density and stunted development of warm-water planktivorous fishes), serious disruption of the previous community structure, and a rapid shift toward smaller-bodied zooplankton.

The morphological changes seen in *Bosmina* are not peculiar to Frains Lake. The occurrence of longer mucro spines on late-glacial *Bosmina* or *Eubosmina* has been reported in sediment from Längsee, Austria (Frey 1955), Esthwaite Water, England (Goulden 1964), the Grosser Segeberger See, West Germany (Hoffman 1977), Linsley Pond and Rogers Lake, Connecticut (Austin 1942, Deevey 1942, 1969). According to Thienemann (1950), the long-spined *Eubosmina longispina* was a typical member of the European glacial "mischfauna." Subsequently, this species was replaced by a sequence of forms, *Eubosmina longispina* to *E. coregoni kessleri* to *E. c. coregoni*, which progressively moved toward mucrones.

As in the case of *Bosmina*, since the modern analogs of the *Eubosmina* occur in lakes of different trophic status, with *Eubosmina* characteristic of oligotrophic conditions and *E. c. coregoni* characteristic of eutrophic conditions (Patalas and Patalas 1966), the replacement sequence has generally been interpreted as representing succession toward eutrophication. Yet the same sequence can be interpreted to reflect a gradual increase of planktivorous fish activity, which results in the reduction or removal of large-bodied predatory copepods.

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Nitrification in the Course of Ecological Succession

Rice and Pancholy (1972) proposed that nitrification—the microbial oxidation of ammonium to nitrite and nitrate—progressively decreases in the course of ecological succession. They suggested that the mechanism causing the decrease is allelochemical inhibition of nitrification, and that the decrease is selectively advantageous to mature ecosystems because it conserves both nitrogen and energy.

Several lines of evidence have been used to support this hypothesis. Warren (1965), Rice and Pancholy (1972, 1973), Todd et al. (1975), Vogt and Edmonds (1977), and Lodhi (1979) have reported that in several secondary seres soil nitrate concentration or numbers of nitrifying bacteria or both tended to decrease with succession, while soil ammonium concentration increased. Less compelling evidence has included increased concentrations of nitrifier toxins in later successional systems (Rice 1974, 1979) and successional changes in the mineral-nitrogen preference of plants (Franz and Haines 1977, Haines 1977).

We believe there are problems with both the evolutionary basis of this hypothesis and the evidence supporting it. In particular, we question the use of nitrate or ammonium pool size and numbers of nitrifiers to indicate relative rates of nitrification. Relying on these measures to indicate nitrification rate implicitly assumes that (a) nutrient pool size reflects the rate of nutrient utilization and (b) reported population sizes of nitrifying bacteria accurately reflect nitrifier activity. We believe that neither assumption is warranted. First, nutrient concentration alone cannot indicate the relative importance of a nutrient. For example, a site with a consistently low concentration of soil nitrate could have a high rate of nitrification if plant uptake, leaching, and/or denitrification were rapidly removing nitrate from the soil. Measures of both nutrient pool size and rate of turnover are needed.

TABLE 1. Characteristics of soils from different stages of a primary sere at the Indiana Dunes and a secondary sere on the New Jersey Piedmont. Values are the unweighted means of either three subsites per site with two replicates per subsite (physical characteristics) or five subsites per site with five replicates per subsite (chemical characteristics), except for PO_4-P which is a site composite with five replicates per site. Different superscripts within each column indicate significantly different sites ($p < .05$) based on analysis of variance. Most-probable-number of ammonium oxidizers (MPN) is based on 10-fold dilutions from 10^{-2} to 10^{-9} with 10 tubes per dilution (Alexander and Clark 1965). MPN values are unweighted means of three subsites; 95% confidence limits appear in parentheses. Samples for all analyses were collected in August 1978.

