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On the quality of soil biodiversity indicators: abiotic and biotic parameters as predictors of soil faunal richness at different spatial scales

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Abstract

Direct measurement of soil biodiversity is expensive, and therefore a substitution of measurement by indication is desirable. We analysed three large datasets for the potential to predict the diversity of soil faunal groups from other parameters. The datasets represent different spatial scales, namely grassland nematodes on an European scale, forest collembola on a regional scale, and grassland ants on a local scale. We tested two groups of parameters as possible surrogates for species richness: (1) environmental parameters, such as climate, soil and vegetation characteristics, and (2) community parameters, such as higher taxon richness, indicator taxa, and maximum dominance.

Climate and soil parameters were significantly correlated with biodiversity in all datasets. However, in spite of the large variety of measurement types analysed, prediction quality of environmental variables was weak and the explained proportion of variance ranged generally below 50%. Richness was subject to considerable stochastic variation among subsamples (CV = 20–60%) thereby evading a narrow correlation with environmental parameters. Higher taxon richness, based on taxa of intermediate hierarchical order, proved the best predictor of richness in collembola and nematodes explaining 55 and 89% of total variance, respectively. A combination of two ant species was the best predictor of ant richness explaining 59% of total variance.

The authors conclude that a rough guess of soil faunal diversity can be cost-effectively derived from environmental data while an estimate of moderate quality can be obtained with reduced taxonomic effort. The precise richness of a soil community, however, is subject to autogeneous community dynamics, to biotic interactions with other populations, and to conditions in the past, and can therefore only be retrieved by immediate investigation of the community itself. Criteria for the quality of indicator parameters are discussed.
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1. Introduction

To measure soil biodiversity requires high taxonomic expertise, takes considerable time-effort and is therefore expensive. With the singular exception of earthworms in temperate and northern soils, the identification of soil fauna poses challenges of extraction efficiency, sample processing, visual recognition, and

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difficult taxonomy. These technical hurdles result, for example, in an average performance of five samples per day for a collembola expert and of two samples per day for a nematode expert. In this paper, we investigate to which degree the diversity of soil faunal groups can be assessed from other parameters which are easier to retrieve than a direct quantification of diversity itself.

Various concepts how to indicate biodiversity have been proposed in the literature, such as indicator groups and higher taxon richness (Mikusinski et al., 2001; Chase et al., 2000; Gaston, 2000; Kerr et al., 2000; Carroll, 1998). Here, we consider the term *diversity* indicator in the broadest sense, we accept any variable that is sufficiently correlated with species richness to serve as a surrogate of richness. As a familiar paradigm of the indicator principle we consider photometry, where colour intensity is used as an indicator of substance concentration. Very much like in photometry, we judged indication quality by the co-linearity and by the scatter of the relation between indicator and target variable. We tried to improve the results by using multivariate measures, corresponding, for example to a differential measurement of two wavelengths in the photometry paradigm. We tested two groups of parameters as possible indicators of soil biodiversity: (1) environmental parameters which are expected to regulate soil fauna composition, such as climate, soil, and vegetation characteristics, and (2) measures inherent to the soil fauna community itself, such as higher taxon richness, indicator taxa, and maximum dominance. We analysed three large datasets representing different spatial scales, namely grassland nematodes on an European scale, forest collembola on a regional scale, and grassland ants on a local scale. Although we present the best richness indicator obtained for each dataset, our main focus is on evaluating the achievable quality of biodiversity indication, rather than on proposing optimal diversity indicators for specific soil faunal groups. The main question addressed is, whether soil biodiversity can efficiently be indicated by environmental parameters, or whether an analysis of the soil fauna itself is essentially inevitable.

2. Material and methods

In this paper, we present a concise description of study sites and methods. Detailed descriptions are provided in Ekschmitt et al. (1999), Frede and Bach (1999), Waldhardt et al. (1999), Wolters et al. (1999), LFU (1994), and Schick and Kreimes (1993). Fig. 1 presents an overview of the geographical location of sample sites, Table 1 summarises the measured parameters, and Table 2 gives an overview of sample sizes and other properties of the sampling designs applied. While sampling and identification of soil fauna followed acknowledged standard methods in each case, the environmental data differed largely among the three investigations. In the European project, actual environmental data were measured for each soil sample. In the regional project, long-term average environmental data were available from the regional authorities. In the local project, environmental information was largely calculated from topographical data present in a GIS database.

