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A Weighted Coenotic Index (WCI): Description and application to soil animal assemblages

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Summary. The Weighted Coenotic Index (WCI) is a single value that unifies total abundance, dominance structure, species richness and ecological weightings, e.g., habitat preferences and positions of species in the r/K continuum. Studies with simulated species assemblages have shown that ecological weightings and dominance structure are major components of the index; the ecological weightings must be related to the group of organisms studied and to the scope of the investigation. The WCI is a relative measure that needs a reference (control) site in each investigation for a conclusive interpretation. Compared to several diversity indexes, the WCI has a much better discriminant ability because it includes ecological weightings and a log-normal dominance structure. This index has been applied to published data from several field studies using protozoa (testate amoebae, ciliates) and earthworms. The results show that the WCI is an appropriate tool to measure changes and to monitor recovery processes in disturbed ecosystems. The index should be calculated separately for each systematic (indicator) group (e.g., ciliates, nematodes, mites) because the information will be more detailed and an overall index could, for instance, mask a high value for one group, such as ciliates, in conjunction with a low value for another group, such as nematodes. The WCI has been developed on a protozoological background owing to the authors' familiarity with this field. Mathematically and practically it is also applicable to other groups of soil and freshwater organisms.

Key words: Weighted coenotic index – WCI – Biotic index – Soil animals – Indicator organism approach – Protozoa – Soil organisms

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Various methods and indexes have been suggested to measure the structure and "quality" of animal and plant assemblages (for reviews see Schwerdtfeger 1975; Wolda 1981; Washington 1984). Those used in terrestrial ecology are generally unweighted, whereas freshwater biologists often ascribe ecological weightings to their "indicator species". Despite being sometimes considered problematic, biased "biotic indexes" have gained great acceptance by field ecologists; saprobity indexes, for example, are widely used to evaluate the quality of running water (Sládeček 1973; Friedrich 1990).

Weighted indexes for soil organisms have been proposed by Lienemann (1982), Beck (1984), Lüftenegger et al. (1985), and Bongers (1990). Lienemann's "ecotype diversity" combines species richness and number of ecotypes at a particular site using the Shannon–Wiener formula. Beck's "Bodenmikrobiologische Kennzahl" combines values for microbial biomass and soil enzymes to quantify microbial activity. Lüftenegger's "C/P Index" and Bongers's "Maturity Index" are based on the proportion of *r*- and *K*-selected ciliates and nematodes, respectively. Such indexes have been successfully applied to measure aspects of natural and disturbed terrestrial ecosystems (e.g., Yeates et al. 1991). Most recently, Ducommun (1991) has suggested a weighted index on the basis of macroinvertebrates, using species abundance and the proportion of phytophages, decomposers and predators.

The published indexes use only a few relevant ecological parameters. The weighted coenotic index (WCI) we propose unifies several basic attributes (species richness, total abundance, dominance structure, and ecological weightings, viz., the degree of autochthonism and the position of species in the *r/K* continuum) of biocoenoses in a single value.

Calculation and background of the Weighted Coenotic Index (WCI)

For samples of the same dimensions

$$\text{WCI} = \sum_{i=1}^{S} \left[10^8 \underbrace{\frac{p_i (1-p_i)^{s-1}}{[o_i (o_{\max} - o_i) + 1]}}_{\text{distribution component}} \times \underbrace{\frac{n_{\max} \tilde{n}_i}{[(n_{\max} - \tilde{n}_i)(\tilde{n}_i - n_{\min}) + 1]}}_{\text{distribution constant}} \times \underbrace{\frac{w_{1i} w_{2i} w_{ni}}{NS}}_{\text{abundances + weightings}} \right] \frac{1}{S}$$

for samples of different dimensions

$$\text{WCI} = \sum_{i=1}^{S} \left[10^8 \frac{p_i (1-p_i)^{s-1}}{\{[o_i - ld(d)]\,[o_{\max} - o_i] + 1\}} \times \frac{n_{\max} \tilde{n}_i}{\{[n_{\max} - \tilde{n}_i]\,[\tilde{n}_i - n_{\min}] + d^2\}} \times \frac{w_{1i} w_{2i} w_{ni} d}{NS} \right] \frac{1}{S}$$

for $p_i = S \neq 1$

d, dimension of the sample, e.g., mass or volume
n_i, number of individuals in species i
$\tilde{n}_i$, median of the n_i values
$n_{\max}$, highest n_i value in a sample
$n_{\min}$, lowest n_i value in a sample
N, total number of individuals
o_i, $1 + ld(n_i)$ = octave species i belongs to
$o_{\max}$, $1 + ld(n_{\max})$ = highest octave in a sample
p_i, n_i/N = relative abundance of species i
S, species richness, i.e., total number of species in all replicates
w_{1i}, weighting 1, e.g., degree of autochthonism in species i
w_{2i}, weighting 2, e.g., the position of species i in the r/K continuum
w_{ni}, further weightings
10^8, factor used to transform values to integers

