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LETTER

Bacterial traits, organism mass, and numerical abundance in the detrital soil food web of Dutch agricultural grasslands

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Abstract

This paper compares responses to environmental stress of the ecophysiological traits of organisms in the detrital soil food webs of grasslands in the Netherlands, using the relationship between average body mass M and numerical abundance N. The microbial biomass and biodiversity of belowground fauna were measured in 110 grasslands on sand, 85 of them farmed under organic, conventional and intensive management. Bacterial cell volume and abundance and electrophoretic DNA bands as well as bacterial activity in the form of either metabolic quotient (qCO_2) or microbial quotient (C_{mic}/C_{org}) predicted the response of microorganisms to stress. For soil fauna, the logarithm of body mass $\log(M)$ was approximately linearly related to the logarithm of numerical abundance $\log(N)$ with slope near -1, and the regression slope and the proportion of predatory species were lower in intensive agroecosystems (more reduced substrates with higher energy content). Linear regression of $\log(N)$ on $\log(M)$ had slope not far from $-3/4$. The approach to monitoring data illustrated in this paper could be useful in assessing land-use quality.

Keywords

Bacterial DNA, body size, collembolans, detritus, food web, microbial quotient, mites, nematodes, qCO_2, soil basal respiration.

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INTRODUCTION

Soil habitats have high biodiversity, heterogeneity and fragmentation. The quantity and diversity of litter are traditionally considered the bottom-up controlling donor (e.g. Scheu & Setälä 2002; Mulder & De Zwart 2003; Moore *et al.* 2004). Consumers can neither directly influence the renewal rate of this basal resource, nor co-evolve further with this food resource. Therefore, detritivores necessarily lack specialization (Scheu & Setälä 2002; Moore *et al.* 2004). As the microbial biomass comprises the majority of the total biomass in soil, the role of top-down regulation at higher trophic positions may appear marginal. However, bottom-up driving forces can be ascribed to bacteria and fungi (cf. Hunt & Wall 2002) and their consumers (Yeates 2003). The bacterial population (reflected by the bacterial-based energy channel) is adapted to use easily degradable substrates in bulk soil (Bloem & Breure 2003; Goddard & Bradford 2003), whereas the natural fungal population is adapted to limited resources like recalcitrant plant tissues in the soil (Ingham *et al.* 1985; Mulder & Breure 2003). Quality (diversity) and quantity of detritus, changes in the soil physical structure and shifts in the biodiversity–functioning relationship affect detrital soil food webs (Breure *et al.* 2002; Moore *et al.* 2004; Wardle *et al.* 2004).

There is little (and often inconsistent) information available on soil decomposers taxonomically refined to species and genera in a quantitative, community-wide context (cf. Naeem & Wright 2003). A useful quantitative approach to an ecological community, and to the soil community in particular, is to measure the numerical abundance N per unit of habitat and the average body mass M of each species, genus or other functional group (such as bacteria or detritus), to plot (N, M) for each group on log–log coordinates, and to superimpose the community food web on this plot by drawing a directed arrow or trophic link from the point (N_r, M_r) to the point (N_c, M_c) if 'c' is the consumer of resource 'r' (*sensu* Cohen *et al.* 2003).

This combination of information on numerical abundance, body mass and the food web has a variety of applications, including community-wide pyramids of trophic height by numerical abundance and by biomass (Jonsson *et al.* in press), community-wide distributions of trophic link length and slopes (Reuman & Cohen 2004), estimation of energetic or biomass flux of all links in a food web (Breure *et al.* 2002; Reuman & Cohen in press), and relations between numerical abundance and body size (Hendriks 1999; Cohen & Carpenter 2005).

In addition to illustrating some of these applications for soil food webs below, we demonstrate here a new application by showing that this plot is a useful indicator of ecosystem functioning in the detrital soil food web under different abiotic conditions (pH, soil fertility, soil texture) associated with organic, conventional, and intensive farming practices. We examine how biotic features at higher resolution, such as bacterial ecophysiological traits, respond to extrinsic factors such as environmental disturbance. To demonstrate these results, nematodes, microarthropods (mites and collembolans), oligochaeta (enchytraeids and earthworms), and bacteria were collected randomly in farms in the eastern Netherlands between 1999 and 2002. In this paper, we examine the detrital soil food web of selected farms plotted in a plane in which the axes are $\log_{10}$ body mass (vertical) and $\log_{10}$ numerical abundance (horizontal), and examine the response of this plot to differences in farm management.