The sites of the nematode dataset lie on a climatic cross-gradient, ranging from oceanic to continental and from boreal to Mediterranean climate, and simultaneously representing six major types of European grassland: Northern tundra (Abisko, Sweden), Atlantic heath (Otterburn, United Kingdom), wet grassland (Wageningen, The Netherlands), semi-natural temperate grassland (Linden, Germany), East European steppe (Pusztaszer, Hungary), and Mediterranean garigue (Mt. Vermion, Greece). To extend the validity of the results beyond any chance effects of 1 year's weather, the microclimate at each site was manipulated using light reflection, shading, wind shelter, rain protection, and irrigation. From a full factorial table with six levels of temperature and six levels of moisture, the optimal set of 14 treatments was calculated as a D-optimal design using Fedorov's method (Cook and Nachtsheim, 1980). In Hungary, an additional treatment with high humidity and intermediate temperature was included. The Swedish experiment was done as a transplantation experiment due to the short vegetation period and the remoteness of the Abisco site.

At all sites, six samples were taken from each treatment during the period from June to December 1996. For each sample, 12 soil cores of 1.65 cm diameter and 10 cm depth were combined and sieved (2 mm mesh) prior to chemical analysis, and five similar cores were combined and used for nematode extraction. In total, 510 bulk samples from 85 treatments were taken for soil analysis, and for nematode analysis, respectively.

