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Computation and Application of Nematode Community Indices: General Guidelines

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Community indices, such as maturity or diversity, condense information regarding the structure and composition of communities into a single metric. Soil health and quality can be inferred from such indices by assuming that communities with different structure and composition function differently. Thus, these indices can be instrumental in monitoring soil and sediment quality as well as assessing ecosystem sustainability and biodiversity.

Historical Perspective

In the 1980s, interest increased for using nematode communities as indicators for environmental monitoring of terrestrial communities (Freckman, 1988; Bongers, 1990). Initially, simple indices of abundance and proportions or ratios of nematodes by trophic group were proposed. Subsequently, diversity indices were employed and a maturity index (MI) was developed for terrestrial nematodes (Yeates, 1970, 1984; Bongers, 1990). Later, the application of the MI was extended successfully to marine and brackish sediments (Bongers *et al.*, 1991). Since then, others have applied the concept to freshwater systems (Beier and Traunspurger, 2003; Höss *et al.*, 2004).

Maturity Indices

Maturity indices are used as a measure of the ecological successional status of a soil community. They are based on the principle that different taxa have contrasting sensitivities to stress or disruption of the successional sequence because of their life-history characteristics. Bongers originally proposed separate indices for free-living (MI) and plant-parasitic (PPI) nematodes. The index is represented by a colonizer–persister ($c-p$) value that ranges from a colonizer ($c-p = 1$) to a persister ($c-p = 5$) with the index values representing life-history characteristics associated

with r - and K -selection, respectively. Those with a $c-p = 1$ are r -selected or colonizers, with short generation times, large population fluctuations and high fecundity. Those with a $c-p = 5$ are K -selected or persisters, produce few offspring and generally appear later in succession (Bongers and Bongers, 1998; Bongers and Ferris, 1999). Small and large $c-p$ weights correspond with taxa relatively tolerant and sensitive to ecological disturbance, respectively (Table 11.1).

Maturity Indices are computed as a weighted mean frequency,

$$MI = \sum \frac{v_i \times f_i}{n}$$

where $v_i = c-p$ value assigned to family, $f_i =$ frequency of family i in sample, $n =$ total number of individuals in a sample. MI may be viewed as a measure of disturbance, with smaller values being indicative of a more disturbed environment and larger values characteristic of a less disturbed environment. The MI decreases with increasing microbial activity and pollution-induced stress when opportunistic nematodes rapidly become dominant. The PPI may (Neher and Campbell, 1994) or may not (Bongers *et al.*, 1997) correlate positively with MI.

Both stress and enrichment result in MI decrease; stress decreases numbers of sensitive species and enrichment increases abundance of opportunists. To differentiate decreases of MI caused by enrichment and pollution from environmental stress, it is better to omit $c-p = 1$ (Bongers and Korthals, 1993; Bongers *et al.*, 1995; Korthals *et al.*, 1996). Opportunistic taxa ($c-p = 1$) are re-evaluated because they are considered enrichment opportunists and their population densities increase rapidly in response to addition of nutrients to soil and may not necessarily reflect long-term changes in soil ecological condition. Those with $c-p$ values between 2 and 5 are more stable temporally and may provide relatively long-term information about environmental conditions. Therefore, it is recommended that marine Oncholaimidae be omitted because they accumulate to generate mono-populations under anoxic enriched conditions known to result in fish dying. Furthermore, dauer larvae of Rhabditidae, Diplogasteridae and Panagrolaimidae are not included because they are non-feeding or inactive stages at the time of sampling.

Yeates (1994) and Wasilewska (1994) proposed a modification of the index based on merging free-living and plant-parasitic nematodes in a soil community (ΣMI). Neher and Campbell (1996) suggested a ΣMI_{25} , which represents a combination of the concepts proposed by Bongers *et al.* (1995) and Yeates (1994). In each

Table 11.1 Colonizer–persister ($c-p$) value assignments for selected nematode families (Bongers and Bongers, 1998).