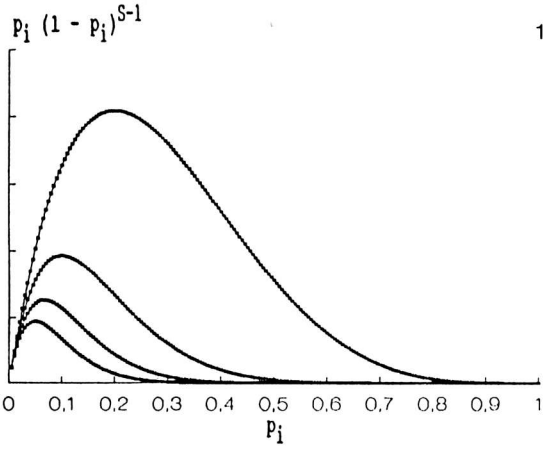
Species richness (S) and total abundance (N) influence the WCI by being in the denominator of the 'abundances + weightings'; thus the index gets proportionally lower (better) with increasing species number and total abundance. Species richness interacts with the numerator of the 'distribution component'; total abundance, however, interacts with the denominator of the 'distribution component', through $ld(n_i)$ which is implied in o_i.

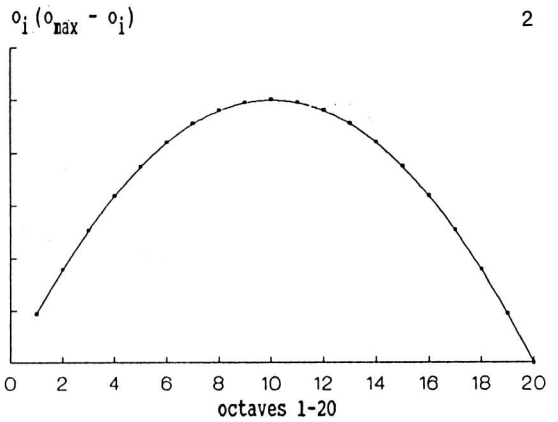
The distribution component and the distribution constant (dominance structure) are based on the log-normal pattern. The logarithmic series fits extremely well to a large number of frequency series drawn from insects, birds, butterflies, and plants (Williams 1944; Preston 1948; Pielou 1969; Wolda 1981; Magurran 1988). Traditionally, the $\log_2$ classes are termed octaves (Preston 1948; Magurran 1988). Since an even distribution, i.e., the same number of individuals per species, represents an abnormal and rare form of dominance structure that occurs only in strongly disturbed or extreme communities (Schwerdtfeger 1975; Magurran 1988), it is considered the most extreme case. This is reflected by the function $f(p_i) = p_i(1-p_i)^{s-1}$ in the numerator of the distribution component. In the case of an even distribution, each p_i equals $1/S$, which is the peak of the above function. Thus, the more the dominance structure approaches an even distribution (the more p_i tends to $1/S$) the worse the index. Since S is in the exponent with a basis of ≤ 1 and > 0, the value of the function decreases, giving better index values for increasing values of S (see simulation experiments). This function, however, produces very low (good) values around the n_i maximum and minimum (Fig. 1), and in the case of extreme species assemblages (n_i values only around the maximum and minimum) function values are irrationally low (good). To compensate for this bias, the deviation of the extremes ($n_{\max}$, $n_{\min}$) from the median ($\tilde{n}_i$) is calculated as:

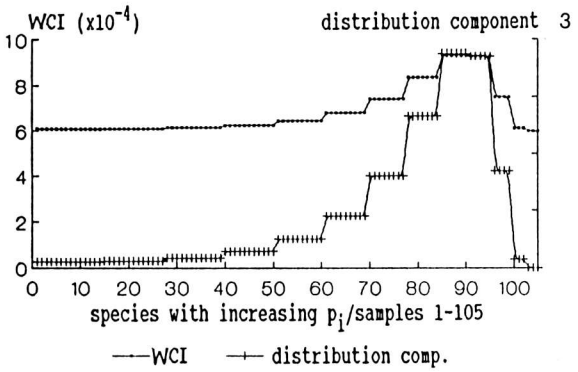
$$\frac{(n_{\max} - \tilde{n}_i)}{n_{\max}} \times \frac{(\tilde{n}_i - n_{\min})}{\tilde{n}_i}$$

This term becomes zero if $n_{\max}$ or $n_{\min}$ equals the median and increases if both strongly deviate from the median. As a large deviation suggests a higher octave number and as the index improves with lower values, this term has been inserted into the denominator. The addition of 1 prevents a division by zero. To compensate for occasionally missing middle octaves, i.e., to fit the dominance structure to the $\log_2$ distribution, an additional weighting has been given: $o_i\ (o_{\max} - o_i)$. Since the middle octaves represent the highest values, this term appears in the denominator (Fig. 2).