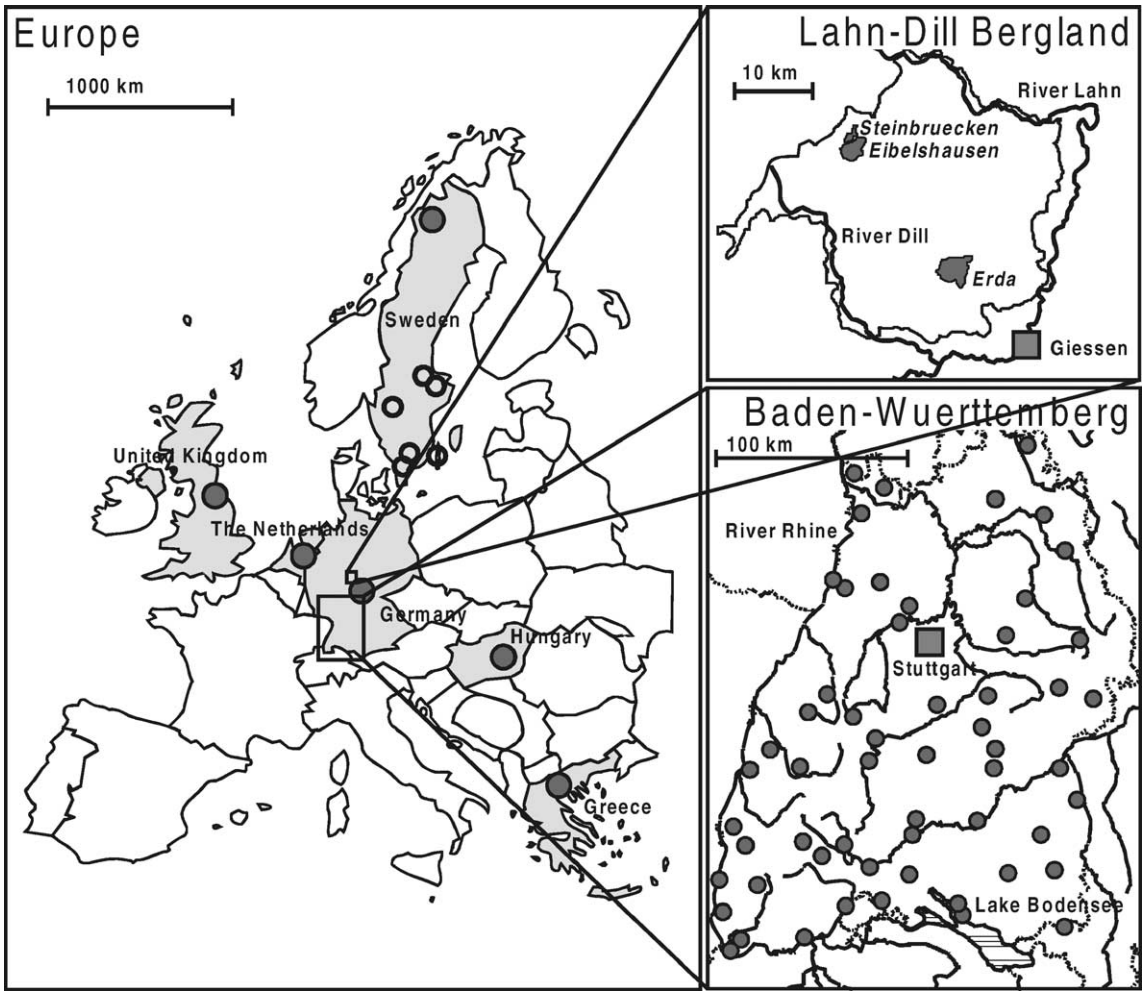


Fig. 1. Geographical locations of sampling sites. (a) Europe: solid circles indicate primary nematode sampling sites, open circles indicate transplantation sites in Sweden. (b) Lahn-Dill region: shaded areas indicate the three locations where ant nests were recorded. (c) State Baden-Wuerttemberg: solid circles indicate the forest sites sampled for collembola. Scales of the maps, and the location of the two smaller maps within Europe are indicated in the figure.

For each sample, soil microclimate was quantified by measuring soil temperature and soil water content. Nematodes were isolated using a modified Cobb's method (s'Jacob and Van Bezooijen, 1984) and were identified to genus level according to Bongers (1988) and Andrassy (1984). Microbial biomass-C was measured using fumigation-incubation (Ross, 1990; Jenkinson and Powlson, 1976). Soil ergosterol content was recorded as a measure of active fungal biomass (Djajakirana et al., 1996). Bacterial substrate utilisation was measured using a modified BIOLOG assay (Vahjen et al., 1995). Soil respiration was measured by absorption in alkali (Isermeyer, 1952). NH_4-N was measured by distillation using MgO to liberate ammonia, NO_3-N was determined by distillation using Devarda's alloy for reduction of NO_3^- to NH_4^+, and organic N of the soil was assessed from Kjeldahl analysis (Allen, 1974).

The regional dataset is based on samples from 57 permanent monitoring sites held by the Baden-Wuerttemberg agency for environmental protection (Landesanstalt fuer Umweltschutz Baden-Wuerttemberg,

Table 1
List of measured parameters[a]

Parameter group	Nematoda	Collembola	Formicidae
Climate	Actual precipitation (mm/day), soil temperature at 5 cm (°C), soil water content (% WHC)	Long-term annual precipitation (mm), long-term annual mean air temperature (°C)	Transport capacity after Moore and topographical wetness index (water balance), hillshade and reflectance map (insulation)
Vegetation	Plant production (dry matter) (g DM/m^2)	Species richness of cormophytes and of mosses, coverage of tree-, shrub-, herb- and moss-layer (%area), Ellenberg indicator values (*Zeigerzahlen*) for light, nitrogen, acidity, temperature and humidity	Plant richness, total plant coverage (%area), vegetation height (cm)
Soil/topography	Microbial biomass (mg C/g DM soil), soil ergosterol content (μg/g DM soil), BIOLOG AWCD (ext. 650/g DM soil), soil contents of NO_3, NH_4 and organic N (mg N/g DM soil)	Proportions of skeletal grain (%vol.), sand, silt and clay (%DM), water holding capacity (%vol.), soil bulk density (g/l), soil organic matter content (μg/g DM soil), soil C/N ratio	Height above drainage channel, slope, hemispherical dispersion after Hodgson (topographical roughness), maximum curvature after wood
Indicator groups	Dominance of feeding types, genera, families and orders	Dominance of species, genera and families	Dominance of species, genera and subfamilies
Maximum dominance	Maximum dominance in each sample of any feeding type, genus, family and order	Maximum dominance in each sample of any species, genus and family	Maximum dominance in each sample of any species, genus and subfamily
Higher taxon richness	Numbers of families and orders	Numbers of genera and families	Numbers of genera and subfamilies

[a] The table gives an overview of the measurements supplied in each of the three datasets. The measured variables are classified into abiotic (climate, vegetation, soil) and biotic parameters (indicator groups, dominance, higher taxon richness).

LFU). The sites are distributed across an area of ca. 230 km × 180 km in Baden-Wuerttemberg, Germany. They represent near-natural woodlands, i.e. they are neither strongly polluted nor intensively managed. Sampling plots are 20 m × 24 m large, surrounded by a buffer zone. No forestry measures are allowed in the plots and in the buffer zones. Most stands are deciduous and mixed forests dominated by beech. Some sites bear coniferous forests dominated by fir and spruce, and there are also a few riverine woods.