$c-p$ value	Family
1	Rhabditidae, Diplogasteridae (s.l.), Panagrolaimidae, Bunonematidae
2	Cephalobidae, Plectidae, Monhysteridae, Aphelenchoididae
3	Teratocephalidae, Chromadoridae, Diphtherophoridae, Prismatolaimidae
4	Alaimidae, Mononchidae, Leptonchidae, Qudsianematidae, Dorylaimidae
5	Aporcelaimidae, Actinolaimidae, Thornenematidae, Belonidiridae

case, the same basic calculation is performed except different combinations of feeding groups (Yeates *et al.*, 1993) and *c-p* groups are included. The difference in these two more comprehensive indices is that they include and exclude *c-p* = 1 nematodes, respectively. As no distinction between free-living and plant-parasitic nematodes is necessary these indices solve a disagreement on whether to include (Bongers, 1990) or exclude (Neher and Campbell, 1996) Tylenchidae in the PPI. The controversy is based on whether Tylenchidae are considered fungal or root feeders.

Diversity

Diversity has been equated solely with numbers of taxa, and the popular press has perpetuated this misconception. Rather, a more appropriate indication of diversity integrates numbers of taxa ('species richness') and equitability among taxa ('species evenness') (Hurlbert, 1971). Two assumptions of most diversity indices include: (i) an index limited to one taxonomic group; and (ii) all species are equal (Cousins, 1991). Good (1953) outlined a generalized diversity index that incorporates richness and evenness into a single value that generally increases with both richness and evenness:

$$H(\alpha, \beta) = \sum_{i=1}^s p_i^\alpha \left\{ -\ln(p_i) \right\}^\beta$$

where p_i is the relative abundance of taxon i , S is the total number of species present and α and β define structural attributes of the algorithm. Good's generalized diversity index demonstrates the mathematical relation of several commonly used diversity, dominance and evenness indices (Table 11.2). Namely, Shannon's diversity index can be interpreted as a variant of Good's diversity index using values of 1 and 1 for α and β , respectively (or $H(1,1)$). Simpson's dominance index can be interpreted as $H(2,0)$. Rényi (1961) defined a notation of this generalized equation, which allows a user to put in different coefficients for species richness and dominance concentration (followed by Hill, 1973), and Baczkowski *et al.* (1997) discuss optimal bounds of α and β for ecological applications. Most other indices constitute logarithmic, exponential, reciprocal, complementary or relative transformations of the Shannon or Simpson indices. In addition to the main indices listed in Table 11.2, numerous alterations have been reported as evenness indices, including $(1-D)/(1-1/S)$, $(1-D)/S$, and $(-\ln D)/(\ln S)$ by Smith and Wilson (1996), and $(1/D-1)/(e^H-1)$ by Alatalo (1981) (D is Simpson's dominance index as in Table 11.2).

These variations on a theme demonstrate unique sensitivities to changes in various structural attributes of an abundance distribution within a community. For example, first, the Camargo diversity index may be more sensitive for assessing structural alterations in aquatic communities than the Shannon (H') and MacArthur indices, which are sensitive to the number of taxa present and the whole spectrum of taxon proportions (Camargo, 1992). Second, the Camargo index typically increases with the addition of subordinate species (those defined as having a relative abundance less than $1/S$) more than most indices, valuing rare species. Beisel *et al.* (1996) argues that such sensitivity to rare species is an undesirable property of a diversity index and favours the Simpson and McIntosh indices that are more sensitive to changes in dominant taxa. Camargo (1997) rebuts with the

Table 11.2 Common indices used to characterize the distribution of abundance within a community.

Name	Equation*	Application	Reference
Diversity indices			
Shannon's diversity	$H' = -\sum (p_i \ln p_i)$	This widely used and versatile index can be applied for both large and small sample sizes. The Shannon index is generally more influenced by rare species than the Simpson index.	Shannon and Weaver (1949)
Hill's diversity	$N_1 = \exp [-\sum (p_i \ln p_i)] = \exp (H')$	An exponential form of Shannon's H' , the value of this index can be interpreted as the number of abundant taxa (Ludwig and Reynolds, 1988).	Hill (1973)
Brillouin's diversity	$H = \frac{1}{N} \log \frac{M!}{\prod N_i!}$	Use only on fully censused communities because it is a true statistic and, thus, free from statistical error.	Brillouin (1962)
Camargo's diversity	$d = \sum \left[P_i - \left(\frac{1}{S} \right) \right]$	Estimates the (structural) asymmetry in relative abundance between dominant and subordinate species, not necessarily differences between dominant species or between subordinate species.	Camargo (1992)
Margalef's diversity	$D_{\text{Marg}} = \frac{(S-1)}{\ln(N)}$	Though simple to calculate, this index is unaffected by evenness or dominance and is sensitive only to species richness and sample size. Thus, its use	Margalef (1958)

should be restricted to comparing species richness among large communities.