DATA

Sample collection and soil extraction

Our basic sampling units were 110 grasslands on Pleistocene sand, 85 managed pastures (dairy cattle) and 25 semi-natural grasslands. Management regimes were organic, conventional, and intensive. Organic farms had average total area of 60 ha, about three times the average of intensive farms (Mulder *et al.* 2003a). Within each managed farm, there were three blocks (pasture, maize fields and other crops), each block sized according to the farming system. Across each grassland, 320 soil cores (diameter 2.3 cm × 10 cm) were taken by a large Eijkelkamp grass plot sampler (Agriresearch Equipment, Giesbeek) at locations determined by generating random x and y GIS-coordinates within the total area of each investigated farm. The cores were mixed in a plastic container. Nematodes were extracted from 100 g soil using funnel elutriation, sieving and cottonwool extraction. Two clean suspensions in 10 mL water were screened with a stereomicroscope to count all individuals. In two permanent mounts in formaldehyde, 150 individuals were counted. Soil nematodes were identified to genus by light microscopy (400–600×) and subsequently assigned to feeding habits according to Yeates *et al.* (1993). Microarthropods were also collected in a randomized design of four cores per farm. These cores (diameter 5.8 cm × 5 cm) were kept separate until extraction. The animals were subsequently sampled, observed at a magnification of 200–1000× with a compound microscope and assigned to feeding guilds on the basis of their carbohydrase activity (Henk Siepel, personal communication). Much of our knowledge about diet width has been derived from microcosm studies using few selected organisms. The trophic status of our micro- and mesofauna is inferred from carbohydrase activity (microarthropods), direct observation of diet of predatory soil nematodes at different developmental stages (cf. Small 1987) or morphology (e.g. the buccal cavities of the nematode genera as described in Yeates *et al.* 1993) and is not based on direct observation or microcosm manipulation (Table S1).

Microbial measurements

Microbiological samples were collected in the upper 10 cm of soil and stored 1 month at a temperature of 12 °C and 50% water holding capacity (WHC). The samples for microbial measurements were pre-incubated at constant conditions to avoid variation caused by weather conditions. Bacterial cells were counted in soil smears by fluorescent staining [5-(4, 6-dichlorotriazin-2-yl)aminofluorescein]. Cell numbers, average cell volume, frequency of dividing cells, cell lengths and widths were determined by direct confocal laser scanning microscopy coupled to a fully automatic image analysis system (Bloem *et al.* 1995a; Paul *et al.* 1999). To estimate the bacterial biomass from the cell number we used the measured cell volume of the entire bacterial population and a biovolume-to-carbon conversion factor of $3.2\ 10^{-13}$ g C μm^{-3} (Van Veen & Paul 1979; Bloem *et al.* 1995b). The carbon content of the bacterial biomass (C_{bac}) was taken to be 50% of the dry weight (Herbert 1976).

As sampling and sieving disturb the soil structure and generally increase microbial activity, we did not take into account the results of the first week of incubation for the calculation of process rates. Microbial activity in soil ecosystems can be determined in two ways: measuring the short-term bacterial growth rate by means of the incorporation of ^{3}H-thymidine into bacterial DNA simultaneously with the incorporation of ^{14}C-leucine into proteins (Michel & Bloem 1993; Bloem & Breure 2003) and/or measuring the long-term specific respiratory rate (microbial respiration rate per unit of microbial biomass) under standardized conditions and without substrate addition. Basal soil respiration by microorganisms can be quantified by measuring CO_2 production – the preferred method – and O_2 consumption. Both can be used to calculate the metabolic quotient: i.e. respiration divided by biomass. As ecosystem properties like climate and soil structure are

supposed to control the ratio of mol CO_2 evolution per mol O_2 uptake, we measured both the CO_2 evolution and the O_2 consumption to estimate the physiological response of soil microbiota (Dilly 2001, 2003). The CO_2 evolution (respiration) was measured between week 1 and week 6 by incubation of soil at 20 °C and 50% WHC. Results of the first week are not used to avoid disturbance effects of sample handling. The accuracy of this technique is high in most Dutch sandy soils in contrast to marine clay, where CO_2 evolution is not reliable due to high amounts of $CaCO_3$ (Bloem & Breure 2003). We measured the metabolic quotient directly in the laboratory during 6 weeks incubation. The metabolic quotient is slightly different from the relative qCO_2, which is calculated as ratio of basal respiration to Substrate-Induced-Respiration after addition of easily degradable glucose (Wardle 1993; Wardle & Barker 1997; Wardle *et al.* 1998).