Table 2
Sampling designs and diversity dimensions[a]

Parameter	Nematoda	Collembola	Formicidae
Dimension of spatial scale	1000 km	100 km	10 km
Number of plots	85	57	20
Samples per plot	6	9	15
Average counts per sample	218 specimens	179 specimens	2 nests
Overall richness observed	121 genera	117 species	13 species
Higher taxon richness 1 observed	55 families	52 genera	4 genera
Higher taxon richness 2 observed	11 orders	5 families	3 subfamilies
Average richness per plot observed	35 genera	37 species	5 species
Average richness per plot, ACE extrapolation	40 genera	43 species	5 species
95%-confidence range of richness across samples	±38%	±71%	±126%

[a] The table presents summary data that characterise the quality of the datasets analysed. Spatial extent, number of plots and sample size are given for each dataset. The taxonomic diversity represented in each of the datasets is indicated by the average abundance and the total richness observed, followed by information on the richness of higher taxa and the richness within single plots.

Altitudes range from 98 m asl near the river Rhine up to 1260 m asl in the Black Forest. Soil acidity of the A-horizon varies between pH 3 and 7 across sites. Long-term annual temperature ranges from 5.5 to 9.5 °C and long-term annual precipitation ranges from 600 to 1700 mm across sites.

Collembola were sampled in the framework of a long-term biomonitoring programme (Oekologisches Wirkungskataster) from 1986 to 1988 and from 1990 to 1993. Half of the sites were visited every year in turns of 2 years. Sampling took place three times a year, i.e. in spring, summer and autumn. Three soil cores of 6.8 cm diameter and 8.0 cm depth were taken from each plot and combined. Soil arthropods were expelled from soil by means of a modified MacFadyen high gradient canister extractor and were stored in 70% ethanol. The Collembola were selected under a dissecting microscope and bleached in a mixture of lactic acid and glycerine, thereafter transferred onto slides. Identification to species level followed the nomenclature of Gisin (1960). Extensive data on vegetation, as well as on physicochemical soil properties were made available by previous investigations and are held in an environmental database by the LFU. Measurement methods are described in a dedicated handbook (LFU, 1994). Since single plant species and soil chemical elements did not show significant correlations with collembola in a previous analysis, a set of integrative plant parameters and mainly soil physical characteristics were selected for the present investigation, in addition to climate parameters (Table 1).

The local dataset is based on studies carried out in the rural districts of Steinbruecken, Eibelshausen and Hohenahr-Erda (Hesse, Germany) in the framework of the Collaborative Research Center "Land-use options for peripheral regions" (DFG, SFB 299). The region is a low mountain range at 270–385 m asl. Major soil types are regosols and cambisols, mean annual temperatures range from 6.5 to 8 °C, and mean annual precipitation varies from 700 to 1200 mm depending on the district. A small-scale mosaic of different land-use types characterises the cultivated area of the region. Poor physical soil conditions, a climate unsuitable for crops, and farm sizes too small to be economically viable resulted in a considerable decrease of cropland since 1950, while grassland and fallow land gradually increased. Much of the area is now covered by moderately managed grasslands, mainly by meadows mown once per year and occasionally grazed by sheep or cattle. *Festuca rubra—Agrostis tenuis* communities dominate the vegetation at the sites converted from cropland to grassland before 1980, whereas no typical plant communities of matured grassland have yet developed on the sites that were converted more recently.

Species richness and nest abundance of ants were determined from June to August 1999 on a number of randomly chosen subplots at each of 20 grassland sites. A minimum of 5 m was left between the subplots to avoid an overestimation of patchily distributed species in seemingly homogeneous habitats (Andersen, 1990). In addition, 2 m were left between the plots and the border zones of the sites to avoid edge effects. Ant nests without conspicuous mounds on the soil surface were recorded by raising the turf with a small chisel. Up to 10 worker ants were collected from each nest and fixed in 70% ethanol immediately. Taxonomic identification to the species level was based on Seifert (1996).

The grassland vegetation was recorded during May–August 1997, excluding a strip of 2 m width along the borders of sites to avoid possible edge effects. GIS-data based on a 20 m × 20 m grid were used from the project's database in order to indicate microclimate by topographic parameters related to insulation and water balance, and to indicate soil properties by parameters related to height, slope, and topographical roughness (Hodgson and Gaile, 1999; Wood, 1996; Moore and Wilson, 1992).

