



A Variance Test for Detecting Species Associations, with Some Example Applications

Author(s): Dolph Schluter

Source: *Ecology*, Vol. 65, No. 3 (Jun., 1984), pp. 998-1005

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1938071>

Accessed: 07/10/2014 12:26

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

A VARIANCE TEST FOR DETECTING SPECIES ASSOCIATIONS, WITH SOME EXAMPLE APPLICATIONS¹

DOLPH SCHLUTER²

*Division of Biological Sciences, University of Michigan,
Ann Arbor, Michigan 48109 USA*

Abstract. A little-used measure of species association is provided by the ratio of the variance in total species number (or total density of individuals) in samples to the sum of the variances of the individual species. Use of this ratio allows a test of the null hypothesis that species do not covary among samples. As the test is simultaneous it is preferable to pairwise 2×2 contingency table analysis and pairwise correlation analysis when the number of species is large. Simulation reveals that this test is also more powerful than Pearson's χ^2 test for comparing observed and expected frequency distributions of species in samples. The variance test was applied to a selection of data from the literature. Results reveal that positive associations are the rule in nature and negative associations are uncommon. Invertebrate species tend to be more positively associated among samples than are vertebrates, although the difference is not significant. Examples of biological processes, especially interspecific interactions, that might produce associations among species are suggested. However one must be cautious not to infer the importance or unimportance of a specific process from the result of the test alone.

Key words: *chi-square; species association; variance test.*

INTRODUCTION

Presently there is interest in the description and statistical analysis of species-abundance patterns. This is especially true in community studies where such patterns can be used to test or to generate hypotheses about the nature of interactions between species in an assemblage; indeed, the patterns have often been used to infer the interactions directly. A common question is: do individuals of a given species occur more or less frequently in a particular place when a second species is also present or abundant (e.g., Lloyd 1967, Pielou and Pielou 1968, Buzas 1970, Taylor 1979, Simberloff and Connor 1981, Wiens and Rotenberry 1981, James and Boecklen, *in press*)?

A number of methods exist for testing whether an association between two species is present. The 2×2 contingency table is most often used for presence/absence data (cf. Pielou 1974). Correlation analysis is frequently applied to population density data (e.g., Wiens and Rotenberry 1981, James and Boecklen, *in press*). However these pairwise techniques are inadequate when $M > 2$ species are found in the study area. All ($\frac{M}{2}$) pairwise associations might be determined, but since the tests are not independent it would be difficult to assign a probability to the distribution of outcomes. Analysis of combinations, using a 2^k contingency table (Pielou 1972), solves this problem for presence/absence data, but the method rapidly becomes impractical as the number of species increases beyond four or five. In this case one might limit the analysis solely to

the number of combinations of species missing from an area (Pielou and Pielou 1968, Simberloff and Connor 1981, Grant and Schluter, *in press*), but not without some loss of information.

This paper investigates a different method for assessing simultaneously whether species in a group are associated. The technique compares the observed variance in the total number of species (or individuals) in samples, with the variance expected under the null hypothesis that density or occurrence of each species is independent of the others. Pielou (1972) was the first to introduce a comparison of this kind, but similar methods have been suggested independently at least three times since then (Diamond and May 1977, Järvinen 1979, Schluter 1982). Robson (1972; see also Schluter 1982) derived a statistic for testing the observed variance against the null model.

Despite the usefulness of the variance comparison, Robson's test has never, to my knowledge, been applied. Thus, two objectives of this paper are to outline the test simply and to indicate the range of situations in which it may be used. The reliability of the statistic is investigated, using simulation on real and contrived datasets. Also, the power of the statistic is compared with that of a second test used by Pielou (1974) and others. Finally the test is applied to a selection of data from the literature. Alternative interpretations of the results are discussed.

VARIANCE TEST

Presence/absence data

I begin by summarizing Robson's result: a typical dataset might consist of a list of species found in independent samples collected from different places in the habitat or from the same place at different points

¹ Manuscript received 1 June 1982; revised 27 January 1983; accepted 1 April 1983.

² Present address: Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A9.

TABLE 1. Example of a data matrix showing presence and absence of M species in N sample collections.