Genetic diversity of the bacteria occurring in grasslands under different management regimes was examined by using denaturing gradient gel electrophoresis (DGGE) after DNA-amplification by polymerase chain reaction (PCR) using a general probe for bacterial 16S-ribosomal DNA (Dilly *et al.* 2004). During electrophoresis these DNA fragments of equal length are running through an increasing concentration of denaturant. Depending on the strength (composition) of the DNA, the fragments start to melt and form a band at a specific denaturant concentration. This technique yields a banding pattern where the number of DNA bands reflects the genotypes of abundant bacteria, and the band intensity reflects the relative abundance of the 'species' (Bloem & Breure 2003). The banding patterns are analysed and quantified by image analysis. By use of specific primers for multiplication of DNA by PCR, it is possible to detect populations with very low numerical abundance. Yet, the available molecular techniques may still appear inaccurate for measurement of fungal remains. Therefore, we performed a palynological treatment in order to determine the fungal concentration by direct microscopy (Mulder & Janssen 1999). One tablet with a known number of exotes (12 500 ± 42) was added to each soil sample at the beginning of the treatment. Fungi were extracted from the dry soil before counting, acetolysed, and finally dehydrated; the obtained hyphae – and exotes – were embedded in silicone-oil 2000 centistokes, sealed with wax and counted (Mulder *et al.* 2003b; Mulder & De Zwart 2003).

Statistical methods

To correlate environmental factors, microbial processes and bacterial- and fungal-feeding nematodes, we used the same Generalized Linear Model (GLM) as in Mulder *et al.* (2003a). For each feeding habit (bacterial or fungal), the nematode abundance N (number of individuals per kg dry soil) was analysed as

$$\log(N) = a + c_1 \times pred_1 + \cdots + c_x \times pred_x + d_1 \times (pred_1)^2 + \cdots + d_x \times (pred_x)^2 + \epsilon$$

where *pred* denotes environmental predictors [pH, plant available nutrients, organic carbon (C_{org}), colloids, livestock density, average temperature and total rainfall during 1 month], and ϵ is the Poisson-distributed error in the counted specimens. For each of three classes of farming systems (organic, conventional and intensive management), one farm was selected which had the highest numerical abundance N predicted by this regression function. These representatives of the three farming systems were selected to see whether differences in farm management affected food web structure and physiological features. Table S2 gives the environmental parameters of the three farms selected by this procedure.

The individual biomass production (P) of soil organisms was inferred at the genus level from specimens grown in litterbags. Soil nematodes were measured after wet-funnel extraction. The length and width of randomly selected animals were measured to estimate biomass C assuming a dry-to-fresh weight ratio of 0.2 and a dry weight C content of 50% (Schouten *et al.* 1998). Most recovered nematodes belonging to 24 genera were microbivores (2101 individuals). The body mass of litterbag-grown nematodes was estimated independently for juveniles, females, and males (excluding the *dauerlarvae* resting stage of some Rhabditida): 1805 bacterial-feeding individuals, 296 hyphal-feeding individuals, 405 plant root-feeding individuals, 35 omnivores and only 15 predators. The following equation (cf. Ernest *et al.* 2003) was used to estimate production:

$$P = \left(\frac{1}{N}\right)\left(\frac{\mathrm{d}N}{\mathrm{d}t}\right)(M) = \left(\frac{1}{N}\right)\left[\frac{\mathrm{d}(NM)}{\mathrm{d}t}\right],$$

where M is the species' average body mass in μg and is time independent, N is the species' average numerical abundance, and t is the sampling date (Julian Day). To adjust for time trends in environmental and climatic data, the GLM regression equation included as predictor variables the means of maximal temperature and average precipitation of the last 3 weeks before sampling, and the interactions of maximal temperature and average precipitation with the Julian Day (Mulder *et al.* 2003a).

Enchytraeids were extracted using wet-funnel extraction, then animals were identified, measured and counted. The enchytraeids' M was estimated from regression equations of fresh weight on length, further assuming that the ratio of dry weight to fresh weight was 0.18 (Berg *et al.* 2001). Collembola and Acarina were extracted with Tullgren funnels, identified and divided into body size classes. The

corresponding dry weight per body size class was calculated based on regression equations of dry weight on length (Berg *et al.* 2001). The respiration metabolism of all microbivores was determined by allometry (Ernest *et al.* 2003), where the metabolic rate per capita (R) is a function of its body mass M: $R \propto M^{3/4}$. The microbial quotient C_{mic}/C_{org} – a measure of the carbon produced by all microorganisms (i.e. bacteria, fungi and protists) living in a soil with given organic resources – was estimated according to Oberholzer & Höper (2000), whose model can be rewritten as