Site	Bulk Density (g/cm³)	Texture		NO3-N (kg/ha)	NH4-N (kg/ha)	PO4-P (kg/ha)	pH	C:N	MPN
		% sand	% silt						
PRIMARY SERE									
Sand	1.66 (0.03)	97.6 (0.5)	1.3 (0.6)	0.01 (0)[a]	1.12 (0.08)[a]	2.85[a]	8.1 (0.1)[a]	31.8 (10.5)	370* (0-1110)[a]
Grass	1.69 (0.01)	98.5 (1.0)	1.1 (0.6)	0.01 (0)[a]	0.57 (0.08)[b]	3.10[a]	7.8 (0.1)[a]	29.4 (6.7)	2400 (1840-2960)[b]
Grass + shrub	1.71 (0.03)	96.4 (0.7)	3.2 (0.7)	0.07 (0.04)[b]	0.97 (0.17)[a]	2.52[a]	7.7 (0.2)[a]	21.0 (1.3)	500 (0-1650)[a]
Pine	1.15 (0.08)	93.0 (1.3)	5.2 (1.8)	0.01 (0)[a]	2.09 (0.35)[c]	2.76[a]	6.5 (0.1)[b]	18.6 (3.8)	530 (0-1450)[a]
Oak (1)	1.04 (0.08)	89.4 (1.5)	6.7 (0.8)	0.04 (0.03)[ab]	4.78 (1.43)[d]	31.5[b]	5.9 (0.4)[c]	14.8 (2.5)	2400 (1620-3180)[b]
Oak (2)	1.07 (0.04)	76.1 (2.1)	18.8 (4.6)	0.11 (0.04)[c]	3.26 (0.34)[d]	14.0[c]	4.2 (0.1)[d]	11.8 (5.1)	240* (0-710)[a]
SECONDARY SERE									
Annual	1.32 (0.01)	21.7 (1.7)	68.8 (2.0)	2.24 (0.17)[a]	2.61 (0.53)[a]	95.0[a]	5.0 (0.02)[a]	11.0 (1.1)	100,000 (38,000-162,000)[a]
Perennial	1.33 (0.02)	18.0 (2.5)	70.7 (1.2)	0.87 (0.15)[b]	2.37 (0.28)[a]	61.4[b]	4.9 (0.7)[a]	10.7 (0.8)	167,000 (0-396,000)[ab]
Shrub	1.22 (0.04)	21.9 (1.9)	68.7 (2.8)	1.63 (0.04)[c]	2.75 (0.17)[a]	106.0[a]	4.9 (0.02)[a]	12.1 (1.4)	113,000 (29,000-196,000)[a]
Old-growth forest	1.01 (0.05)	23.1 (0.9)	66.3 (2.5)	2.33 (0.27)[a]	3.56 (0.18)[b]	35.7[c]	4.4 (0.06)[b]	19.7 (5.7)	25,000 (0-51,000)[b]

*Two of the three subsites in these sites had < 90 cells/g; these were treated as zeroes.

Second, numbers of nitrifiers do not necessarily reflect activity. The most-probable-number (MPN) technique that is used to count nitrifiers counts only those adapted for rapid growth under the specific conditions of the incubation procedure (Belser and Schmidt 1978, Focht and Verstraete 1977). Further, the technique does not account for well-documented differential metabolic activities among counted cells (Ardakani et al. 1974, Boylen 1973, Fliermans and Schmidt 1975, McLaren 1973, Schmidt 1973).

These difficulties can be avoided by using nitrification potentials—the net rate of nitrate production in incubated soils. This approach was used by Coile (1940), Lamb (1979), and Montes and Christensen (1979), who measured nitrification potentials of soils from different stages of secondary successions. Although there are difficulties with the interpretations of these studies, none reported clear trends with succession.

Our study was designed to investigate successional changes in nitrification potential in two well-defined seres and thus to test the hypothesis that nitrification progressively decreases through succession. The primary sere was at the Indiana Dunes on the southern edge of Lake Michigan. Plant succession in this area has been extensively studied by Cowles (1899, 1901) and Olson (1958). Included in this study were six sites along a north-south transect: sand, grass, grass plus shrub, pine, oak (1), and old-growth oak (2) stages of succession.

The secondary sere was at the Hutcheson Memorial Forest on the New Jersey Piedmont. This is an old-growth mixed-oak stand with adjoining 1 ha known-age abandoned fields maintained as an ecological preserve by Rutgers University. The successional vegetation of the area has been well-documented (Bard 1952, Forman and Elfstrom 1975, Frye 1978, Lang and Forman 1978, Monk 1961, Monte 1973, Small et al. 1971). Four sites in this tract were studied: annual, perennial herb, shrub, and old-growth forest stages of succession. Table 1 presents properties of soils from sites along both seres.

