
FREQUENCY CALCULATIONS FROM SEVERAL DIFFERENT FOREST ECOLOGICAL SAMPLING METHODS¹

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In forest ecology, the concept of the phytosociological relationship species frequency is associated most commonly with the quadrat and has been defined essentially as the number of quadrats containing the species divided by the total number of quadrats (Curtis and McIntosh, 1950). Greig-Smith (1957) defines the frequency of a species, determined by a particular size sample, as the chance of finding the species within any one trial. Frequency has also been similarly defined as the probability of encountering the species in a specific subsample (Shiue and Beazley, 1957). The numerical value of species frequency will vary with the particular definition of subsample, even for the same stand. The dependency of species frequency upon the definition of subsample has led to the consideration that species frequency may not be characteristic of the population sampled, but rather of the sampling method itself (Kylin, 1926).

The purpose of this study is to show that species frequencies, as estimated from several different sampling methods with different definitions of subsample, can be compared if for all sampling methods, species frequency, species density, and relative species density are reduced to common terms.

For the purposes of this study, the terms species frequency, species density, and relative species density are defined as follows: Species frequency is the probability of encountering the species of interest in a specific subsample (Shiue and Beazley, 1957); Species density is the number of stems of the species of interest per unit area (a variation of species density is subsample species density which is defined as the number of stems of the species of interest per subsample); Relative species density is the probability of encountering the species of interest sampling the stems one at a time. Relative species density therefore equals subsample species density when the subsample is one stem. Actual sampling measurements then are used to estimate these population parameters. In order to distinguish

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the density of a single species from the density of the stand the term species density is used and to keep the usage uniform the adjective species has to be used with frequency. Subsample is used in its most general sense and may relate to any sampling method.

METHODS AND DISCUSSION

A tract of Maple-Basswood forest, with a White Pine overstory, in the Itasca State Forest, Minnesota, 40 x 120 meters was mapped and sampled. The mapping was accomplished by means of a plane table and all tree species individuals with stems one inch or more DBH were identified and located on the map. Since the map was a nearly exact scale duplication of the forest stand, all sampling was performed using the map. Sampling was accomplished by establishing a coordinate system on the map and selecting random pairs of coordinates to position subsamples by means of a table of random numbers. The coordinate system used consisted of a 40 point ordinate and a 120 point abscissa, with the points 1 meter apart making possible the selection of 4800 total non-repeated subsamples. However sampling was carried out with replacement.

TABLE 1
Subsample density, (10 x 10 meter quadrat), and relative density for the quadrat, plotless variable radius, and the point quarter sampling methods

	Subsample density ² (Quadrat)			Relative species density		
	Q ³	PVR ⁴	PQ ⁵	Q	PVR	PQ
<i>Acer saccharum</i> Marsh. ¹	2.000	1.930	3.986	0.329	0.128	0.338
<i>Tilia americana</i> L.	1.225	1.088	1.226	0.202	0.088	0.106
<i>Populus tremuloides</i> Michx.	0.850	0.562	1.515	0.140	0.163	0.131
<i>Quercus rubra</i> L.	0.750	0.204	1.515	0.123	0.059	0.131
<i>Pinus strobus</i> L.	0.575	0.304	1.948	0.095	0.374	0.169
<i>Quercus macrocarpa</i> Michx.	0.225	0.350	0.288	0.037	0.009	0.025
<i>Acer rubrum</i> L.	0.175	0.152	0.577	0.029	0.009	0.050
<i>Betula papyrifera</i> Marsh.	0.100	0.146	0.216	0.018	0.038	0.019
<i>Populus grandidentata</i> Michx.	0.100	0.039	0.288	0.018	0.007	0.025
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.050	0.434	0.072	0.008	0.021	0.006
<i>Ulmus americana</i> L.	0.025	0.007	xxxxx*	0.004	0.002	xxxxx
<i>Pinus resinosa</i> Ait.	xxxxx	0.030	xxxxx	xxxxx	0.021	xxxxx

¹Nomenclature after Fernald (1950).