Sam- ple	Species										Num- ber of spe- cies
	1	2	3	4	5	.	.	.	i	.	M
1	1	0	1	1	0	T_1
2	0	0	0	0	1	T_2
3	0	1	1	1	0	T_3
4	1	1	1	0	0	T_4
.
j	T_j
N	T_N
	n_1	n_2	n_3	n_4	n_5	.	.	.	n_i	.	n_M

in time. Species occurrence within such samples can be represented by the data matrix shown in Table 1. The digits 1 and 0 indicate presence and absence, respectively, of a species in a given sample. The total number of samples in which a species i is found is given as n_i , and $T = T_j$ is the total number of species in sample j .

We are interested in determining whether the M species are associated. It is known from probability theory (Feller 1950) that the variance of a sum of random variables is equal to the sum of the variances plus twice the sum of the covariances. Applying this to species occurrences in samples (Table 1),

$$\begin{aligned} \text{Var}(T) &= \sum_i^M \text{Var}(X_i) \\ &+ 2 \sum_{i < l}^M \text{Cov}(X_i, X_l), \end{aligned} \tag{1}$$

where X_i is the "occurrence" for species i in samples. The null hypothesis of no association (H_0) states that the sum of the covariances is zero. This will be true when species are independently distributed among samples, but may also result when positive and negative covariances cancel each other out. H_0 is thus tested against the alternative hypothesis that there is a net positive or negative association among species.

The variance terms in Eq. 1 are unknown, but they may be estimated from the data. Let σ_i^2 be the sample estimate of $\text{Var}(X_i)$; for presence/absence data,

$$\sigma_i^2 = p_i(1 - p_i),$$

where $p_i = n_i/N$. Estimate variance in total species number, $\text{Var}(T)$, as

$$s_T^2 = (1/N) \sum_j^N (T_j - t)^2, \tag{2}$$

where t is the observed mean number of species per sample. Under H_0 the conditional expected value of s_T^2 ,

$$E(s_T^2 | p_1, \dots, p_M) = \Sigma \sigma_i^2.$$

The ratio

$$V = s_T^2 / \Sigma \sigma_i^2 \tag{3}$$

thus serves as an index of species association in samples. The expected value of V under H_0 is 1. A value $>$ (or $<$) 1 indicates that overall the species covary positively (or negatively) in presence/absence.

We require a statistic for testing whether a deviation from 1 is larger than chance alone would dictate. It is known from the Central Limit Theorem (Feller 1950) that the sum of a large sequence of independent random variables is approximately normal. This will often be true of sums of species occurrences (Table 1), providing M is not too small, and hence T will be approximately normal. If, in addition, N is not too small a modification of the association index V ,

$$W = VN = s_T^2 N / \Sigma \sigma_i^2 \tag{4}$$

will, under H_0 , be approximately chi-square distributed, with N degrees of freedom.

Eq. 4 is essentially Robson's result. Critical values for rejecting the null hypothesis may be obtained from a table of critical values for the chi-square distribution (e.g., Rohlf and Sokal 1969). For example if the species do not covary the probability is .90 that W will lie between the limits

$$\chi^2_{.05, N} \leq W \leq \chi^2_{.95, N}.$$

We require a check on the procedure, given realistic values for M and N . The reliability of the test was thus investigated for a hypothetical case under H_0 (case 1). One hundred data matrices of five species and 20 samples were constructed in the manner of Table 1. Occurrence of each species in samples was generated as a binomial(1, p) random variate, using simulation in MIDAS (Michigan Interactive Data Analysis System). Probabilities of occurrence for the five species (p) were set to .8, .6, .5, .3, and .2, respectively. For each resulting random matrix, the test statistic W was computed. The empirical distribution of these values was not significantly different from a χ^2_{20} distribution (Kolmogorov-Smirnov [K-S], $P > .10$).