In order to eliminate sampling errors of richness estimates depending on sample size, extrapolated total richness, rather than observed richness was used as diversity parameter throughout this study. Richness extrapolations were calculated according to the ACE-estimator (Chazdon et al., 1998; Chao et al., 1993). Where ACE did not apply due to numerical restrictions, the CHAO1-estimator was used, as recommended by Colwell (1997). All calculations were programmed and conducted in MS Excel (Microsoft, Redmont, USA). The quality of indicators was tested by multivariate regressions comprising linear and quadratic terms. Regression models were confined to contain only significant variables by applying forward stepwise inclusion of independent parameters. Indicator quality was primarily assessed by the coefficient of determination R^2. If a regression model explained less than 50% of richness variance ($R^2 < 0.5$) then

Table 3
Overview of regression results[a]

Parameter	Nematoda	Collembola	Formicidae
(a) Environmental variables			
Climate			
Best single parameter	Average soil temperature, linear + quadratic ($R^2 = 0.24$, Rel.Err. = 32%, $P < 0.0001$)	Long-term annual precipitation, linear ($R^2 = 0.18$, Rel.Err. = 17%, $P = 0.0011$)	Reflectance map (insulation), linear + quadratic ($R^2 = 0.38$, Rel.Err. = 29%, $P = 0.0167$)
Best multiple model	Identical with univariate model above	Identical with univariate model above	Identical with univariate model above
Vegetation			
Best single parameter	Annual plant production, linear + quadratic ($R^2 = 0.10$, Rel.Err. = 37%, $P = 0.0289$)	Percentage coverage of tree layer, linear ($R^2 = 0.12$, Rel.Err. = 17%, $P = 0.0092$)	Plant richness, coverage, vegetation height (not significant)
Best multiple model	Not available	Coverages of tree layer and herb layer, linear + quadratic ($R^2 = 0.21$, Rel.Err. = 17%, $P = 0.0062$)	Plant richness, coverage, plant height (not significant)
Soil/topography			
Best single parameter	Soil microbial C, linear ($R^2 = 0.43$, Rel.Err. = 28%, $P < 0.0001$)	Soil organic matter, linear + quadratic ($R^2 = 0.16$, Rel.Err. = 17%, $P = 0.0189$)	Hemispherical dispersion (roughness), linear ($R^2 = 0.29$, Rel.Err. = 26%, $P = 0.0185$)
Best multiple model	Soil microbial C, ergosterol and BIOLOG, linear + quadratic ($R^2 = 0.54$, Rel.Err. = 25%, $P < 0.0001$)	Identical with univariate model above	Height above drainage channel, hemispherical dispersion, linear ($R^2 = 0.47$, Rel.Err. = 23%, $P = 0.0062$)
Climate, vegetation and soil combined			
Best multiple model	Soil microbial C, ergosterol and annual plant production, linear + quadratic ($R^2 = 0.57$, Rel.Err. = 26%, $P < 0.0001$)	Long-term annual precipitation, coverages of tree layer and herb layer, linear + quadratic ($R^2 = 0.34$, Rel.Err. = 15%, $P = 0.0002$)	Reflectance map, height above drainage channel and hemispherical dispersion, linear ($R^2 = 0.60$, Rel.Err. = 21%, $P = 0.0027$)
(b) Community parameters			
Indicator taxa			
Best single parameter	Dominance of family Paratylenchidae, linear ($R^2 = 0.61$, Rel.Err. = 23%, $P < 0.0001$)	Dominance of family Onychiuridae, linear + quadratic ($R^2 = 0.13$, Rel.Err. = 17%, $P = 0.0256$)	Dominance of *M. rubra*, linear ($R^2 = 0.44$, Rel.Err. = 27%, $P = 0.0014$)
Best multiple model	Paratylenchidae, Teratocephalidae and Diphtherophoridae, linear ($R^2 = 0.82$, Rel.Err. = 16%, $P < 0.0001$)	Isotomidae, Onychiuridae and Sminthuridae, linear ($R^2 = 0.15$, Rel.Err. = 17%, $P = 0.0324$)	*M. rubra* and *M. schencki*, linear ($R^2 = 0.59$, Rel.Err. = 24%, $P = 0.0006$)
Dominance			
Best regression	Maximum dominance of orders, linear ($R^2 = 0.51$, Rel.Err. = 25%, $P < 0.0001$)	Maximum dominance of families, linear + quadratic ($R^2 = 0.18$, Rel.Err. = 19%, $P = 0.0049$)	Maximum dominance at any taxonomic level (not significant)
Higher taxon richness			
Intermediate level taxon	Richness of nematode families, linear ($R^2 = 0.89$, Rel.Err. = 12%, $P < 0.0001$)	Richness of collembolan genera, linear ($R^2 = 0.55$, Rel.Err. = 12%, $P < 0.0001$)	Richness of ant genera, linear ($R^2 = 0.36$, Rel.Err. = 29%, $P = 0.0048$)
High level taxon	Richness of nematode orders, linear + quadratic ($R^2 = 0.38$, Rel.Err. = 29%, $P < 0.0001$)	Richness of collembolan families (not significant)	Richness of ant subfamilies, linear ($R^2 = 0.35$, Rel.Err. = 29%, $P = 0.0062$)

[a] The table lists the best regressions found in each category of potential richness indicators, together with an indication whether quadratic terms were significant. Where appropriate, multivariate models are included. Regression quality is specified by the coefficient of determination (R^2), the relative error of estimate (Rel.Err.) and the error probability (P).

indicator quality was judged as weak. The Statistica for Windows package (StatSoft Inc., Tulsa, USA) was used for all statistical tests.