²Analysis of variance for both density and relative density indicate no significant differences among the methods at either the 0.05 or 0.01 levels of significance.

³Quadrat Method

⁴Plotless Variable Radius Method

⁵Point Quarter Method

*Did not occur in the sample

The methods compared in this study are the quadrat (10 m x 10 m), the point-centered-quarter method (Cottam and Curtis, 1956) and (Cottam et al., 1953) and the plotless-variable-radius method (Bitterlich, 1947) and (Grosenbaugh, 1952). The samples consist of 40 quadrats, 40 point-centered-quarter 4-tree subsamples, and 25 plotless-variable-radius points. The number of subsamples in each case are consistent with common usage. The sampling for any one method was completely independent of all other methods.

Since the primary concern of this paper is with the comparison of species frequency estimates, much of the information that would be normally presented in a full scale comparison of methods is omitted.

In table 1 are given estimated species densities for all species in all sampling methods. Inasmuch as quadrats are beyond doubt the most frequently used

sampling devices, all values are reduced to estimated quadrat species density; i. e., the density for each species for each method is given on a stems-of-the-species per 100 sq m basis.

The quadrat method yielded estimated quadrat species density directly. The plotless-variable-radius method estimated species density in stems per acre which was then converted to stems per 100 sq m. The point-centered-quarter-area calculations are based on the approximate spacing of trees in squares in which the average of the four measurements is considered to be $\frac{1}{2}$ the diagonal of the square. The area occupied by the 40 sets of 4 trees was then calculated and the appropriate transformation was made to trees per 100 sq m.

TABLE 2
Estimated species frequency and frequency derived from subsample (quadrat) species density, for all species and methods

	Estimated frequency			Density derived frequency ¹		
	Q	PVR	PQ	Q	PVR	PQ
<i>Acer saccharum</i> Marsh.	0.850	0.920	0.850	1.000	1.000	1.000
<i>Tilia americana</i> L.	0.625	0.720	0.300	1.000	1.000	1.000
<i>Populus tremuloides</i> Michx.	0.450	0.960	0.350	0.350	0.562	1.000
<i>Quercus rubra</i> L.	0.525	0.760	0.425	0.750	0.204	1.000
<i>Pinus strobus</i> L.	0.350	1.000	0.525	0.575	0.304	1.000
<i>Quercus macrocarpa</i> Michx.	0.175	0.120	0.100	0.225	0.350	0.288
<i>Acer rubrum</i> L.	0.175	0.120	0.200	0.175	0.152	0.577
<i>Betula papyrifera</i> Marsh.	0.100	0.440	0.100	0.100	0.146	0.216
<i>Populus grandidentata</i> Michx.	0.100	0.040	0.100	0.100	0.039	0.288
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.050	0.200	0.025	0.050	0.434	0.072
<i>Ulmus americana</i> L.	0.025	0.040	xxxxx	0.025	0.007	xxxxx
<i>Pinus resinosa</i> Ait.	xxxxx	0.360	xxxxx	xxxxx	0.030	xxxxx

¹Analysis of variance for density derived frequencies indicate that there are no significant differences among the methods at either the 0.05 or 0.01 level of significance.

It is possible to estimate species frequency directly by dividing the number of subsamples containing the species by the total number of subsamples. Table 2 contains estimated species frequencies based on this procedure.

The sample area for quadrats is 100 sq m with an average of 6.08 stems per subsample. The average subsample area for the plotless-variable-radius method is 500.37 sq m, containing 16.88 trees per subsample and for the point-centered-quarter method the average subsample size is 34.67 sq m with 4 trees per subsample. These estimates of species frequencies are not directly comparable for they are based on systems using different area measures.

Because direct comparisons of the estimated species frequencies among methods are out of the question other aspects of species frequency must be examined.

As stated previously, species frequency can be defined as the probability of encountering a given species in a specific subsample. Thus species frequency can be estimated from species density and can be illustrated with an example.