Behavior of the statistic near the critical limits was also checked. Under H_0 , 5 of the 100 simulated values for W are expected to be greater than $\chi^2_{.95, 20}$, and 5 are expected to be less than $\chi^2_{.05, 20}$. The number actually observed is shown in Table 2. Also shown in this table is the number of type 1 errors for two more simulations of 100 presence/absence data matrices, this time using binomial parameter values derived from sources in the literature. All three presence/absence cases indicate a good fit between observed and expected. In no case is the number of errors at each tail significantly different from 5 (separate binomial tests for each tail; all $P \geq .24$), despite small numbers of species in two of the studies and a small number of samples in the third.

TABLE 2. Number of cases in 100 random simulations for which the value of W falls outside the 90% critical range for χ^2_N (type I errors). Figure in parentheses gives two-tailed probabilities (binomial test) that the difference between the observed number of errors at each tail and 5 is produced by chance. Parameter values are derived from the sources listed.

Study number	Type	Source	No. species	No. samples	No. $\leq \chi^2_{.05,N}$	No. $\geq \chi^2_{.95,N}$
1	Presence/absence	Hypothetical case 1	5	20	2 (.24)	4 (.87)
2	Presence/absence	Simberloff 1976*	26	3	5 (1.0)	7 (.26)
3	Presence/absence	Culver 1970†	6	28	4 (.87)	4 (.87)
4	Density data	Hypothetical case 2	5	5	7 (.26)	5 (1.0)
5	Density data	James and Boecklen, <i>in press</i> ‡	29	7	2 (.24)	7 (.26)

* Parameters from 26 arthropod species whose occurrence is variable over three post-defaunation sampling periods on a mangrove island (ST2).

† Parameters from six species of crustaceans and 28 caves. *G. porphriticus* excluded.

‡ Parameters from seven years data on 29 upland forest Maryland birds.

Population density data

Robson designed his test specifically with reference to presence/absence data. However, the test may be generalized to handle population density data. In this situation we are interested in determining whether the abundances of M different species covary among samples. To test this, the observed variance in the total number of individuals per sample (s_T^2 , all species combined) is compared with the sum of the variances of individual species densities ($\sum \sigma_i^2$). In this case

$$\sigma_i^2 = (1/N) \sum_j^N (X_{ij} - t_i)^2, \tag{5}$$

where X_{ij} is the density of species i in sample j , and t_i is the observed mean density of species i . As before, the ratio V provides an index of association (Eq. 3). A value for $V >$ (or $<$) 1 indicates that the species tend to covary positively (or negatively) in their abundance in samples.

For population density data the statistic W (Eq. 4) may be used to test an association, as for presence/absence data. While the abundance of individual species in samples may not be normal, it will often be the case that, under H_0 , the total density in samples (all species combined) will approximate a normal distribution (Feller 1950). In this case W will be approximately χ^2_N distributed.

The reliability of the assumptions for density data was investigated with a second hypothetical case. One hundred data matrices were constructed of five species with independent normal densities in five samples. The distribution of resulting values for W was not significantly different from a χ^2_5 distribution ($K-S, P > .10$). Correspondingly, the observed number of errors at the tails was not different from that expected (Table 2).

The last example in this table simulated normal densities using species parameters from James and Boecklen's study of Maryland forest birds (provided by F. C. James). Tail error frequencies again indicate a good fit to χ^2_N .

COMPARISON WITH OTHER TESTS

Excepting 2^k analysis (Pielou 1972), there are few alternatives to the variance test for detecting species associations in presence/absence data. However, Pielou (1974) and Taylor (1979) compared the frequency distribution of species number per sample with the distribution expected under the null hypothesis of no association. Taylor compared the observed distribution to both that of a fitted Poisson and a simulated distribution based on observed numbers of occurrences. Pielou, using instead techniques provided by Barton and David (1959), computed expected number of species per sample under H_0 as a binomial (K, P) distribution, where the parameters K and P are derived from species occurrence frequencies. Both Pielou and Taylor compared observed and expected frequencies with Pearson's χ^2 . With this test, rejection of H_0 indicates a significant positive or negative association.