We apply two kinds of weightings (w_{1i}, w_{2i}) in three steps (1, 2, 4) to each species, viz., the species are weighted according to their degree of association with the soil (autochthonism, parameter w_{1i}) and their position in the r/K continuum (w_{2i}). Step 4, for instance, indicates a low degree of autochthonism (occurring regularly also in freshwater in the case of protozoa) or an r-selected life strategy. The distance between steps 1 and 2 and steps 2 and 4, respectively, is disproportional, to give stenoecious or K-selected persisters more weight. The product of w_{1i} and w_{2i} allows five states, i.e. species weightings (1, 2, 4,







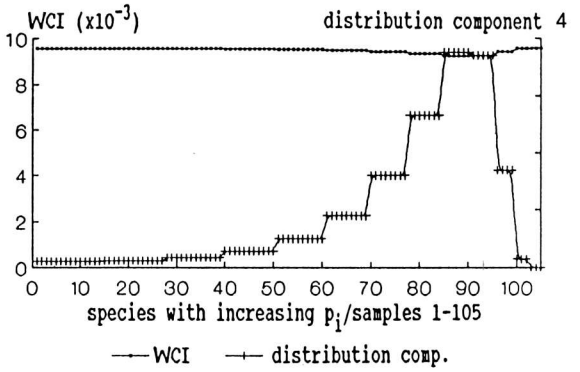


Fig. 1. Relations of species number and dominance structure, i.e., of $p_i (1-p_i)^{s-1}$. With increasing S the values decrease and the curves steepen. Simultaneously, the peak moves away from $p_i = 1$ towards $p_i = 0$. The curves have low values if p_i gets very high or low

Fig. 2. Properties of o_i $(o_{max} - o_i)$ calculated with $d = 1$. The sample calculated includes 20 octaves, each having one species

Fig. 3. Relation between ecological weightings (w) and dominance structure illustrated by a log-normally distributed sample with 105 species. In a given biocoenosis all species but one have $w_{1i}/w_{2i} = 1$; one species has $w_{1i}/w_{2i} = 4$. The WCI is calculated S times, whereby the weightings $w_{1i}/w_{2i} = 4$ pass through all species from 1 to S. For the species having $w_{1i}/w_{2i} = 4$ the distribution component is calculated; its curve runs parallel to that for the WCI

Fig. 4. Like figure 3 but with reverse weightings ($w1 = w4$; $w4 = w1$)

8, 16). The two sets of weighting pairs $w_{1i} = 1$, $w_{2i} = 2$ and $w_{1i} = 2$, $w_{2i} = 1$ as well as $w_{1i} = 1$, $w_{2i} = 4$ and $w_{2i} = 4$, $w_{2i} = 1$ cause identical changes in the index. A more sophisticated differentiation is premature, in view of the present incomplete knowledge of species autecology. The weightings are expressed linearly in the WCI, so that a doubling of the weightings doubles the index. For protozoa, $w_{1i} = 1$ refers to species found exclusively in terrestrial habitats, $w_{1i} = 2$ to species strongly associated (very likely restricted) with soil, and $w_{1i} = 4$ to species frequently recorded in freshwater also. The weighting $w_{2i} = 1$ refers to *K*-selected species which are usually rather large, divide slowly, adapt poorly, are found in temperate, uniform habitats, and are vigorous competitors (Lüftenegger et al. 1985). The opposite applies to the *r*-selected species ($w_{2i} = 4$); $w_{2i} = 2$ corresponds to intermediate species (some ciliates and many testaceans). The autochthonism weightings (w_{1i}) of the testacean species were determined according to the faunal lists given by Chardez and Lambert (1981) and Aescht and Foissner (1989). The *r*/*K* weightings (w_{2i}) were primarily determined according to organism size and the material used for shell building, e.g., $w_{2i} = 1$ was ascribed to large, *K*-selected species bearing xenosomes. Furthermore, the relationships among production, mortality, and abundance were taken into account (Schönborn 1983). Since the weightings of soil testaceans are a synopsis of data available in the literature, those for the more common species are listed in Table 1. The w_{1i} classification of ciliates is almost entirely from table 14 in Foissner (1987; ***1, **2, *4). Most taxa of the Polyhymenophora are classified as *K*-selected with $w_{2i} = 1$, except for *Keronopsis* spp. and *Paraholosticha* spp., which exhibit multiple division in reproductive cysts and do not persist; consequently they are *r*-selected ($w_{2i} = 4$).

Table 1. Ecological weightings of common soil testaceans (species include subspecies). w1 = degree of association with the soil; w2 = position in the *r/K* continuum; w3 = pH preference