If *Pinus strobus* has a subsample (quadrat) species density of 0.575 (see table 1), 0.575 stems of *Pinus strobus* occur on the average in each subsample (10 x 10 m quadrat), one stem would occur on the average in about every 2 quadrats, or *Pinus strobus* stems would occur on the average in about $\frac{1}{2}$ the quadrats. If this is true, then *Pinus strobus* would have an estimated species frequency of about 0.5.

If *Acer saccharum* were chosen with its subsample (quadrat) species density of 2.000 (table 1), its estimated species frequency would be approximately 1.0, for with two stems per quadrat, the chances are good that almost every subsample would have at least one *Acer saccharum* stem.

TABLE 3

Estimated species frequency derived with the use of the Poisson Series and estimated species frequency derived with the use of the Binomial Series for all species and all methods

	Poisson frequency ¹			Binomial frequency		
	Q	PVR	PQ	Q	PVR	PQ
<i>Acer saccharum</i> Marsh.	0.865	0.855	0.976	0.797	0.422	0.808
<i>Tilia americana</i> L.	0.706	0.663	0.701	0.595	0.308	0.362
<i>Populus tremuloides</i> Michx.	0.572	0.430	0.780	0.530	0.510	0.430
<i>Quercus rubra</i> L.	0.528	0.141	0.780	0.409	0.216	0.430
<i>Pinus strobus</i> L.	0.437	0.262	0.854	0.329	0.847	0.524
<i>Quercus macrocarpa</i> Michx.	0.168	0.295	0.250	0.140	0.036	0.186
<i>Acer rubrum</i> L.	0.161	0.141	0.438	0.111	0.036	0.186
<i>Betula papyrifera</i> Marsh.	0.095	0.136	0.194	0.071	0.144	0.074
<i>Populus grandidentata</i> Michx.	0.095	0.038	0.250	0.070	0.028	0.096
<i>Ostrya virginiana</i> (Mill.) K. Koch	0.049	0.239	0.070	0.032	0.083	0.023
<i>Ulmus americana</i> L.	0.024	0.007	xxxxx	0.016	0.008	xxxxx
<i>Pinus resinosa</i> Ait.	xxxxx	0.030	xxxxx	xxxxx	0.021	xxxxx

¹Analysis of variance for both groups indicate no significant differences among the methods at either the 0.05 or 0.01 level of significance.

If the stems are distributed in a random or uniform manner, estimated subsample density should be a good estimate of species frequency. If the stems are clumped the species frequency estimates will be high.

The tendency for species to be randomly distributed and to be clumped may well exist in the same stand simultaneously. Whitford (1949) has shown that the tendency toward random or clumped distributions is related to the age of the stand.

Table 2 contains estimates of species frequencies computed from subsample (quadrat) species density. When compared to estimated quadrat frequency, the estimates of species frequencies for quadrats derived from estimates of species density appear to be too high. Most of the plentiful species have estimates of species frequencies of 1.000 and this is borne out even with the other methods. However, the transformation from estimated species density to estimated species frequency yielded values that were all biased in the same direction. Since this method of calculating species frequency depends entirely upon the random or uniform distribution of the stems in areal extent, there is a strong presumption that this is not so.

If an hypothesis involving the randomness or nonrandomness of the areal distribution of the species underlies the sampling method, other relationships among species frequency, species density and relative species density may be derived from the hypothesis.

The hypothesis that the species were distributed in the population of quadrat subsamples according to the Poisson series, and the hypothesis that the species were distributed in the population of point-centered-quarter subsamples according to the binomial series were tested. From the results of a Chi-square test for goodness of fit, it could be concluded that there was not sufficient evidence to reject the hypothesis for the major species for the Poisson series, nor was the evidence sufficient to reject the hypothesis for any of the species for the binomial.

For the Poisson distribution the expectation of the occurrence of subsamples containing 0, 1, 2, 3, . . . of the species is given by the sequence $\frac{n}{e^d}$, $\frac{nd}{e^d}$, $\frac{nd}{2e^d}$, $\frac{nd}{6e^d}$, . . ., where n equals the number of subsamples, e is the base of the natural logarithms, and d is the mean occurrence of the species in the subsamples (Snedecor, 1946). The factor d is subsample or quadrat species density.