I compared the previous test (hereafter called Pielou's method, for convenience) to the variance test in its ability to detect associations among species in presence/absence data. First, I simulated 100 random data matrices of five species and 20 samples. Unlike earlier simulations, occurrence of different species was not generated independently. Instead a uniform (0, 1) random number, u_j , was selected and assigned to each sample of the data matrix. This was repeated independently for all 100×20 samples. Occurrence of species 1–3 was then simulated as a binomial (1, u_j) random variate, and species 4–5 occurrence was generated as a binomial (1, $u_j/2$). Since the probability of occurrence of any given species in a sample is a simple constant function of the occurrence probabilities of all other species, there is a tendency for them to be positively associated.

Actually, since occurrence is still largely random, resulting data matrices range from having species that appear to be distributed independently to having species that appear very highly associated. Assuming that both the variance test and Pielou's method have the same

TABLE 3. Relative ability of variance test and Pielou's (1974) test to detect species associations ($\alpha = .05$). Figures are from three hypothetical examples of 100 simulations.

No. species	No. samples	No. significant associations	
		Variance test	Pielou's test
5	20	68	22
10	10	94	5
10	5	13	0

probability of a type I error, then the number of random matrices that are detected as being associated by each test will serve as a measure of their relative power. I computed W for each data matrix and counted the number of significant results ($\alpha = .05$). I also determined P and K (Pielou 1974) for each matrix and the expected frequencies of samples containing zero to five species. Pearson's χ^2 was used to test observed and expected frequencies; adjacent cells were combined so that the expected number of samples was at least two, a not overly conservative minimum. Results (Table 3) show that Pielou's method detected only 22 matrices as associated, whereas the variance test found 68.

I repeated this procedure twice using different values for number of species and samples. The results (Table 3) uphold the conclusion from the previous comparison. For the 10 species and 10 samples example, the variance test detected 94 associated matrices, against 5 by Pielou's test. In the third example of 5 samples and 10 species power was low in both tests (Table 3), but again the variance test detected the greater number.

For density data I know of no statistical tests for association with which to compare the variance test.

EXAMPLES FROM THE LITERATURE

Comparison of a measure of association against the statistical null hypothesis is important to determine if species are more than randomly associated. Comparison with an actual distribution of values for V may be equally illuminating. What types of associations are most commonly found in nature? To answer this I have searched through recent issues of several available ecological journals for tabular information on presence/absence or population densities of species. Examples were selected from the animal literature, and an attempt was made to represent a wide variety of groups and degrees of taxonomic relatedness. To control for area effects on species number I ensured that samples were similar in size or effort; I occasionally relaxed this restriction for density data (e.g., Nilsson 1977). Data collected from along a successional sequence were not included. The consequent list of 37 references is given in the Appendix.

A problem with directly comparing values for V among different studies is that the distribution of val-

ues expected under H_0 is asymmetric around 1. I used instead a scaled version, Q , which is the probability of obtaining a value $\leq W = VN$ from a χ^2_N distribution. Q is also advantageous in that it takes into account differences between studies in the number of samples, N . Values for both V and Q are furnished in the Appendix; these data are summarized in Fig. 1. A significant departure from randomness at $\alpha = .10$ is indicated when Q is $<.05$ or $>.95$.

Under the null hypothesis of no association among species the distribution of values for Q will be uniform between 0 and 1. The actual distribution, shown in Fig. 1, is highly significantly different from randomness. In 30 of 37 studies Q was $>.5$ (two-tailed binomial test, $P = .0002$), corresponding to values for V greater than the median under H_0 . At $\alpha = .10$ only one study showed a significant negative association, a desert rodent community studied by Rosenzweig and Winakur (1969). Other Q values below the median are from a variety of groups, including freshwater crustaceans in localities of a lake (Halvorsen and Gullestad 1976), slugs in plots of different tree species (Beyer and Saari 1977), coral reef fishes on different sites (Anderson et al. 1981), and breeding birds in different years (James and Boecklen, *in press*).

In contrast, species in 11 studies were significantly positively associated at $\alpha = .10$. Again a wide variety of groups are represented, ranging from marine polychaetes (Kohn and Lloyd 1973), Foraminifera (Buzas 1970), and coprophagous beetles (Hanski 1980) in different sites to annual surveys of breeding birds (Lack 1969). There seems to be no relationship between type of association and level of taxonomic relatedness. Q values for vertebrate species are $>.5$ slightly more frequently than for invertebrates (Fig. 1), though the difference is not significant (Fisher's exact test, $P = .46$). Possibly this trend is a result of differences in the importance of certain biological interactions (e.g., competition), or in the effects of climate or resource variability, in the two animal groups.