Dominance indices	$D = \sum p_i^2$	Probability that two randomly chosen individuals of an infinite community belong to the same class, thus inversely related to diversity. It is often reported as $1-D$, but see Hurlbert's PIE.	Simpson (1949)
Simpson's dominance (infinite community)	$N_2 = (\sum p_i^2)^{-1} = 1/D$	The reciprocal of Simpson's D , the value of this index can be interpreted as the number of very abundant taxa (Ludwig and Reynolds, 1988)	Hill (1973)
Simpson's dominance (finite community)	$\lambda = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$	Similar to Simpson's D , but corrected for finite communities. Mathematically, it is usually more appropriate in ecological studies than Simpson's D , but is used less often.	Simpson (1949)
Probability of interspecific encounter (PIE)	$PIE = \left(\frac{N}{N-1}\right) \left(1 - \sum p_i^2\right)$	Simpson's dominance index D converted to a diversity index and corrected for finite communities	Hurlbert (1971)
McIntosh dominance	$D1 = \frac{(N - \sqrt{\sum n_i^2})}{(N - \sqrt{N})} \approx \sqrt{\frac{\sum n_i^2}{N}}$	Recommended by Beisel <i>et al.</i> (1996) as the most relevant dominance index since most sensitive to variations on dominant taxa and not highly sensitive to variations on rare or medium taxa.	McIntosh (1967)

Table 11.2 Continued. Common indices used to characterize the distribution of abundance within a community.

Name	Equation*	Application	Reference
Evenness indices			
Brillouin's maximum diversity	$H_{\max} = \frac{1}{N} \ln \frac{N!}{\left(\frac{N}{S}\right)^{s-1} \left[\left(\frac{N}{S}\right) + 1\right]^r}$	Represents maximum possible evenness of a sample of N individuals and S species such that $N = S[N/S] + r$ where $[N/S]$ is the integer portion of N/S and r is the remainder.	Brillouin (1962)
Brillouin's minimum evenness	$H_{\min} = \frac{1}{N} \ln \frac{N!}{(N - S + 1)}$	Represents minimum possible evenness of a sample of N individuals and S species.	Brillouin (1962)
Brillouin's evenness	$J = \frac{H}{H_{\max}} \text{ or } J' = \frac{H'}{\ln S}$	Use J for samples (and J' for collections) to determine the evenness portion of diversity; J or J' represent observed and maximum diversity, respectively.	Pielou (1966)
Brillouin's relative evenness	$V = \frac{H - H_{\min}}{H_{\max} - H_{\min}}$	Unlike J and J' , V is not influenced by species richness (S)	Hurlbert (1971)
Heip's evenness	$E_{\text{Heip}} = \frac{(e^{H'} - 1)}{(S - 1)}$	Hypothesized by Beisel <i>et al.</i> (2003) to be more sensitive to variations in rare species richness and/or abundance.	Heip (1974)

(Dis) Similarity indices

Morisita's similarity

$$C_H = \frac{2 \sum (p_{ij} p_{ik})}{\sum_j p_{ij}^2 + \sum_k p_{ik}^2}$$

Quantitative data; represents the degree of overlap between segment j and all segments combined (k). It ranges from 0 (no similarity in community structure) to 1 (complete similarity) and is often expressed as a percentage ($C_H * 100$).

Morisita (1959)

Bray-Curtis dissimilarity

$$BC_{ij} = \sum \frac{|n_{ik} - n_{jk}|}{(n_{ik} + n_{jk})}$$

Quantitative data; an alternative to Morisita's similarity.

Bray and Curtis (1957)

Jaccard similarity

$$S_J = 100 * \frac{c}{(a + b + c)}$$

Binary data (presence/absence); represents the percent of taxa present that are similar to both groups.

Jaccard (1912)

Sørensen similarity

$$CC = 100 * \frac{2c}{(a + b + 2c)}$$

Represents the percent similarity of each group with respect to taxa present.