If the hypothesis that nitrification is progressively inhibited in the course of ecological succession is correct, we would expect our incubations to yield two results: First, the amount of nitrate produced in the incubations (in the absence of nitrate uptake, leaching, and substantial denitrification) should decrease in the older sites. Second, nitrate should represent a
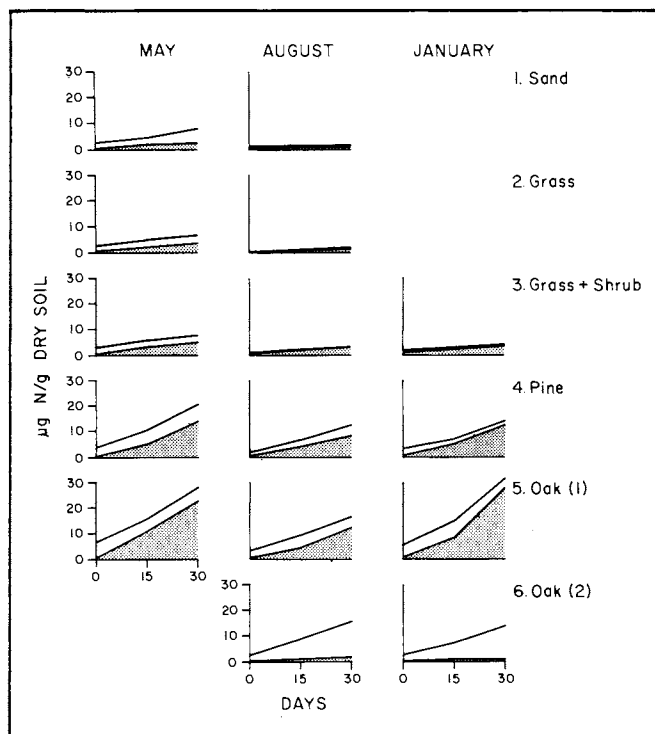

FIGURE 1. Net NO_3-N and total mineral nitrogen (NH_4-N plus NO_3-N) accumulation in soil samples collected along a primary sere at the Indiana Dunes in May, August, and January 1978-79 and incubated for 0, 15, or 30 days. The upper line in all cases represents total mineral-N accumulation; the lower line (shaded underneath) represents NO_3-N accumulation. Values plotted are the unweighted means of either three subsites per site with three replicates per subsite (May samples) or five subsites per site with five replicates per subsite (August and January samples) for each incubation period. Incubated soils were kept at 21°C and 60% field capacity in dark controlled-environment cabinets.
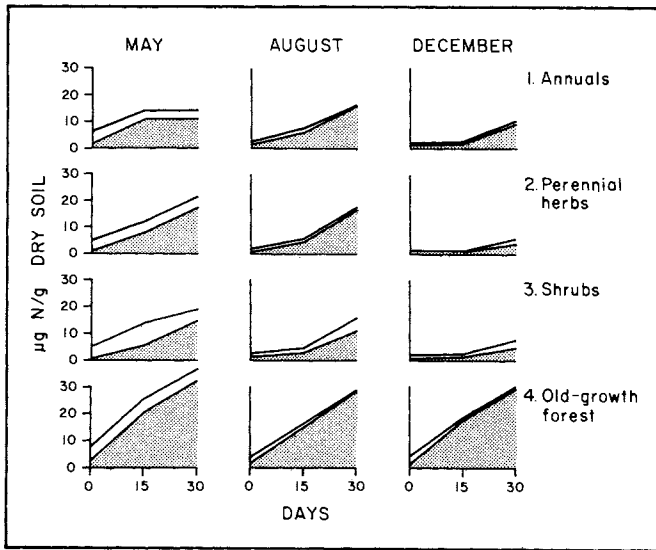
FIGURE 2. Net NO₃-N and total mineral nitrogen accumulation in soil samples collected along a secondary sere on the New Jersey Piedmont in May, August, and December 1978 and incubated for 0, 15, and 30 days. See Figure 1 legend for further explanation.

progressively smaller proportion of the net nitrogen mineralized in each sere.

The results of this study did not yield the pattern predicted by the hypothesis. Overall nitrate production increased with successional age until the last stage of the primary sere (Figure 1), whereas nitrate production in the secondary sere (Figure 2) showed no consistent pattern except that soils from the oldest stage produced the most nitrate. Moreover, most of the nitrogen mineralized was transformed to nitrate in most of the sites. Only in the older oak site in the primary sere was there clear, consistent evidence that nitrogen was mineralized but not converted to nitrate.