If these results may be generalized, it can be con-

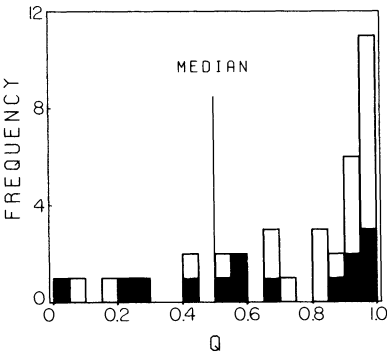


FIG. 1. Frequency distribution of values for Q computed from the literature. Shaded values are from vertebrate studies.

TABLE 4. Ecological processes which may result in a positive or negative association among species, with emphasis on interspecific interactions.

Association	Interaction	Example of process
Negative	Competition	Interference or resource mediated, producing occasional exclusion or negatively covarying population sizes.
Negative	None	Different resource requirements or climatic tolerances with negatively covarying resource/climate states.
Negative	Mutualism	Resources compete and are used exclusively by species. Local overharvest of some resources decreases abundance of consumer species, but density of remaining consumer species increases due to release of resources from competition (modification of Vandermeer 1980).
Negative	Predation	High predator densities produce a local depression of prey and result in negatively covarying population sizes.
Positive	Competition	Population sizes of competing species fluctuate in unison in response to fluctuations in their identical, limiting resources.
Positive	None	Common response to changes in climate or in supply of unlimiting resources.
Positive	Mutualism	Species enhance each other's survival probabilities, etc.
Positive	Predation	Predator abundance fluctuates in positive response to variation in prey abundance.

cluded that positive associations are nearly the rule, at least in the animal kingdom. This may be seen as a consequence of a variety of possible factors, some of which will be discussed in the next section. By this, however, one is forced to conclude that “randomness” is not very appropriate as a model for species associations in nature. Of course the null hypothesis of no association must still provide the standard from which to make statistical inferences about a collection of species in samples. Nonetheless it may be just as important to attempt to weigh values of V against some empirical distribution, not necessarily “null” (e.g., Fig. 1). For example one might regard *any* value for $Q < 0.5$ to be highly unusual and demanding of further research, even if the association index V is not significantly different from 1.

SECONDARY ASSOCIATIONS

An additional application of the variance test is the detection of “secondary associations” among species. These are associations remaining after some environmental component has been used to account in part for species presence or density. I (Schluter 1982) used the test to decide whether differences between finch density observed at sites and density predicted from food supply were independent for different finch species. The technique is the same as for density data except that the data matrix uses residuals from regression (each species regressed against an independent variable). For finch densities in sites (see Appendix) residuals are found to be slightly negatively associated ($V = 0.52$, $P = .18$). Presence/absence data may often be dealt with similarly. For example Diamond and Marshall (1977: Table 4) list occurrence of 17 bird species on 14 New Hebridean islands. The species are positively associated ($V = 2.09$, $P < .05$), but this may be explained by area effects. To remove this effect occurrence of each species was independently regressed against log island area using a probit analysis (Finney 1971).

Deviations between actual and expected occurrence were then determined and tested for association. The result ($V = 1.34$) indicates that a positive but nonsignificant association persists among the species ($P = .35$) after the linear effects of log island area on probability of occurrence are removed.

INTERPRETATION

In general the variance test gave similar results to those of the respective authors (Appendix) in the few cases where these were determined by other means. In at least one case, however, a different conclusion was reached; e.g., Nilsson (1977) argued for the presence of density compensation in a group of island birds, yet my own computations reveal a positive overall association in density ($P = .01$). The conflicting interpretations reveal some advantages but also some shortcomings of the variance test. The technique cannot always be sensitive to associations among subsets of species in a collection. There may be situations with some species covarying positively among themselves but negatively with other species, yet an overall result of no association is discovered. On the other hand since there will always be positive and negative associations between pairs of species (sometimes significant) even in a random assemblage, the variance test is appropriate when one is dealing with a large number of species. In addition, this test will often detect significant overall associations when pairwise techniques do not. Where, in a set of species, some pairwise associations are found and thought to be important, these should be verified by additional sampling. Or, ecological data on the species may be used to subdivide large collections of species into smaller sets of interest prior to using the variance test.