Sørensen (1948)

p_i represents the proportion of the i -th taxa in a sample, or n_i the number, with M individuals and S total species.

†Quantitative data: p_{ij} or p_{ik} represents the proportion of the i -th taxa in sample j or k , or n_j the number; binary data: a the number of taxa unique to group A, b the number of taxa unique to group B, and c the number of taxa common to both group A and group B.

argument that the 'conviction that rare taxa should not contribute to the response of a dominance index is absurd'. In fact, the Camargo index is one of few diversity indices developed from an *a priori* ecological definition that dominance is the appropriation of potential niche space of certain subordinate species by other dominant species (McNaughton and Wolf, 1970).

The debate defining 'dominance' and 'diversity' raises a second question, that of which taxa to include in an index. Ideally a summary statistic such as a diversity index could relate the abundance structure of an entire community. For a freshwater nematode community, this would include all the bacterivores, algivores, herbivores, predators and omnivores. However, if the McNaughton and Wolf (1970) definition of dominance is accepted as a complement to diversity, then logically only one trophic group should be included in any diversity or dominance index. This creates a practical problem because the specific feeding habits of most nematode species are diverse, changing or unknown. In fact, first, the effect of each species on ecosystem processes has not been determined (Chapin *et al.*, 1992). Second, the reduction of diversity indices to specific functional groups entirely contradicts the intended use of indices, i.e. to summarize complex and varied community data into a single useful datum (Beisel, 1997).

Not all indices are contested so vigorously. Although the sensitivities of respective indices are still unclear, some generalization can be made from the literature. Typically, Shannon's (H') index is sensitive to rare taxa and Simpson's (λ) index weights common taxa (Boyle *et al.*, 1990). Hill's family of diversity numbers are easy to interpret ecologically because the indices define units as taxa (Peet, 1974) but they are not necessarily superior from a statistical perspective (Heip *et al.*, 1988; Ludwig and Reynolds, 1988). Hill's diversity numbers N_0 , N_1 and N_2 are defined as numbers of all taxa, abundant taxa and very abundant taxa, respectively (Ludwig and Reynolds, 1988). N_1 equates with an antilog of a Shannon index (eH') and N_2 equals the reciprocal of a Simpson index ($1/\lambda$).

Diversity is linked artificially to the taxonomic resolution an investigator employs. Even though diversity is most often equated with species, it can be applied at various taxonomic levels of resolution, such as genotype, genus, family and trophic group. For free-living nematodes, it is more common to apply diversity indices to taxonomic levels above species because species identifications based on morphology are difficult. Appropriate caution must be taken when applying indices at the family or trophic group levels. Unfortunately, ambiguity in trophic classification of nematodes usually occurs because it is inferred by morphology rather than actual experiments on feeding preferences (Yeates *et al.*, 1993). Furthermore, feeding-habit groupings may be ambiguous and/or not mutually exclusive in some cases. For example, abundant populations of *Aphelenchoides*, *Tylenchus*, *Tylencholaimus* and *Ditylenchus* can be classified as 'plant-/fungal-feeding' nematodes (Sohlenius *et al.*, 1977), or some 'predaceous' *Mesodorylaimus* sp. can grow and reproduce by feeding on bacteria (Russell, 1986). *Tylenchus* spp. are often considered fungivores in ecological studies, but the basis of the judgement is dubious because several species feed and reproduce on roots. In other cases, some species may always be placed in one category and may have developmental stages or generations that fit in another category.

As diversity indices are based on relative abundances of community species they are insensitive to taxonomic differences between species. Alternatively, biodiversity indices are based on taxonomic relations among species and ignore species abundances. However, in many environmental planning and protection programmes, there is interest in both species composition and relative distribution. Therefore, new combined indices have been proposed such as the quadratic entropy index (Q), which incorporates relative abundances of both species and a measure for the pairwise taxonomic differences between species (Izsak and Papp, 2000; Ricotta, 2002). Unfortunately, these new combined indices violate part of the mathematical properties of an ecological diversity index, so they are dubbed 'weak diversity indices'.

