remains to be seen. The intermediate stands 6 and 4 may move toward one of the two clusters of moss communities or may remain as transition communities. Within either the stand 8 or stand 3 camp, the moss species ensembles appear to be much like random subsets of the entire species pool.

Acknowledgments

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Literature Cited

Andersen, A. J. B., 1971. Ordination methods in ecology. J. Ecol. 59:713-726.

Botkin, D. B., J. F. Janak, and J. Wallis, 1972. Some ecological consequences of a competition model of forest growth. J. Ecol. 60:849-872.

Braun, E. L., 1950. Deciduous Forests of Eastern North America. Hafner, New York.

Bray, J. R. and J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 22:217-234.

Cairns, J. and R. L. Kaesler, 1969. Cluster analysis of Potomac River survey stations based on protozoan presence-absence data. Hydrobiologia 34:414-432.

Cole, L. C., 1949. The measurement of interspecific association. Ecology 30: 411-424.

Curtis, J. T., 1959. The Vegetation of Wisconsin: An Ordination of Plant Communities. Univ. of Wisconsin Press, Madison. 657 pp.

Dahl, E., 1960. Some measures of uniformity in vegetation analysis. Ecology 41:805-808.

Darlington, H. T., 1964. The Mosses of Michigan. Cranbrook Institute Science Bull. No. 47.

Dice, L. R., 1945. Measures of the amount of ecologic association between species. Ecology 26:297-302.

Dixon, W. J. and M. B. Brown (eds.), 1977. BMDP-77: Biomedical Computer Programs P-Series. Univ. of California Press, Berkeley. 880 pp.

Fager, E. W., 1957. Determination and analysis of recurrent groups. Ecology 38:586-595.

Goodall, D. W., 1970. Statistical Plant Ecology. In: Ann. Rev. Ecol. System, Vol. I. Johnston, R. F., Frank, P. W., and C. D. Michener, eds. Annual Reviews Inc. pp. 99-124.

Grout, A. J., 1928. The Moss Flora of North America. Vol. III. Published by Author.

Grout, A. J., 1933. The Moss Flora of North America. Vol. II. Published by Author.

Grout, A. J., 1936. The Moss Flora of North America. Vol. I. Chronica Botanic Co., Waltham, Mass.

Grout, A. J., 1965. Mosses with Handlens and Microscope. Eric Lundberg, Ashton, Md.

Hairston, N. G., 1964. Studies on the organization of animal communities. J. Anim. Ecol. 33 (Suppl.):227-239.

Jaccard, P., 1902. Gesetze der Pflanzenverteilung der Alpinen Region. Flora 1902:349-377.

Jaccard, P., 1912. The distribution of flora in the alpine zone. New Phytol. 11:37-50.

Lambert, J. M., and M. B. Dale, 1964. The use of statistics in phytosociology. Advances Ecol. Res. 2:59-99.

Langford, A. N. and M. F. Buell, 1969. Integration, identity, and stability in the plant association. Adv. Ecol. Res. 6:83-135.

MacArthur, R. H., 1965. Patterns of species diversity. Biol. Rev. 40:510-533.

Morisita, M., 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. of Science, Kyushu Univ., Series E (Biology) 3:65-80.

Nichols, G. E., 1935. The hemlock-white pine-northern hardwood region of eastern North America. Ecology 16:403-422.

Odum, E. P., 1943. The vegetation of the Edmund Niles Huyck Preserve, New York. Am. Midl. Nat. 29:72-88.

Orloci, L., 1973. Ordination of resemblance matrices. In, Ordination and Classification of Communities, R. H. Whittaker, ed. pp. 249-286.

Preston, F. W., 1948. The commonness and rarity of species. Ecology 41:611-627.

Preston, F. W., 1962. The canonical distribution of commonness and rarity. Ecology 43:185-215, 410-432.

Roback, S. S., J. Cairns, and R. L. Kaesler, 1969. Cluster analysis of occurrence and distribution of insect species in a portion of the Potomac River. Hydrobiologia 34:484-502.