3. Results

In total, 121 nematode genera, 117 collembola species and 13 ant species were recorded, corresponding to an average extrapolated total richness of 40 nematode genera, 43 collembola species and 5 ant species per sampling site (Table 2). Variation of richness estimates between replicate samples was high, leading to 95% confidence ranges of 25–55 genera for nematodes, 13–74 species for collembola and 0–10 species for ants, per sample on average.

Regression results are summarised in Table 3. The table depicts the indicators with the highest coefficient of determination (R^2) found among the tested variables in the categories climate, vegetation, soil, indicator taxa, maximum dominance and higher taxon richness.

Climate was a significant but weak ($R^2 < 0.25$) predictor of richness in all three datasets, showing a strongly humped regression line on the largest scale (Fig. 3b). Vegetation parameters were weak predictors of collembolan richness ($R^2 = 0.2$), poor predictors of nematode richness ($R^2 = 0.1$), and they were not significantly correlated with ant richness. Soil parameters and topographical parameters showed better but still weak correlations with nematode richness ($R^2 = 0.4$–0.5) and ant richness ($R^2 = 0.3$–0.5), and the correlation with collembola did only explain less than 20% of richness variance ($R^2 = 0.16$). A combination of climate, vegetation and soil parameters yielded R^2 values of ca. 0.6 for nematode and ant richness, and 0.35 for collembolan richness. To summarise, within the set of 44 environmental parameters tested, only six parameters and parameter combinations correlated with soil faunal richness by an R^2 higher than 0.4. The large majority of environmental parameters, including multivariate parameter combinations, explained less than 25% of variance in soil faunal richness, or were not significantly correlated with soil faunal richness at all.

In contrast to the environmental variables, parameters derived from community composition repeatedly exhibited R^2 larger than 0.5. Higher taxon richness, based on taxa of intermediate hierarchical order,

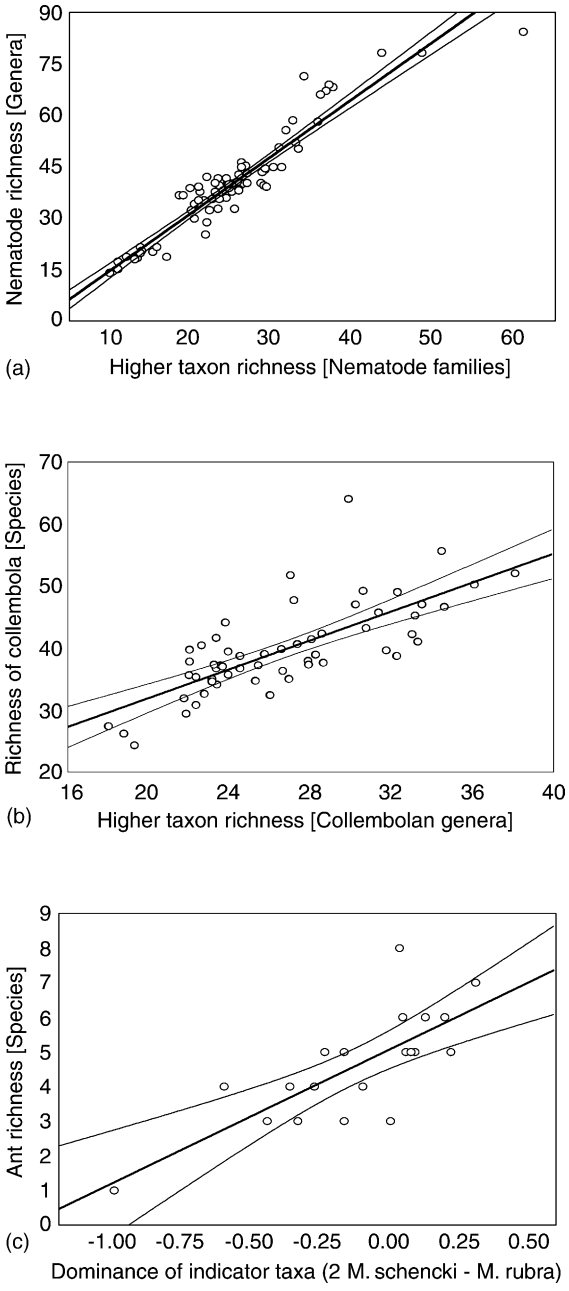


Fig. 2. The best community-based indicators found. Among all parameters tested, higher taxon richness proved the best predictor for nematode richness (a) and collembolan richness (b). Ant richness was well predicted by the combined dominance of the ant species *M. schencki* and *M. rubra* (c).