Critical to valid interpretation of diversity indices are appropriate sampling and statistical techniques. Generally, stratified- or simple-stage cluster sampling are touted as generating less bias in diversity estimates than simple random sampling (Gimaret-Carpentier *et al.*, 1998; Mayoral, 1998; di Battista, 2002). Commonly, diversity indices are analysed statistically with traditional ANOVA procedures. However, care must be taken to ensure that assumptions of normality and equal variances are met, especially for small sample sizes. Sometimes, distributions can be transformed to resemble a Gaussian distribution by application of log and log-normal scales (Hill *et al.*, 2003). Rogers and Hsu (2001) propose an asymptotically correct method for diversity indices with unequal variances, when sample sizes are equal, and transformations cannot remedy the situation.

Trophic Group Ratios

Ratios of trophic groups have been proposed to describe the relative balance of positive to negative impacts of nematodes on primary productivity or stage of decomposition. Wasilewska (1989) proposed a ratio that computes the sum of fungivores and bacterivores divided by plant parasites. A ratio greater than 1 suggests that the positive impacts of nematodes outweigh the negative impacts on plant productivity. Two forms of decomposition pathway indices have been proposed, differing in the denominator. Statistically, the form fungivores divided by the sum of fungivores and bacterivores [$F/(F+B)$] is considered mathematically more stable than simply dividing fungivores by bacterivores (F/B). Because each variation gives a contrasting result, it is critical that the user defines the ratio employed in the results of a report. Typically, individual or ratios of trophic groups have not withstood the level of statistical rigour that maturity and trophic diversity indices do in their ability to differentiate the ecological condition of soils on a large geographic scale (Neher *et al.*, 1995; Neher and Campbell, 1996).

Multivariate Approaches

Canonical Correspondence Analysis (CCA) is useful to compare suites of taxon data with suites of environmental variables. Environmental variables can include treatment classes as nominal 0 or 1 variables or chemical properties or pollutants as continuous variables. CANOCO (ter Braak and Smilauer, 2002) and PRIMER-E

(<http://www.pml.ac.uk/primer/index.htm>) software are simple tools to perform these procedures. In CANOCO, abundances are transformed as $\log(x + 1)$ before analysis. Transformations are unnecessary in PRIMER because the scaling is non-metric multi-dimensional scaling. CCA results are displayed graphically with biplots. In CCA biplots, each vector for an environmental variable defines an axis, and site or genera scores can be projected on to that axis (Jongman *et al.*, 1995). An indication of relative importance of a vector is its length; the angle indicates correlation with other vectors and CCA axes. Eigen values for CCA axes indicate the importance of the axes in explaining relationships in the genera–environment data matrices. Unfortunately, CCA analyses are restricted to illustrating one instance at a time.

Principal response curves (PRC) is a multivariate method for the analysis of repeated measurement design. PRC is based on redundancy analysis (RDA); each experimental unit and sampling times and unit by time interactions are treated as dummy explanatory variables. The result is a diagram showing the sampling periods on the *x*-axis and the first principal component of the variance explained by treatment on the *y*-axis. For illustrative purposes, undisturbed condition was treated as a ‘control’, representing a zero baseline, and ‘disturbed’ of the same experimental unit as the ‘treatment’ to focus on the ‘differences’ between the two states of condition through time. Monte Carlo permutation tests permuting whole time series are applied to compute statistical significance. van den Brink *et al.* (2003) provide a review of the analytical procedure and detailed instruction is provided in the manual of CANOCO Version 4.5 software (ter Braak and Smilauer, 2002).

References

- Alatalo, R.V. (1981) Problems in the measurement of evenness in ecology. *Oikos* 37, 199–204.
- Baczkowski, A.J., Joanes, D.N. and Shamia, G.M. (1997) Properties of a generalized diversity index. *Journal of Theoretical Biology* 188, 207–213.
- Beier, S. and Traunspurger, W. (2003) Seasonal distribution of free-living nematodes in the Krahenbach, a fine-grained submountain carbonate stream in southwest Germany. *Nematology* 5, 113–136.
- Beisel, J.N. (1997) Assessing changes in community structure by dominance indices: a comparative analysis – response. *Journal of Freshwater Ecology* 12, 641–646.
- Beisel, J.N., Thomas, S., Ussegliopolatera, P. and Moreteau, J.C. (1996) Assessing changes in community structure by dominance indices: a comparative analysis. *Journal of Freshwater Ecology* 11, 291–299.
- Beisel, J.N., Usseglio-Polatera, P., Bachmann, V. and Moreteau, J.C. (2003) A comparative analysis of evenness index sensitivity. *International Review of Hydrobiology* 88, 3–15.
- Bongers, T. (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83, 14–19.
- Bongers, T. and Bongers, M. (1998) Functional diversity of nematodes. *Applied Soil Ecology* 10, 239–251.
- Bongers, T. and Ferris, H. (1999) Nematode community structure as a bioindicator in environmental monitoring. *Trends in Evolution and Ecology* 14, 224–228.
- Bongers, T. and Korthals, G. (1993) The maturity index, an instrument to monitor changes in the nematode community structure. *Proceedings of the International Symposium on Crop Protection* 45, 80.
- Bongers, T., Alkemade, R. and Yeates, G.W. (1991) Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. *Marine Ecology Progress Series* 76, 135–142.