A related problem is that since certain species are always more variable than others, especially with density data, the result of the test is more sensitive to associations within the more variable group. In such

situations a procedure that standardizes the species densities before use of the test will sometimes be justified.

Finally, it should be noted here that there is no necessary correspondence between the result of the variance test and any ecological process. Researchers frequently seem wont to infer the existence of a particular interaction between species (e.g., competition) on the basis of a statistical test of this kind, but such inference is usually not valid. In order to discourage this practice with the variance test, I have constructed a "list of causes" (Table 4), which gives examples of processes (especially interactions) that may produce species associations. I have not included the "no association" outcome in the Table, but for any interaction this may result from a balancing of negative and positive forces.

It is clear from Table 4 that any conclusion about the variance ratio is consistent with all hypotheses that any or no interaction among the species has produced it. I show this not to invalidate the statistic but to emphasize its proper use. If a sufficient knowledge has been gained about the biology of the species, then the variance test may be used to distinguish among rival mechanistic hypotheses. Alternatively it may be used as a simple descriptor of species patterns, the causes of which can be investigated subsequently.

ACKNOWLEDGMENTS

Frances James provided both the stimulus to write this paper and some data on Maryland birds, for which I thank her. I'm also grateful to George Estabrook, Gary Fowler, and Neil Oden for assistance at various developmental stages. Gary Fowler, Peter Grant, Frances James, Robert Poole, and Trevor Price made comments on the final version. Computer funds were provided by the Division of Biological Sciences at the University of Michigan.