proved the best predictor of richness in collembola and nematodes explaining nearly 60 and 90% of richness variance, respectively ($R^2 = 0.55$ and 0.89). A combination of the ant species *Myrmica rubra* and *Myrmica schencki* was the best predictor of ant richness explaining nearly 60% of richness variance ($R^2 = 0.59$) (Fig. 2).

4. Discussion

In this paper, we investigate the potential of a range of parameters to serve as indicators of soil biodiversity. To this end, we analysed three datasets of a very different nature. If results share similarities across these datasets then we assume that the similarities point to a general rule and that comparable results can be expected in future investigations.

Among the three datasets analysed, the data on grassland nematodes presented the largest gradients covering a spatial scale of thousands of kilometres, while simultaneously providing actual environmental data from the immediate vicinity of each soil sample. This dataset represents a typical "researcher's" situation, where specific measurements are available for each single sample. The data on forest collembola, in contrast, represent an "environmentalist's" situation where data covering a regional scale have been collected over several years. Data from different categories, such as vegetation and soil originate from separate sampling campaigns and are loosely linked in time and space. They characterise the medium term average local situation. Finally, the data on grassland ants represent a modern perspective where environmental information is not based on direct measurement, but is indirectly inferred from topographical data and remote sensing data integrated into a GIS database.

Our results confirm the general hypothesis that soil biodiversity is driven by environmental factors, such as climate, vegetation and soil properties. At the same time, the results elucidate that soil biodiversity is only partly formed by the state of the environment. Environmental variables explained roughly half (34–60%) of the variance in soil animal richness, leaving the other half unexplained and therefore unpredictable from environmental factors alone. Soil animal richness varied considerably between replicate samples (CV = 20–60%) indicating a high degree of independence of richness from environmental conditions.

Fig. 3 illustrates three major causes why many environmental parameters did not prove good indicators of soil faunal richness: high scatter, non-linearity and non-representativeness. The most general cause was evidently a highly scattered relationship between indicator variable and richness (Fig. 3a). Furthermore, the relationship was strongly non-linear in many cases (Fig. 3b), as is demonstrated by the significance of quadratic terms in the regression results (Table 2). While a non-linear relationship between indicator and richness does not present a strict cut-off criterion, it complicates the indication of biodiversity because there is no unequivocal coincidence of increase, or decrease, of richness with an increase of the indicator value. A third and important deficiency of indicator quality is demonstrated in Fig. 3c. Here, the overall correlation was based on a few data points located to the right of the graph, while the majority of data, marked in the graph by a circle, exhibited a complete lack of correlation between indicator variable and richness. Thus, the overall correlation was not representative for most of the data and a prediction of richness from this data appears less justified. High scatter, non-linearity, non-representativeness, and combinations of these excluded many of the tested environmental variables from the list of potential biodiversity indicators.

However, there are more impediments to the prediction of soil faunal richness from environmental data than statistical properties of regressions. As has been forcefully argued by Salt and Hollick (1946), the observed distribution pattern of soil animals can bear little relation to presently measured environmental conditions, because the faunal distribution pattern is influenced: (1) by autogeneous dynamics of the population under consideration itself, (2) by interaction of this population with predators, parasites and competitors, as well as (3) by conditions and forces active in the past but indiscernible in the present. Depending on the quantitative importance of these mechanisms, distribution patterns of populations and therefore composition and diversity of communities can be largely independent from presently observed environmental patterns. Based on these arguments, we assume that correlations between environmental variables and soil faunal richness exhibiting R^2 values as high as 0.6,