- Bongers, T., de Goede, R.G.M., Korthals, G. and Yeates, G.W. (1995) Proposed changes of c-p classification for nematodes. *Russian Journal of Nematology* 3, 61–62.
- Bongers, T., van der Meulen, H. and Korthals, G. (1997) Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. *Applied Soil Ecology* 6, 195–199.
- Boyle, T.P., Smillie, G.M., Anderson, J.C. and Beeson, D.R. (1990) A sensitivity analysis of nine diversity and seven similarity indexes. *Research Journal of the Water Pollution Control Federation* 62, 749–762.
- Bray, J.R. and Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27, 325–349.
- Brillouin, L. (1962) *Science and Information Theory*, 2nd edn. Academic Press, New York.
- Camargo, J.A. (1992) New diversity index for assessing structural alterations in aquatic communities. *Bulletin of Environmental Contamination and Toxicology* 48, 428–434.
- Camargo, J.A. (1997) Assessing changes in community structure by dominance indices: a comparative analysis – rebuttal. *Journal of Freshwater Ecology* 12, 637–641.
- Chapin, F.S., Schulze, E.D. and Mooney, H.A. (1992) Biodiversity and ecosystem processes. *Trends in Ecology and Evolution* 7, 107–108.
- Cousins, S.H. (1991) Species diversity measurement: choosing the right index. *Trends in Ecology and Evolution* 6, 190–192.
- di Battista, T. (2002) Diversity index estimation by adaptive sampling. *Environmetrics* 13, 209–214.
- Freckman, D.W. (1988) Bacterivorous nematodes and organic-matter decomposition. *Agriculture, Ecosystems, and Environment* 24, 195–217.
- Gimaret-Carpentier, C., Pelissier, R., Pascal, J.P. and Houllier, F. (1998) Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9, 161–172.
- Good, I.J. (1953) The population frequencies of species and the estimation of population parameters. *Biometrika* 40, 237–264.
- Heip, C. (1974) A new index measuring evenness. *Journal of the Marine Biological Association* 54, 555–557.
- Heip, C., Herman, P.M.J. and Soetaert, K. (1988) Data processing, evaluation, and analysis. In: Higgins, R.P. and Thiel, H. (eds) *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, DC, pp. 197–231.
- Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432.
- Hill, T.C.J., Walsh, K.A., Harris, J.A. and Moffett, B.F. (2003) Using ecological diversity measures with bacterial communities. *FEMS Microbiology Ecology* 43, 1–11.
- Höss, S., Traunspurger, W., Severin, G.E., Jüttner, I., Pfister, G. and Schramm, K.W. (2004) Influence of 4-nonylphenol on the structure of nematode communities in freshwater microcosms. *Environmental Toxicology and Chemistry* 23, 1268–1275.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.
- Izsak, J. and Papp, L. (2000) A link between ecological diversity indices and measures of biodiversity. *Ecological Modelling* 130, 151–156.
- Jaccard, P. (1912) The distribution of flora in the alpine zone. *The New Phytologist* 11, 37–50.
- Jongman, R.H.G., ter Braak, C.J.F. and van Tongeren, O.F.R. (1995) *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge, UK.
- Korthals, G.W., de Goede, R.G.M., Kammenga, J.E. and Bongers, T. (1996) The Maturity Index as an instrument for risk assessment of soil pollution. In: van Straalen, N.M. and Krivolutski, D.A. (eds) *Bioindicator Systems for Soil Pollution*. Kluwer Academic, Dordrecht, The Netherlands, pp. 85–93.
- Ludwig, J.A. and Reynolds, J.F. (1988) *Statistical Ecology: A Primer on Methods and Computing*. John Wiley & Sons, New York.
- Margalef, R. (1958) Information theory in ecology. *General Systems* 3, 36–71.
- Mayoral, M.M. (1998) Rényi's entropy as an index of diversity in simple-stage cluster sampling. *Information Sciences* 105, 101–114.