Genus/species	w1	w2	w3	Genus/species	w1	w2	w3
Arcella arenaria	2	2	2	*Geopyxella sylvicola*	1	1	2
Arcella crenulata	1	2	2	*Heleopera petricola*	2	4	2
Arcella rotundata	4	2	2	*Heleopera rosea*	2	1	2
Assulina muscorum	2	2	4	*Heleopera sphagni*	2	1	2
Assulina seminulum	2	2	4	*Heleopera sylvatica*	2	1	2
Bullinularia gracilis	1	1	2	*Hoogenraadia spp.*	1	1	2
Bullinularia indica	2	1	2	*Hyalosphenia elegans*	2	1	2
Centropyxis aculeata	4	2	2	*Hyalosphenia subflava*	2	4	2
Centropyxis aerophila	2	2	2	*Nebela collaris*	2	2	4
Centropyxis cassis	2	2	2	*Nebela dentistoma*	2	2	2
Centropyxis constricta	2	1	1	*Nebela lageniformis*	2	2	2
Centropyxis deflandriana	2	1	2	*Nebela militaris*	2	2	4
Centropyxis elongata	2	1	1	*Nebela parvula*	2	2	4
Centropyxis gibba	2	2	2	*Nebela penardiana*	4	2	2
Centropyxis laevigata	4	2	2	*Nebela tincta*	2	2	4
Centropyxis minuta	2	2	1	*Nebela wailesi*	2	2	2
Centropyxis oomorpha	1	2	2	*Paraquadrula spp.*	4	1	1
Centropyxis orbicularis	4	1	2	*Phryganella acropodia*	2	2	2
Centropyxis plagiostoma	1	1	1	*Phryganella paradoxa*	2	1	2
Centropyxis platystoma	4	2	2	*Plagiopyxis callida*	2	1	4
Centropyxis serrahni	2	2	4	*Plagiopyxis declivis*	2	2	2
Centropyxis sylvatica	4	2	2	*Plagiopyxis labiata*	2	2	4
Centropyxis vandeli	1	2	2	*Plagiopyxis minuta*	2	1	1
Corythion asperulum	2	2	4	*Plagiopyxis oblonga*	1	1	2
Corythion dubium	2	2	4	*Plagiopyxis ovalis*	1	1	2
Cryptodifflugia compressa	4	4	2	*Pseudawerintzewia calcicola*	2	1	1
Cryptodifflugia oviformis	2	4	1	*Pseudawerintzewia orbistoma*	1	1	2
Cyclopyxis ambigua	1	1	2	*Pseudodifflugia fascicularis*	4	2	2
Cyclopyxis arcelloides	4	1	1	*Pseudodifflugia gracilis*	2	2	2
Cyclopyxis eurystoma	2	2	2	*Quadrulella symmetrica*	4	2	2
Cyclopyxis kahli	4	2	2	*Schoenbornia humicola*	1	4	4
Difflugia bryophila	2	2	1	*Schoenbornia viscicula*	1	4	1
Difflugia lucida	4	2	2	*Schwabia terricola*	1	1	1
Difflugia oblonga	4	1	2	*Tracheleuglypha dentata*	2	2	2
Difflugia parva	4	2	2	*Trachelocorythion pulchellum*	2	2	4
Difflugiella vulgaris	2	4	4	*Trigonopyxis arcula*	2	2	4
Edaphonobiotus campascoides	1	2	2	*Trigonopyxis minuta*	2	2	4
Euglypha ciliata	4	4	2	*Trinema complanatum*	2	2	2
Euglypha compressa	4	4	2	*Trinema enchelys*	4	4	2
Euglypha cristata	2	4	2	*Trinema lineare*	4	4	2
Euglypha laevis	4	4	2	*Trinema penardi*	2	2	1
Euglypha rotunda	4	4	2	*Valkanovia delicatula*	2	2	2
Euglypha strigosa	2	4	2	*Valkanovia elegans*	1	2	2
Euglypha tuberculata	4	1	1				

All colpodids are classified as $w_{2i} = 4$; species from other ciliate groups are pooled as "diverse" ($w_{2i} = 2$).

Since the WCI uses abundances, the sample dimension should be taken into account. This is expressed by the inclusion of the variable d in the index, so that the abundances are transformed into a uniform dimension. However, samples of equal size should be preferred since the number of species cannot be transformed.

As the denominator of the index increases to high values, the WCI value decreases to very low values; it is thus convenient to multiply values with a factor such as 10^8.

For replicated samples (e.g., random blocks), we recommend calculating the median WCI, to remove outliers and to avoid incorporating skewed distributions. Furthermore, we recommend using total species richness because it reflects the natural situation better than the mean species number; in addition, values become more independent of the species minimal area.

Calculation example

The calculation of the WCI is exemplified for an assemblage of six species ($S_1 - S_6$) with different abundances (n_i) and ecological weightings (w_{1i}, w_{2i}). Each step of the calculation is shown and can be performed either by hand, which is rather time-consuming, or by computer. We have divided the formula into simple portions which can be used to develop an algorithm for computer routines.

Assemblage parameters used and calculation of the distribution component

S_i	n_i	w_{1i}	w_{2i}	p_i	$p_i(1-p_i)^{s-1}$	o_i	$o_i(o_{max}-o_i)+1$	$w_{1i}w_{2i}$
1	2	4	1	2/187 = 0.011	$0.011 \cdot 0.989^5 = 0.010$	1 + ld (2) = 2.00	2.00·5.64 + 1 = 12.28	4
2	6	1	1	6/187 = 0.032	$0.032 \cdot 0.968^5 = 0.027$	1 + ld (6) = 3.58	3.58·4.06 + 1 = 15.54	1
3	12	2	4	12/187 = 0.064	$0.064 \cdot 0.936^5 = 0.046$	1 + ld (12) = 4.58	4.58·3.06 + 1 = 15.02	8
4	25	2	1	25/187 = 0.134	$0.134 \cdot 0.866^5 = 0.065$	1 + ld (25) = 5.64	5.64·2.00 + 1 = 12.28	2
5	42	4	4	42/187 = 0.255	$0.225 \cdot 0.775^5 = 0.063$	1 + ld (42) = 6.39	6.39·1.25 + 1 = 9.00	16
6	100	1	2	100/187 = 0.535	$0.535 \cdot 0.465^5 = 0.012$	1 + ld (100) = 7.64	7.64·0.00 + 1 = 1.00	2