The first term of the series will yield the expected number of subsamples in the total sample that do not contain the species. The next term will yield the expected number containing one of the species, the next, the number containing two, etc.

If the expected number of subsamples containing none of the species can be derived from the Poisson series, then by subtraction the expected number with the species can be determined. This information, together with the total number of subsamples, is all that is necessary to estimate species frequency.

Using estimated quadrat densities for all methods (table 1), the expected species frequencies for all species for all methods were computed using the Poisson series. This was done by substituting the estimated quadrat densities for d in the Poisson series.

Table 3 contains estimates of species frequencies for all species, for all methods computed from estimated quadrat density and using the Poisson series. With the Poisson distribution it is a fact that some degree of clumpedness will occur. This is in keeping with the expectation that with the Poisson most or many of the subsamples will not contain the species of interest and that some of the subsamples will have 1, 2, 3, 4, or more of the species of interest each. The general effect is to lower the species frequencies of the abundant species while leaving virtually unchanged the species frequencies of the less abundant ones. F-ratios indicate no significant differences for the three methods, indicating that each method estimated the quantity species density within bounds such that the subsequent transformations yield differences that were not significant.

For the point-centered-quarter method the binomial distribution was applied in the following way. Assuming relative species density to be the probability of encountering the species in the stand in subsamples of 1, a binomial expression was formulated in terms of relative density, and is: $(p+q)^k=1$, where p is the probability of encountering the species in the stand (relative species density), where q is the probability of not encountering the species, and where k is the number of trees in the subsample. In the point-centered-quarter method, $k=4$.

When this binomial expression is expanded and its terms multiplied by the total number of subsamples, (40 for the point-centered-quarter method), the expected numbers of subsamples containing $k \dots 3, 2, 1$, and 0 of the individual species are obtained. The expansion for the point-centered-quarter is: $np^4+n4p^3q+n6p^2q^2+n4pq^3+nq^4$, where n equals the total number of subsamples.

This led to another series of calculations of expected species frequencies based on the binomial series, where nq^4 , the expected number of subsamples without the species, was evaluated for each species. With this information estimates of species frequency of each species was calculated using the relative densities of table 1 for all methods.

Table 3 contains estimates of species frequencies for all species, for all methods computed from relative species densities and using the binomial series. Much the same has occurred with estimated species frequencies calculated from the binomial mathematics as had occurred with the Poisson. Again the expectation with the binomial is that a definite proportion of the subsamples will have none of the species of interest, while some others will have 1, 2, 3, or more depending upon the power of the binomial. F-ratios indicate no significant differences among the methods, again indicating that the method of estimating relative species density was such that nonsignificant differences of estimated species frequency resulted. The results from both the Poisson and the binomial would seem to indicate that in order to make good estimates of species frequencies, good estimates of species density must first be made since species frequencies can be thought of as a function of species density as limited by subsample size. Since nonsignificant differences were found within each method tested, it is apparent that the calculation and com-

parison of estimated species frequency also depends to a great extent upon the assumptions underlying the sampling technique.

CONCLUSIONS

It is concluded from the foregoing analysis that as far as the stand under study is concerned, estimated species frequency from several sampling methods including area sampling methods and plotless methods may be compared. The only requisite of the comparison is that the terms of species frequency be identical and this may be accomplished by transforming them into common terms.

Species frequency derived from estimated species density and based upon the assumption of the random distribution of trees areally yields estimated species frequencies values that are biased in the direction of being high. However, statistically the differences between estimates from all methods tested were not significant indicating that all estimates are biased in the same direction.

Estimated species frequencies calculated from Poisson and binomial distributions were also statistically nonsignificant but the estimated species frequencies for the most abundant species were somewhat reduced.

SUMMARY

By transforming the data for estimated species frequency from each of three different sampling methods into common terms, a comparison of estimated species frequencies was made. Analysis of variance conducted on each method of computing estimated species frequency indicated no significant differences among the methods.

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