Russell, N. H., 1955. Natural forests of the Edmund Niles Huyck Preserve, New York. Proc. Iowa Acad. Sci. 62:231-244.

Siegel, S., 1956. Nonparametric statistics for the Behavioral Sciences. McGraw Hill Book Co.

Southwood, T. R. E., 1968. Ecological Methods. Chapman and Hall, London. 391 pp.

Welch, W. H., 1958. Mosses of Indiana. Bookwalter Co., Indianapolis.

Whittaker, R. H. (ed.), 1973. Ordination and Classification of Communities. Dr. W. Junk Publishers, The Hague. 737 pp.

Wilcoxon, F., 1945. Individual comparisons by ranking methods. Biomet. Bull. 1:80-83.

Williams, C. B., 1964. Patterns in the Balance of Nature and Related Problems of Quantitative Ecology. Academic Press, New York.

Williams, W. T. and J. M. Lambert, 1959. Multivariate methods in plant ecology. I. Association-analysis in plant communities. J. Ecol. 47:83-101.
Williams, W. T., and J. M. Lambert, 1966. Multivariate methods in plant ecology. V. Similarity analyses and information analysis. J. Ecol. 54:427-446.
Williams, W. T., G. N. Lance, L. J. Webb, J. G. Tracey, and M. B. Dale, 1969. Studies in the numerical analysis of complex rainforest communities. III. The analysis of successional data. J. Ecol. 57:515-536.
Williamson, M. H., 1978. The ordination of incidence data. J. Ecol. 66:911-920.

	Moss Species	General Occurrence No. Stands	No. Samples	No. of samples for each stand containing the species Stand No. 1	2	3	4	5	6	7	8	9	10	11	PC	LP
22.	Brachythecium starkei	1	1													1
23.	Brachythecium velutinum	3	3		1			1				1				
24.	Brotherella recurvans	5	30	11	4		6					3				6
25.	Brotherella tenuirostris	1	4											4		
26.	Bryum capillare	2	3		1											2*
27.	Bryum pseudotriquetrum	1	3													3*
28.	Bryhnia graminicolor	3	4										1		1*	2
29.	Bryhnia novae-angliae	6	9	1	1		2		1		1					3*
30.	Calliergon cordifolium	3	12		1									1		10
31.	Calliergonella cuspidata	1	2												2	
32.	Campylium chrysophyllum	6	16	4			6	1			2	1				2*
33.	Campylium hispidulum	3	3		1			1				1				
34.	Campylium polygamum	3	3										1		1*	1
35.	Ceratodon purpureus	1	6					6								
36.	Climacium americanum	1	7													7
37.	Ctenidium molluscum	2	2						1		1					
38.	Dicranella heteromalla	9	22	2	1	2	2	3			2	3	1			6
39.	Dicranella refescens	3	4					1				2	1			
40.	Dicranella schreberiana	1	1			1										
41.	Dicranella varia	2	2			1		1								
42.	Dicranum flagellare	3	3		1					1						1
43.	Dicranum fuscescens	2	2									1				1

	Moss Species	General Occurrence		No. of samples for each stand containing the species												
		No. Stands	No. Samples	Stand No.												
				1	2	3	4	5	6	7	8	9	10	11	PC	LP
44.	Dicranum montanum	7	32	4	12	1	3				1	1				10
45.	Dicranum sabuletorum	1	1													1*
46.	Dicranum scoparium	5	12	1				1*				2	2			6
47.	Dicranum undulatum	1	2					2								
48.	Dicranum viride	10	27	1	3		5	1	4	5	4	1	1			2
49.	Discelium nudum	1	1					1								
50.	Ditrichum pallidum	2	6	3												3
51.	Ditrichum pusillum	2	4					3								1
52.	Drepanocladus aduncus	1	2													2
53.	Drepanocladus fluitans	1	1					1								
54.	Drepanocladus sendtneri	1	1													1*
55.	Ephemerum crassinervium	3	5					1	1	3						
56.	Eurhynchium hians	6	7	2		1		1	1						1*	1
57.	Eurhynchium pulchellum	5	12							2			1	2	2	5*
58.	Fissidens adiantoides	1	1				1									
59.	Fissidens bushii	3	4											1	2	1
60.	Fissidens bryoides	2	2					1*	1							
61.	Fissidens cristatus	1	1	1												
62.	Fissidens minutulus	4	4								1			1	1*	1
63.	Fissidens osmundioides	1	1	1												
64.	Fontinalis novae-angliae	1	1													1
65.	Gymnostomum	1	1											1		