- McIntosh, R.P. (1967) An index of diversity and the relation of certain concepts to diversity. *Ecology* 48, 392–404.
- McNaughton, S.J. and Wolf, L.L. (1970) Dominance and the niche in ecological systems. *Science* 167, 131–139.
- Morisita, M. (1959) Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Japan, Series E. (Biol.)* 3, 65–80.
- Neher, D.A. and Campbell, C.L. (1994) Nematode communities and microbial biomass in soils with annual and perennial crops. *Applied Soil Ecology* 1, 17–28.
- Neher, D.A. and Campbell, C.L. (1996) Sampling for regional monitoring of nematode communities in agricultural soils. *Journal of Nematology* 28, 196–208.
- Neher, D.A., Peck, S.L., Rawlings, J.O. and Campbell, C.L. (1995) Measures of nematode community structure for an agroecosystem monitoring program and sources of variability among and within agricultural fields. *Plant and Soil* 170, 167–181.
- Peet, R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics* 5, 285–307.
- Pielou, E.C. (1966) Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370–383.
- Rényi, A. (1961) On measures of entropy and information. *Proceedings of the Fourth Berkeley Symposium on Mathematical Statistics and Probability* 1, 547–561.
- Ricotta, C. (2002) Bridging the gap between ecological diversity indices and measures of biodiversity with Shannon's entropy: comment to Izsak and Papp. *Ecological Modelling* 152, 1–3.
- Rogers, J.A. and Hsu, J.C. (2001) Multiple comparisons of biodiversity. *Biometrical Journal* 43, 617–625.
- Russell, C.C. (1986) The feeding habits of a species of *Mesodorylaimus*. *Journal of Nematology* 18, 641.
- Shannon, C.E. and Weaver, W. (1949) *The Mathematical Theory of Communication*. University of Illinois, Urbana, Illinois.
- Simpson, E.H. (1949) Measurement of diversity. *Nature* 163, 688.
- Smith, B. and Wilson, J.B. (1996) A consumer's guide to evenness indices. *Oikos* 76, 70–82.
- Sohlenius, B., Persson, H. and Magnusson, C. (1977) Distribution of root and soil nematodes in a young Scots pine stand in central Sweden. *Ecological Bulletins (Stockholm)* 25, 340–347.
- Sørensen, J. (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Danske Videnskabers Selskabs Biologiske Skrifter* 5, 1–34.
- ter Braak C.J.F. and Smilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide, Software for Canonical Community Ordination* (version 4.5), Biometris, Wageningen and České Budějovice, The Netherlands, 500 pp.
- van den Brink, P.J., van den Brink, N.W. and ter Braak, C.J.F. (2003) Multivariate analysis of ecotoxicological data using ordination: demonstrations of utility on the basis of various examples. *Australasian Journal of Ecotoxicology* 9, 141–156.
- Wasilewska, L. (1989) The role of nematodes in agroecosystems. *Żeszyty Problemowe Postępów Nauk Rolniczych* 358, 7–16.
- Wasilewska, L. (1994) The effect of age of meadows on succession and diversity in soil nematode communities. *Pedobiologia* 38, 1–11.
- Yeates, G.W. (1970) The diversity of soil nematode faunas. *Pedobiologia* 10, 104–107.
- Yeates, G.W. (1984) Variation in soil nematode diversity under pasture with soil and year. *Soil Biology and Biochemistry* 16, 95–102.
- Yeates, G.W. (1994) Modification and qualification of the nematode Maturity Index. *Pedobiologia* 38, 97–101.
- Yeates, G.W., Bongers T., de Goede, R.G.M., Freckman, D.W. and Georgieva, S.S. (1993) Feeding habits in soil nematode families and genera – an outline for soil ecologists. *Journal of Nematology* 25, 315–331.