LITERATURE CITED

- Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russel, and E. F. Talbot. 1981. The community structure of coral reef fishes. *American Naturalist* **117**:476-495.
- Anderson, N. H., and J. L. Wold. 1972. Emergence trap collections of Trichoptera from an Oregon stream. *Canadian Entomologist* **104**:189-201.
- Askew, R. R. 1962. The distribution of galls of *Neuroterus* (Hym: Cynipidae) on oak. *Journal of Animal Ecology* **31**:439-455.
- Barton, D. E., and F. N. David. 1959. The dispersion of a number of species. *Journal of the Royal Statistical Society B* **21**:190-194.
- Beyer, W. N., and D. M. Saari. 1977. Effect of tree species on the distribution of slugs. *Journal of Animal Ecology* **46**:697-702.
- Buzas, M. A. 1970. Spatial homogeneity: statistical analyses of unispecies and multispecies populations of Foraminifera. *Ecology* **51**:874-879.
- Culver, D. C. 1970. Analysis of simple cave communities. I. Caves as islands. *Evolution* **24**:463-474.
- Davidson, D. W. 1977. Species diversity and community organization in desert seed-eating ants. *Ecology* **58**:711-724.
- Diamond, J. M., and A. G. Marshall. 1977. Distributional ecology of New Hebridean birds: a species kaleidoscope. *Journal of Animal Ecology* **46**:703-727.
- Diamond, J. M., and R. M. May. 1977. Species turnover rates on islands: dependence on census interval. *Science* **197**:266-270.
- Dondale, C. D., B. Parent, and D. Pitre. 1979. A six-year study of spiders (Araneae) in a Quebec apple Orchard. *Canadian Entomologist* **111**:377-380.
- Feller, W. 1950. An introduction to probability theory and its applications. Volume I. Wiley, New York, New York, USA.
- Finney, D. J. 1971. Probit analysis. Third edition. Cambridge University Press, London, England.
- Freeland, W. J. 1979. Primate groups as biological islands. *Ecology* **60**:719-728.
- Gardarsson, A. 1979. Waterfowl populations of Lake Mývatn and recent changes in numbers and food habits. *Oikos* **32**:250-270.
- Golini, V. I., and R. E. Wright. 1978. Relative abundance and seasonal distribution of Tabanidae (Diptera) near Guelph, Ontario. *Canadian Entomologist* **110**:385-398.
- Grant, P. R. 1976. An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. *Canadian Journal of Zoology* **54**:2156-2173.
- Grant, P. R., and D. Schluter. *In press*. Interspecific competition inferred from patterns of guild structure. *In* D. R. Strong, D. S. Simberloff, and L. G. Abele, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Hafner, M. S. 1977. Density and diversity in Mojave desert rodent and shrub communities. *Journal of Animal Ecology* **46**:925-938.
- Halvorsen, G., and N. Gullestad. 1976. Freshwater crustaceans in some areas of Svalbard. *Archiv Für Hydrobiologie* **78**:383-395.
- Hanski, I. 1980. Spatial patterns and movements in coprophagous beetles. *Oikos* **34**:293-310.
- Hartzband, D. J., and W. D. Hummon. 1974. Sub-community structure in subtidal meiobenthic Harpacticoida. *Oikos* **14**:37-51.
- Holmes, R. T., and F. W. Sturges. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. *Journal of Animal Ecology* **44**:175-200.
- James, F. C., and W. Boecklen. *In press*. Interspecific morphological relationships and the densities of birds. *In* D. R. Strong, D. S. Simberloff, and L. G. Abele, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Järvinen, O. 1979. Geographical gradients of stability in European land bird communities. *Oikos* **38**:51-69.
- Kohn, A. J., and M. C. Lloyd. 1973. Polychaetes of truncated reef limestone substrates on Eastern Indian Ocean coral reefs: diversity, abundance and taxonomy. *Internationale Revue der gesamten Hydrobiologie* **58**:369-399.
- Lack, D. 1969. Population changes in the land birds of a small island. *Journal of Animal Ecology* **38**:211-218.
- Lindegård, C. 1979. A survey of the macroinvertebrate fauna, with special reference to Chironomidae (Diptera) in the rivers Laxá and Kráká, northern Iceland. *Oikos* **32**:281-288.
- Lindegård, C., and P. M. Jónasson. 1979. Abundance, population dynamics and production of zoobenthos in Lake Mývatn, Iceland. *Oikos* **32**:202-227.
- Lindegård, C., and J. Thorup. 1975. The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical, and horizontal distribution. *Archiv für Hydrobiologie* **75**:109-139.
- Lloyd, M. 1967. "Mean crowding." *Journal of Animal Ecology* **36**:1-30.
- Macan, T. T. 1976. A twenty-one year study of the waterbugs in a moorland fishpond. *Journal of Animal Ecology* **45**:913-922.
- Nilsson, S. G. 1977. Density compensation and competition

- among birds breeding on small islands in a South Swedish lake. *Oikos* **28**:170–176.
- . 1979. Density and species richness of some forest bird communities in South Sweden. *Oikos* **33**:392–401.
- Petr, T. 1972. Benthic fauna of a tropical man-made lake (Volta Lake, Ghana 1965–1968). *Archiv Für Hydrobiologie* **70**:484–533.
- Pielou, D. P., and E. C. Pielou. 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *Journal of Theoretical Biology* **21**:202–216.
- Pielou, E. C. 1972. 2^k contingency tables in ecology. *Journal of Theoretical Biology* **34**:337–352.
- . 1974. *Population and community ecology: principles and methods*. Gordon and Breach, New York, New York, USA.
- Robson, D. S. 1972. Statistical tests of significance. Appendix to a paper by E. C. Pielou (1972). *Journal of Theoretical Biology* **34**:350–352.
- Rohlf, F. J., and R. R. Sokal. 1969. *Statistical tables*. W. H. Freeman, San Francisco, California, USA.
- Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* **50**:558–572.
- Schluter, D. 1982. Distributions of Galapagos ground finches along an altitudinal gradient: the importance of food supply. *Ecology* **63**:1504–1517.
- Shorrocks, B. 1975. The distribution and abundance of woodland species of British *Drosophila* (Diptera: Drosophilidae). *Journal of Animal Ecology* **44**:851–864.
- Simberloff, D. S. 1976. Species turnover and equilibrium island biogeography. *Science* **194**:572–578.
- Simberloff, D. S., and E. F. Connor. 1981. Missing species combinations. *American Naturalist* **118**:215–239.
- Taylor, W. D. 1979. Sampling data on the bacterivorous ciliates of a small pond compared to neutral models of community structure. *Ecology* **60**:876–883.
- Vandermeer, J. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist* **116**:441–448.
- Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* **51**:21–41.
- Wood, T. G. 1974. The distribution of earthworms (Megascolidae) in relation to soils, vegetation, and altitude on the slopes of Mt. Kosciusko, Australia. *Journal of Animal Ecology* **43**:87–106.