	Moss Species	General Occurrence No. Stands	General Occurrence No. Samples	No. of samples for each stand containing the species Stand No. 1	2	3	4	5	6	7	8	9	10	11	PC	LP
66.	Haplocladium virginianum	1	7					7								
67.	Hedwigia ciliata	1	2													2*
68.	Helodium paludosum	1	1													1*
69.	Helodium blandowii var. helodioides	1	1													1
70.	Heterophyllium haldanianum	6	26	7	5		2				1				1	10
71.	Homomallium adnatum	11	22	2	2	2		1	4	2	3		1	1	2	2
72.	Hygroamblystegium fluviatile	2	5												3	2
73.	Hygroamblystegium fluviatile var. orthocladon	2	5											3	2	
74.	Hygroamblystegium tenax	3	4								1				1	2*
75.	Hypnum cupressiforme	7	11		2			1*	2		1	1	1			3*
76.	Hypnum curvifolium	2	6	1												5
77.	Hypnum imponens	7	17	2	4			1		3		5	1			1*
78.	Hypnum lindbergii	2	2									1				1
79.	Hypnum pallescens	9	43	5	7			1	4	6	8	5	3			4
80.	Hypnum pratense	1	2													2
81.	Isopterygium micans	1	2													2*
82.	Isopterygium muellerianum	3	3				1								1	1
83.	Isopterygium striatellum	3	3				1	1				1				
84.	Leptodictyum brevipes	3	3			1									1	1*
85.	Leptodictyum laxirete	2	3											1	2	

	Moss Species	General Occurrence No. Stands	No. Samples	No. of samples for each stand containing the species												
				Stand No.												
				1	2	3	4	5	6	7	8	9	10	11	PC	LP
86.	Leptodictyum riparium	6	14			1			1		1	1			4	6
87.	Leptodictyum sipho	1	1											1		
88.	Leptodictyum trichopodium	6	12					2*				1	1	1	3	4*
89.	Leptodictyum trichopodium var. kochii	1	1					1								
90.	Leptodictyum vacillans	1	1													1*
91.	Leptobryum pyriforme	2	4									3	1			
92.	Leskea gracilescens	1	1										1			
93.	Leskea polycarpa	2	2					1*					1			
94.	Leskeella nervosa	5	6		1			1*	2	1						1*
95.	Leucobryum glaucum	6	21	1			6			2		2	5			5*
96.	Mnium affine	8	10				3	1		1	1	1	1	1	1	
97.	Mnium cuspidatum	11	29		1	1	4		4	1	1	2	2	2	2*	9
98.	Mnium hymenophylloides	2	2									1				1
99.	Mnium lycopodioides	1	2												2	
100.	Mnium marginatum	6	14				2			1		6	2	1		2*
101.	Mnium medium	2	2								1					1*
102.	Mnium punctatum	5	15	2	1									2	4	6*
103.	Mnium rostratum	2	2		1											1
104.	Mnium spinulosum	3	4	2	1		1									
105.	Mnium stellare	1	1				1									
106.	Nanomitrium megalosporum	1	1								1					
107.	Oncophorus wahlenbergii	1	1	1												