These results further suggest that rates of nitrification may in general be controlled by rates of nitrogen mineralization in these seres. This explanation may also fit situations in which nitrification rates are higher in early successional systems. These systems include a northern hardwoods forest shortly after clearcutting (Likens et al. 1970, Smith et al. 1968), a tulip-poplar forest shortly after stem girdling (Johnson and Edwards 1979), and may also include recently fertilized abandoned agricultural land (Woodwell 1979). The seres studied by Rice and Pancholy (1972, 1973, 1974) may fall into this latter category, although they do not report fertilization history. All of these situations have in common a high availability of mineral nitrogen early in succession. Thus the apparent pattern of rates of nitrification with succession reported by Rice and Pancholy (1972) and others may be caused not by progressive allelochemical inhibition of nitrification in older sites, but by systematically elevated nitrogen availability early in certain kinds of succession.

If this suggestion is correct, we would expect the pattern of nitrification in primary succession to be the reverse of that suggested by Rice and Pancholy (1972). Primary seres start with a nitrogen-poor substrate and gradually increase in total-nitrogen pool size (Stevens and Walker 1970). Consequently, rates of nitrogen mineralization and nitrification should progressively increase for many years. The results from the Indiana Dunes sere are in accordance with this suggestion (Figure 1). It is not clear that any consistent pattern should be expected in secondary succession.

Although we believe that in general nitrogen mineralization potentials are a good predictor of nitrification potentials, a number of sites such as our older oak site in Indiana have been studied in which this association does not hold (Ellenberg 1977, Johnson and Edwards 1979, Melillo 1977, Nakos 1977, Vitousek et al. 1979). The relatively low rates of nitrification in these sites could be caused by the allelochemic inhibition of nitrification (Rice and Pancholy 1972), or by low pH (Weber and Gainey 1962), by competition between nitrifiers and decomposers for some other limiting nutrient (Purchase 1974), or by low initial populations of viable nitrifiers (Sabey et al. 1959). Further research designed to determine which of these mechanisms are important and why they occur in particular kinds of sites would be most useful to our understanding of the control of nitrification.

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Measuring Fluctuating Environments

Many recent ecological hypotheses have been framed in terms of the differences expected between "stable" and "fluctuating" or "predictable" and "unpredictable" environments. Such hypotheses appear in discussions of life histories, species diversity, niche breadths, community stability, and genetic polymorphisms. If we are to test them rigorously, we need measures of environmental variation, independent of the organisms under study, that are sensitive to differences among habitats and that permit significance tests. Colwell (1974) developed measures of constancy, contingency, and predictability that do just that for nonmetric data. His measures are associated with log-likelihood (G) values approximated by the chi-square distribution for significance tests. He did not investigate the accuracy of that approximation, nor did he compare his measures with other measures of the association of cross-classified variables.

This paper describes the exact small-sample behavior of Colwell's measures, examines the adequacy of the significance tests he proposed, and compares his measures with two others proposed by Goodman and Kruskal (1954). It then demonstrates that Colwell's measures are sensitive to decisions that must be made in working up the data, compares their sensitivity in detecting periodicities to that of Fourier transforms, and provides both rules of thumb for working up data and tables for use in significance tests.

Colwell's measures partition the predictability (P) of a time-series into the separate contributions of constancy (C) and contingency (M). They are calculated by casting the raw data into a frequency matrix in which the rows represent the states the data can take, and the columns represent time periods. By calculating contingency for frequency matrices with various numbers of columns, one can locate the natural periodicities in the data: M is maximal when the number of columns matches the natural period.

Goodman and Kruskal's (1954) measures complement Colwell's. One measures the proportional reduction in error gained by predicting the row category given knowledge of the column category, relative to the prediction made under the assumption of independence of rows and columns. The other measures the proportion of variation in row categories explained by column categories. Although correlated in periodic series, the measures are not identical. One should first use M to locate the natural periodicities, then calculate Goodman and Kruskal's measures for additional insight.

My method involved generating on a computer, with Monte-Carlo techniques, artificial time-series appropriate to testing the null hypothesis that either constancy or contingency was zero. I then calculated Colwell's and Goodman and Kruskal's measures for each series, measured the number of Type I and Type II errors made in 10,000 such calculations, then contrasted those results with the number predicted by the significance tests. More than 320,000 time-series were used.

For large samples and data with strong periodicities, all measures were well-behaved, but for small samples and weak signals, the number of Type I errors exceeded those expected under the chi-square distribution, and the number of Type II