APPENDIX

Association index (V) for a selection of data from the literature. Q refers to the cumulative distribution of a χ^2_N density evaluated at $W = VN$.

Author	Organism	Table in reference	Lower level of taxonomic relatedness	No. species	No. samples (N)	V	Q
Presence-absence data							
Wood 1974	earthworms	1	family	8	24	0.62	.077
Halvorsen and Gullestad 1976	crustaceans	2	class	31	31	0.76	.191
Freeland 1979	Protozoa	2	phylum	10	11	0.99	.574
Diamond and May 1977	birds	1	class	16	29	1.02	.561
Lindegaard 1979	chironomids	2	family	34	9	1.20	.710
Davidson 1977	ants	2	family	16	10	1.42	.835
Lindegaard 1979	oligochaetes	2	class	7	9	1.84	.944
Petr 1972	chironomids	4	family	19	6	6.20	>.999
Rosenzweig and Winakur 1969	rodents						
James and Boecklen, <i>in press</i>	birds	4	order	6	11	0.41	.047
Anderson et al. 1981	fish	...	class	29	7	0.65	.286
Hafner 1977	rodents	5	family	7	10	0.70	.246
Beyer and Saari 1977	rodents	1	order	9	6	0.81	.439
Rosenzweig and Winakur 1969	slugs	1	order	6	13	0.88	.432
Holmes and Sturges 1975*	rodents	4	order	13	15	0.98	.524
Lindegaard and Jónasson 1979	birds	1	class	11	4	0.99	.590
Schluter 1982	chironomids	4	family	9	5	1.11	.650
Lindegaard and Thorup 1975†	birds	...	genus	4	12	1.14	.681
Lloyd 1967	arthropods	5	phylum	19	5	1.19	.689
Askew 1962	arthropods	2	phylum	7	48	1.19	.825
Askew 1962	gall wasps	1	genus	4	75	1.23	.912
Culver 1970	gall wasps	1	genus	4	50	1.25	.889
Grant 1976‡	crustaceans	Appendix	class	6	28	1.28	.849
Shorrocks 1975	mammals	2	class	9	10	1.59	.897
Gardarsson 1979	<i>Drosophila</i>	1	genus	14	5	1.87	.905
Golini and Wright 1978	ducks	8	family	14	6	1.98	.936
Holmes and Sturges 1975§	deer flies	3	family	18	4	2.03	.912
Macan 1976	birds	1	class	29	5	2.06	.932
Kohn and Lloyd 1973†	corixid bugs	2	family	5	9	2.32	.987
Buzas 1970	polychaetes	2	class	19	5	2.50	.972
Dondale et al. 1979†	Foraminifera	1	order	4	16	2.50	.999
Lack 1969	spiders	1	class	12	6	2.57	.983
Hartzband and Hummon 1974	birds	1	class	8	27	2.60	>.999
Nilsson 1977	copepods	1	order	33	9	2.61	.994
Anderson and Wold 1972	birds	2	class	14	8	2.75	.995
Hanski 1980	Trichoptera	1	order	43	4	3.20	.988
Nilsson 1979	beetles	Appendix	order	42	5	6.28	>.999
	birds	2	class	44	8	8.53	>.999

* Data for period XI (winter).

† Unnamed species not included.

‡ June data only.

§ Data for period IV (early summer).

|| Excludes 1938, 1939, 1952, 1953, 1957, 1963 and Meadow Pipit in all years due to incomplete data.