Calculation of constants

Parameter	Terms
$S = 6$	$n_{max} \cdot \tilde{n}_i = 100 \cdot 18.5 = 1850$
$N = 187$	$(n_{max} - \tilde{n}_i) \cdot (\tilde{n}_i - n_{min}) + 1 = (100 - 18.5) \cdot (18.5 - 2) + 1 = 1345.75$
$n_{max} = 100$	$N \cdot S = 187 \cdot 6 = 1122$
$n_{min} = 2$	
$\tilde{n}_i = 18.5$	
$o_{max} = 7.6$	

Calculation of WCI

d.comp.	d.const.	a. & w.	WCI_i
$10^8 \cdot (0.010/12.28) \cdot$	(1850/1345.75)·	(4/1122) =	399.1
$10^8 \cdot (0.027/15.54) \cdot$	(1850/1345.75)·	(1/1122) =	212.9
$10^8 \cdot (0.046/15.02) \cdot$	(1850/1345.75)·	(8/1122) =	3001.9
$10^8 \cdot (0.065/12.28) \cdot$	(1850/1345.75)·	(2/1122) =	1297.1
$10^8 \cdot (0.063/ 9.00) \cdot$	(1850/1345.75)·	(16/1122) =	13722.5
$10^8 \cdot (0.012/ 1.00) \cdot$	(1850/1345.75)·	(2/1122) =	2940.5
Summation of individual values		$\sum$ =	21574.0
Divide sum by number of species:		WCI = 21574/6 =	3596

Interpretation of the WCI

The WCI produces relative values. Accordingly, it needs representative samples collected over minimal areas and a reference site in each investigation for a conclusive interpretation. Compared to the total abundance and species number, the WCI discriminates biocoenoses more sharply, i.e., the proportions between measures become distinctly larger. This is due to the weighting of species and the inclusion of a log-normal dominance structure (see field studies, below).

Whether changes in the WCI indicate an improvement or deterioration of the biotope may depend on the group of soil organisms investigated; however, a decrease usually indicates improvement. With testate amoebae, for instance, comparatively low or decreasing values of the index indicate natural (e.g., undisturbed) or improved soil conditions; high or increasing values of the index indicate unnatural (e.g., disturbed) or extreme soil conditions (e.g., litter layer). With ciliates the index demands a different interpretation because very few ciliates are active in natural, evolved soils due to the suppressive effects of ciliatostasis (Petz and Foissner 1988; Foissner 1989a); thus a high index may indicate either natural (evolved) or unfertile soil conditions or a toxic influence (see field studies, below).

Simulation experiments

Simple data sets (coenoses) were taken to test the sensitivity of the WCI to changes in species richness, total abundance, dominance structure, and ecological weightings. These simulation experiments often reveal the properties of an index more clearly than data from natural assemblages (Wolda 1981). Low index values are generally achieved in samples with large numbers of species, a high total abundance, a dominance structure approaching log-normal distribution, and a majority of autochthonous and *K*-selected species (Figs. 1–4).

Changes in the total abundance and species richness produce inversely proportional changes in the WCI since S and N are in the denominator. This property is strengthened by the terms $p_i(1-p_i)^{s-1}$ and $o_i(o_{max}-o_i)$. Species richness and total abundance are thus closely connected with distribution (Figs. 1, 2). With an increasing species number but a constant dominance structure the term $p_i(1-p_i)^{s-1}$ decreases, giving greater significance to the parameter S (Fig. 1). With increasing total abundance N but a constant dominance structure the term $o_i(o_{max}-o_i)$ increases, giving greater significance to the parameter N, through a higher n_i value being included in the variable o_i.

The term $p_i(1-p_i)^{s-1}$ is important to approach log-normal distribution. It has a peak at $p_i = 1/S$. With an increasing number of species the peak moves from $p_i = 1$ towards $p_i = 0$, since $1/S$ tends towards zero. At the same time the gradient of the term becomes steeper; p_i values at a great distance from $p_i = 1/S$ are low (Fig. 1). There are two extreme cases: if $S = 2$, $p_i(1-p_i)^{s-1}$ turns into the quadratic function $p_i - p_i^2$, and the graph becomes a parabola with an apex at $p_i = 0.5$; if $S = 1$, the exponent is zero, and accordingly the term turns into a linear function.

The term $o_i(o_{max}-o_i)$ is a quadratic function with the apex at the middle octave (Fig. 2). Its zero positions are at $o_i = 0$ and $o_i = o_{max}$. Since the term belongs to the denominator and $o_i = 0$ does not occur in the index, lower octaves have a slight preference over high ones.