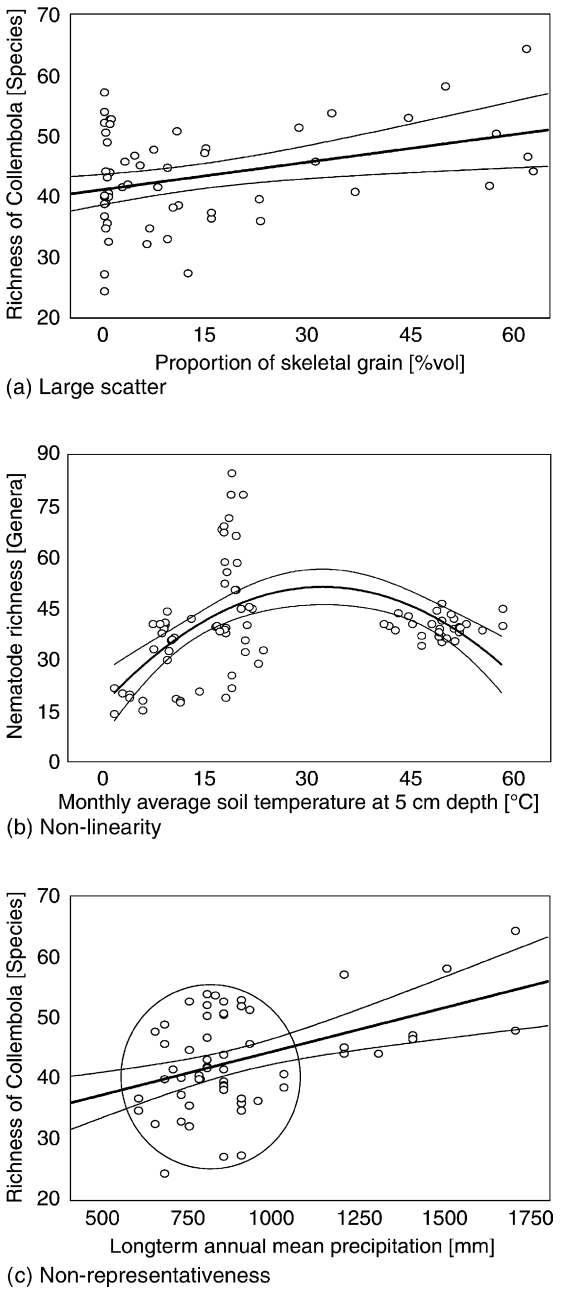


Fig. 3. Examples of undesirable indicator properties. The figure demonstrates three types of relationships between indicators and target variables that deteriorate the quality of indication: (a) indicator variable and target variable show a scattered relation, (b) the relation between indicator variable and target variable is strongly non-linear, (c) the regression between indicator and target variable is coined by a minority of data points and is not generally valid in the majority of datapoints.

as they were observed in this study, represent a good achievement and will not generally be improvable by performing more or different measurements, nor by augmenting sampling effort. An inevitable consequence of such limited correlation strength is that prediction accuracy is also limited. In the present analysis, soil faunal richness as predicted from environmental variables deviated from measured richness by a coefficient of variation of ±15–26%, depending on the faunal group. This implies that 95% of predictions deviated up to ±30–51% from the true value, while 5% of predictions fell even beyond this range.

Given the partial independence of richness patterns from environmental conditions, it appears promising to retrieve information on biodiversity from the community itself and to save labour effort by reducing the amount of taxonomic identification. In fact, correlations based on community information such as higher taxon richness or indicator species yielded R^2 values of 0.55 up to 0.89. In nematodes and collembola, these correlations improved substantially over the best correlations with environmental variables, and in ants the same level of R^2 as with environmental variables was achieved. In all three faunal groups, the relationships between richness and the best community-based indicators were highly linear and representative (Fig. 2). However, even the best community-based indicators exhibited correlations, which would be seen far from acceptable as a calibration of a photometric measurement. The improvement of correlation quality meant that 95% of richness predictions ranged within ±24% of the true value in nematodes and collembola, and within ±46% of the true value in ants.

5. Conclusions

The authors conclude that a rough guess of soil faunal diversity can be cost-effectively derived from environmental data. Here, particularly the good predictions of ant richness provided by topographical data suggest that basic predictions of soil biodiversity can be developed in the future from GIS databases. The richness of a soil community is however likely to depend on autogeneous community dynamics, on biotic interactions with other populations, and on conditions in the past. Our results suggest that this fact is rather independent of the spatial extent and the spatial resolution at which

measurements are made. Reliable richness estimates can therefore only be retrieved by immediate investigation of the community itself. Here, higher taxon richness proved a good diversity indicator in nematodes and collembola, where a large number of 40 taxa was present. In contrast, the richness of ant communities, which exhibited a low number of only five species per plot, was best predicted by a small set of indicator species. Indicator species may apply more generally to groups in which a relatively small number of species is present (Andersen, 1995). Even in these improved, community-based indicators, accuracy of richness predictions remained fairly low. We conclude that a full identification of the community at high taxonomic resolution is inevitable whenever precise knowledge on the diversity of a soil community is desired.

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