	Moss Species	General Occurrence No. Stands	No. Samples	No. of samples for each stand containing the species Stand No. 1	2	3	4	5	6	7	8	9	10	11	PC	LP
108.	Orthotrichum obtusifolium	2	2			1								1		
109.	Orthotrichum pumilum	2	3								1			2		
110.	Orthotrichum sordidum	1	1								1					
111.	Orthotrichum stellatum	1	1			1										
112.	Orthotrichum strangulatum	1	3												3	
113.	Physcomitrella patens	1	1													1
114.	Plagiothecium denticulatum	11	56	3	5		12	2*		3	1	7	3	1	1	18
115.	Plagiothecium latebricola	1	1													1
116.	Plagiothecium roseanum	3	5				1								1*	3
117.	Plagiothecium sylvaticum	9	22		2		5	1*			1	5	1	1	2	4*
118.	Platydictya confervoides	2	3			2									1	
119.	Platydictya jungermannoides	1	1										1			
120.	Platydictya jungermannoides var. minutissimum	1	1			1										
121.	Platygyrium repens	10	59	3	7		6	3	7	8	11		7	4		3*
122.	Pleuridium subulatum	1	1					1*								
123.	Pleurozium schreberi	4	6				1	3					1		1	
124.	Pohlia nutans	5	17	1	1			3*					1			11
125.	Pohlia wahlenbergii	2	12										1			11
126.	Polytrichum commune	2	6					3								3*
127.	Polytrichum formosum	1	1	1												
128.	Polytrichum juniperinum	3	4				1	2					1			

	Moss Species	General Occurrence		No. of samples for each stand containing the species												
		No. Stands	No. Samples	Stand No. 1	2	3	4	5	6	7	8	9	10	11	PC	LP
129.	Polytrichum ohioense	1	1			1										
130.	Polytrichum piliferum	1	1					1								
131.	Pottia truncata	1	1													1
132.	Ptilium crista-castrensis	1	1					1								
133.	Pylaisiella intricata	4	8							4	2	1	1			
134.	Pylaisiella polyantha	2	2						1	1						
135.	Pylaisiella selwynii	5	8			1			3	1	1		2			
136.	Rauiella scita	1	1		1											
137.	Rhodobryum roseum	1	1													1*
138.	Rhynchostegium serrulatum	12	39	3	4	3	4	1	1		2	1	1	3	4	12
139.	Rhytidiadelphus triquetrus	2	2				1	1								
140.	Sematophyllum adnatum	4	11						1		4	2	4			
141.	Sematophyllum marylandicum	1	1			1										
142.	Tetraphis pellucida	6	19	1			2				2	2	2			10
143.	Thuidium delicatulum	10	21	3			5	2	1	1	1	2	1	1		4*
144.	Thuidium recognitum	5	12	1		1	4	5								
145.	Tortella tortuosa	1	1				1									
146.	Trichostomum tenuirostre	1	1			1										
147.	Ulota crispa	6	9		3	1		1*	1	1				2		

* Species record dropped by equalization of sampling effort (see text).

Appendix table 2. Principal components analysis ordination for moss and tree species assemblages. (1) is the ordination for all 13 stands using the adjusted data set. (2) is the same as (1) except PC and LP were dropped in order to compare only the same 11 stands for both trees and mosses. (3) is the ordination of the trees. All lists arranged in order of decreasing factor score.

	(1) Mosses	(2) Mosses		(3) Trees	
Stand	Factor 1 Score	Factor 1 Score	Stand	Stand	Factor 1 Score
8	1.232	1.215	8	4	1.254
9	1.177	1.163	9	7	1.254
10	1.096	1.078	10	8	1.219
4	1.085	1.072	4	6	1.200
1	1.065	1.056	1	10	1.102
LP	1.065	0.997	2	9	0.951
2	1.004	0.943	5	5	0.937
5	0.951	0.939	7	3	0.896
7	0.924	0.893	6	11	0.787
11	0.891	0.847	11	1	0.572
6	0.877	0.682	3	2	0.416
PC	0.789				
3	0.706				
% =	85	87		92	

% is the % of the variance explained by factor 1.