The ecological weightings (w_{1i}, w_{2i}, w_{ni}) are closely related to the dominance structure. A species $w_{1i}/w_{2i} = 4$ has the greatest weight if the distribution component is very high. A change in this component produces a proportional change in the WCI (Fig. 3). If a species $w_{1i}/w_{2i} = 1$ is combined with a high-value distribution component, its significance is much lower than that of a species having $w_{1i}/w_{2i} = 4$ (Fig. 4).

Field studies

The WCI was calculated for species assemblages of some natural and experimental sites using published data (Table 2). This is a widely used, independent test method (Magurran 1988).

Vertical distribution of protozoa in a spruce forest soil (Table 2)

Data are based on the paper by Petz and Foissner (1988). The WCI clearly reflects the different habitat preferences, i.e., the spatial separation of testaceans and ciliates. For testate amoebae the WCI was lowest (best) in the fermentation layer (1 – 3 cm) which is known to be their optimal habitat (Schönborn 1966). With ciliates the WCI was lowest (best) in the litter layer (0 – 1 cm) due to the suppressive effects of ciliatostasis in the deeper, more evolved soil layers (Petz and Foissner 1988). The diversity index (H′) was, however, higher at 1 – 3 cm, although there were fewer individuals and species, reflecting the more even distribution (higher evenness) of individuals.

Effects of fertilization on protozoa in the soil of levelled revegetated ski slopes (Table 2)

Data are based on the paper by Lüftenegger et al. (1986). Two organic fertilizers (Biosol, dried fungal biomass; ARA, dried bacterial biomass) and a synthetic NPK fertilizer were applied as different treatments to experimental plots. The testate amoebae had barely recovered 3 years after levelling and recultivation of the ski slopes, as evident from their very low numbers and the very high (bad) WCI values. The abundances in treated plots were too low to allow an assessment of differences between treatments. In contrast, ciliate numbers had increased significantly in the fertilized sites, which were clustered BA, BAM, BAM/KN (Bray and Curtis species-abundance similarity). This fact is also reflected in the WCI. The organically fertilized plots differed in individual numbers, again reflected by the WCI, since the site with the lower abundance (ARA) had a higher (worse) WCI than that with the higher abundance (Biosol). The difference between the organic and mineral fertilizers was well expressed by the WCI, in accord with the interpretation by

Table 2. Weighted coenotic index (WCI) and Shannon & Wiener diversity (H′) of soil testacean and ciliate assemblages. N = total abundance (individuals g^{-1} soil dry mass), S = species number

Sites and treatments (designated according to the original papers)	Testaceans				Ciliates			
	N	S	WCI	H′	N	S	WCI	H′
Spruce forest								
Organic layer (0 – 1 cm)	11138	9	6	1.299	350	30	47	2.425
Organic layer (1 – 3 cm)	31408	25	0.2	2.420	109	24	636	2.634
Organic layer (3 – 9 cm)	17385	14	2	1.974	14	9	254345	1.680
Fertilization experiment								
Undisturbed soil (N)	540	23	87	2.628	2	5	874631	1.495
Organic (biosol; B)	9	2	440000000	0.693	332	18	83	1.988
Organic (ARA; A)	1	1	Calculation invalid		225	17	237	2.153
NPK (M)	1	1	Calculation invalid		57	21	1614	2.525
Revegetated, unfertilized (K)	0	0	Calculation invalid		5	9	425863	1.642
Soil compaction experiment					Not investigated			
Control (chamber effect; b)	1816	11	36	1.489				
Soil compaction 10% (c)	1709	10	248	1.924				
Soil compaction 30% (d)	906	8	973	1.802				
Soil compaction 50% (e)	151	5	263719	1.519				
Agricultural soils								
Organically farmed	884	28	33	2.896	379	37	17	2.416
Conventionally farmed	528	25	111	2.898	405	35	21	2.719
Vineyard soils					Not investigated			
Minimal (A; reference site)	270	13	2285	1.279				
Conventional (B)	156	12	46123	1.335				
Biodynamic (C)	239	14	18730	1.552				
Organic-biological (D)	347	16	2181	1.557				
Semi-biological (E)	748	21	162	1.706				
Pesticide experiment								
Control, day 15 (C)	11467	12	16	2.020	1057	33	5	2.386
Control, day 90 (C)	9698	12	21	1.989	259	26	53	2.272
Mancozeb, day 15 (M)	12600	12	7	1.976	1035	31	4	2.050
Mancozeb, day 90 (M)	13952	11	9	1.980	214	21	94	2.050
Mancozeb (10×), day 15 (Mt)	9534	12	9	1.838	728	31	9	2.147
Mancozeb (10×), day 90 (Mt)	9823	11	13	1.770	294	24	48	2.004
Lindane, day 15 (L)	7557	12	28	2.106	66	18	3624	2.620
Lindane, day 90 (L)	7641	9	61	1.942	161	18	413	2.014
Lindane (10×), day 15 (Lt)	7522	9	28	1.750	9	3	36213990	1.099
Lindane (10×), day 90 (Lt)	5706	8	77	1.739	388	11	218	1.329

Lüftenegger et al. (1986), but in contrast with the Shannon–Wiener diversity, which was highest for the site fertilized with NPK, although individual abundance was very low; this is due to the unnatural, almost even distribution (high evenness). Ciliatostasis clearly had a strong suppressive effect, as shown in the high (bad) WCI value in the natural climax soil; the high value of the WCI in the revegetated, unfertilized plot (K) was obviously caused by shortage of food.

Effects of soil compaction on the testate amoebae of an alpine pasture (Table 2)

Data are based on the paper by Berger et al. (1985). The sites clustered cb, cbd, cbde (Bray and Curtis species-abundance similarity index). This pattern and the strongly detrimental effect of 50% soil compaction are exactly reflected in the WCI values. The diversity index (H′) differentiated this pronounced effect poorly.

Protozoa in organically and conventionally farmed fields (Table 2)

Data are based on Foissner (1989b). The number of testate amoebae was significantly lower in the conventionally farmed fields ($P<0.01$; ANOVA) which is clearly reflected in the WCI values, but not in the diversity index (H′). The total abundance and species richness of ciliates were almost identical ($P>0.1$). This was corroborated by the WCI values. The organically farmed sites, however, had a slightly lower (better) WCI.

Testate amoebae in soils of conventionally and organically farmed vineyards (Table 2)

Data are based on the paper by Lüftenegger and Foissner (1989). The sites clustered CD, CDB, CDBA, CDBAE (Bray and Curtis species-abundance similarity index). A rather similar ranking was obtained with the WCI values; however, the conventionally farmed vineyard was more distinctly separated from the organically farmed sites. Again, the Shannon-Wiener diversity (H′) reflected these rather pronounced differences poorly.

Effects of pesticides on protozoa in a spruce forest soil (Table 2)

Data are based on the paper by Petz und Foissner (1989). For ciliates, the sites clustered MtC, MtCM, MtCM/LLt and MC, MCMt, MCMtL, MCMtLLt on days 1 and 90 after treatment, respectively (Bray and Curtis species–abundance similarity index). The corresponding clusters for testate amoebae were CL, CLM, CLMLt, CLMLtMt and MMt, Mt/CL, Mt/CL/Lt. According to Petz and Foissner (1989), the ciliates showed more pronounced changes than the testate amoebae and the insecticide lindane influenced the protozoa much more than the fungicide mancozeb. This was confirmed by the WCI values. The high (bad) WCI values, i. e., low numbers of individuals and species for the ciliates, were the result of adverse pesticide effects and not of suppressive effects (ciliatostasis) as seen in the fertilization experiment (example 2).

Table 3. Effects of electromagnetic fields on earthworms

Species	Weighting	Test	Control
D. octaedra	4	42.7	203.0
D. rubidus	2	0.2	0.8
L. rubellus	2	81.4	5.7
L. terrestris	2	–	+
A. tuberculata	1	271.9	–
A. longa	1	30.1	–
A. calliginosa	1	–	232.6
A. trapezoides	1	–	54.9
Abundance		426.3	497.0
Species number		5	6
WCI		448	617

Effects of electromagnetic fields on earthworms (Table 3)

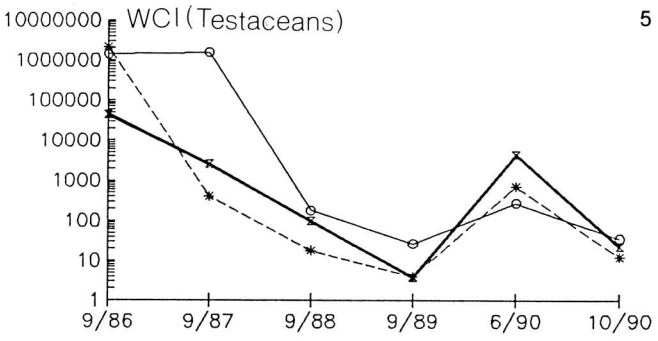
Data are from Snider and Snider (1988). The distribution of earthworms in the *r/K* spectrum follows Satchell (1980). Weightings were applied as for protozoa, i.e., *r*-selected species were weighted 4, *K*-selected species 1, and other species 2. Differences in numbers of earthworms were small and not significant; some changes in the community structure were found. These small differences were more clearly shown by the WCI.

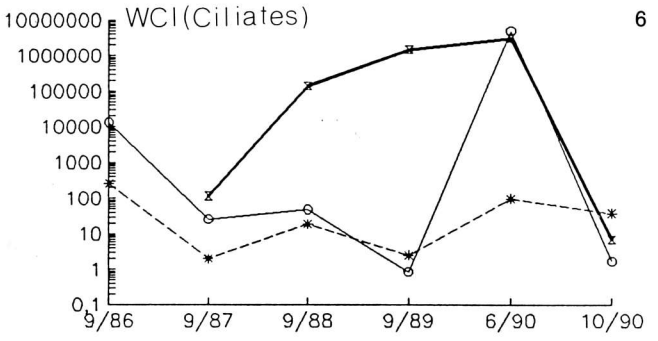
Monitoring with the WCI (Figs. 5, 6)

The WCI is valuable in monitoring changes over time, following either natural (e.g., season) or anthropic influences. Our example is from a reafforestation trial with different kinds of fertilizers (Aescht and Foissner 1992). In this experiment a further weighting (beside the *r/K* and habitat preferences) was used, viz., the pH preference of certain testacean species. Those living in acid humus were weighted (w_{3i}) 4, those living in mild (mull) humus 1, and those which are indifferent were weighted 2 (Table 1). The testate amoebae were distinctly disturbed by planting seedlings (disturbance of the humic soil layer), but recovered within about 1–2 years. The increase (getting worse) in the WCI in June 1990 was the result of a seasonal decline (reflecting summer dryness) in numbers of individuals and species. The individual and species number of the ciliates was markedly higher in the fertilized plots, especially in those treated with the organic fertilizer. Four years after the tree seedlings had been planted, the WCI values for both testate amoebae and ciliates were very similar in all treatments, indicating that the fertilizer effects did not last.

Discussion

Previous mathematical descriptions of natural and stressed soil animal assemblages have been based on numbers of individuals and species and/or relative abundances. Numerous similarity and diversity indexes that combine two of these parameters have been proposed (for reviews see Schwerdtfeger 1975; Perkins 1983; Washington 1984; Magurran 1988). The WCI that we suggest combines the





Figs. 5, 6. Monitoring the effects of fertilizers in a reafforestation trial by the weighted coenotic index (WCI) of testaceans and ciliates. Very similar WCI values occur at the end of the investigation period, indicating that the fertilizer effects did not last. – × – control, – * – organic fertilizers, – ○ – NPK

number of species and the total individual abundance with two further measures, viz., the log-normal dominance structure of the taxocoenosis and several ecological weightings of species or of groups of species. The ecological weightings that we include are similar to the biotic and chemical indexes used by freshwater biologists (Sládeček 1973; Washington 1984; Bach 1986) and to the Bodenmikrobiologische Kennzahl proposed by Beck (1984) to quantify soil microbial activity.

The WCI is intended to provide information about stressed assemblages of organisms. A comparison of the results described in the field studies and our subsequent evaluation shows that the WCI not only reflects the verbally expressed conclusions, but often makes differences more distinct, particularly compared to the classical diversity index of Shannon-Wiener (Table 2). Since the WCI is a relative measure, a reference (control) site is needed in each investigation, as required for the diversity indexes, because different biotope types (e.g., forests and meadows) cannot be compared. It is not really possible at present to rank very diverse assemblages of soil animals on an absolute scale. Most biotic indexes for freshwater coenoses (e.g., saprobity indexes) indicate a single main factor, viz., the amount of readily oxidizable organic matter (saprobity). A single key factor is difficult to find for soil ecosystems, although pH would probably be a good choice for some studies. Compared to conventional indexes and classic ecological methods, the WCI provides more detailed information, because it is highly discriminatory and considerably reduces the complexity of the data; it may therefore be more comprehensible to non-specialists. It certainly should not be used as a substitute for classic methods of describing assemblages of organisms but should be used to summarize the data.

The WCI should be calculated separately for each systematic (indicator) group (e.g., ciliates, nematodes, mites) because the information will be more detailed and an overall index could, for instance, mask a high value for one group, such as ciliates, in conjunction with a low value for another group, such as nematodes. However, if only few indicator species from various systematic groups are used, a pooled evaluation may be more useful. This question needs further examination.

In constructing a biotic index, the most difficult task is the weighting of species, i.e., to find the right proportions for w_{1i} to w_{ni}. At present all have the same relevance in the WCI. The question of whether one of these should bear more weight needs further examination and a more detailed knowledge of the autecology. Compared to the r/K weighting (w_{2i}), the autochthonism weighting (w_{1i}) poses less problems, since many faunistic data are available. The addition of further parameters and a more detailed weighting scale is possible, and could improve the WCI (see example 8).

To apply meaningful species weightings, a very detailed knowledge of the selected group or groups of organisms is necessary. Generally, autochthonous and/or stenoecious species and K-selected persisters should "improve" the WCI value because it is reasonable to assume that biotopes that harbour more of these species are relatively undisturbed and of higher "quality" than biotopes that harbour fewer of these species. The weighting of individual species must be related to the preferred habitat of the group. It is reasonable to assume that species which live at the ends of the group's occurrence scale indicate extreme conditions and should thus "weaken" the WCI. For example, it is widely accepted that earthworms are neutrophilic (Lee 1985). An increased occurrence of acidophilic species in a beech forest soil could indicate acidification (e.g., by industrial emissions). In contrast, a pH of 8.5 in an agricultural soil could indicate salinization (e.g., by irrigation). For the WCI to reflect these conditions, suitable species weightings must be applied, e.g., 1 for optimal species preferring pH 7–8, 2 for indifferent species living at pH 6–7, and 4 for species tolerating the extremes of pH <6 or >8. The kinds of ecological properties of certain taxa that are used depend on the scope of the investigation. For example, nematodes could be ranked according to feeding type (e.g., fungal feeders, microbivores, plant parasites) if they are used to determine whether a particular influence (e.g., fertilization) changes their community structure.

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