$$C_{mic}/C_{org} = 10^{[1.143+0.093\times pH+0.0005\times F]} \times (CLAY_{fraction})^{0.311} \times (C_{org})^{-0.671}$$

where F is the number of mm of local rainfall measured during the last 12 months before sampling and $CLAY_{fraction}$ is the percentage of soil particles with a size < 2 μm. In that way, we predicted the total carbon content of microorganisms (microflora and microfauna) C_{mic}. The comparison between the measured C_{bac}/C_{org} and the expected C_{mic}/C_{org} provided a way to evaluate whether the microbial quotient (which summarizes the physiological rate of the complete microbial community of a given soil) was greater than expected from only microbial pulses in immature systems ($C_{bac} > C_{mic}$ showed an observed bacterial carbon content higher than the predicted carbon content of all the microorganisms).

RESULTS

To illustrate the approach of this study, Fig. 1 presents data from an organic farm predicted by GLM to have the highest numerical abundance of non-parasitic soil nematodes. This figure, plotted according to the methods of Cohen *et al.* (2003), shows that the detritus, the bacterial population and most species of the terrestrial fauna fell near a diagonal where the slope of the body mass log(M) as a function of the numerical abundance log(N) (in 1 kg soil) was −0.99 ± 0.11 SE of estimate. The slope of a regression line and its (counterclockwise) angle are interchangeable, but we prefer slopes when presenting allometric results, and angles otherwise. A slope equal to −1 for an individual trophic link from a resource to a consumer (equivalently, an angle of 135° with respect to the horizontal x-axis) implies that a consumer's total biomass equals its resource's total biomass (Cohen *et al.* 2003). Thus, the total biomass of both our predators (consumers) seemed on average to equal the total biomass of their resource in this illustrative organic farm. In Fig. 1 most taxa fell near the diagonal with slope close to −1. As in Tuesday Lake, Michigan (Reuman & Cohen 2004), here in detrital soil food webs long trophic links deviated less in slope from the diagonal than did short links. Also as in Tuesday Lake, here different functional groups tended to clump together, the predators (omnivores) showing short links and the bacterivores showing very long links (approximately five-times longer than for predators/omnivores) with a median quite close to the food web diagonal (+5%).

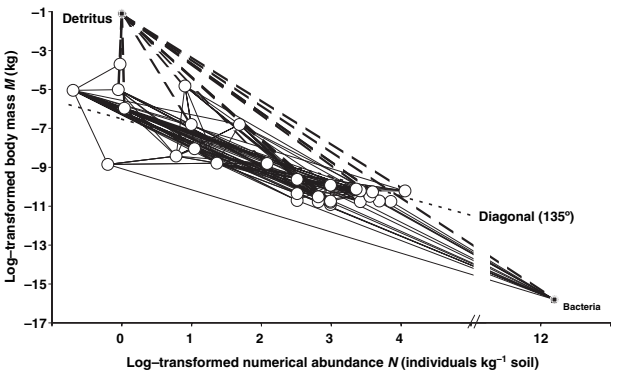

Figure 1 Numerical abundance N (individuals per kg dry soil) and average body mass M of belowground organisms in the detrital soil food web of an organic farm in the Netherlands. M derived from litterbag-grown individuals. Both axes display logarithms to base 10. The upper circle represents the detritus (including fungal mycelium and plant debris). Apart from the bacteria, the taxonomical resolution is at the genus level. The slope of the diagonal for all the soil organisms and including detritus is very close to −1.

The variation in the body size of litterbag-grown soil organisms increased with increasing M (Table 1). Nevertheless, the estimates of the mass of consumers and predators from their N were very accurate. Bacteria were an outlier in the detrital soil food web with a Studentized residual higher than | 2 |. Thus average cell volume (bacterial M) was not predictable from their numerical abundance N only. Figure 1 spans micro- (nematodes), meso- (mites, collembolans and enchytraeids) and macrofauna (earthworms). The mesofauna was the most complete subunit of our community webs. For the mesofauna of Fig. 1 (rows 27–38, bottom Table S1), the biomass $N \times M$ differed three orders of magnitude between prey and predators. If we exchange the axes of Fig. 1 and recalculate for soil detritivores the slope of log(N) as a function of log(M), we obtain −0.79, not far from −0.83 with a 99% confidence interval of (−0.96, −0.70) for Tuesday Lake in 1984 and also not far from −0.74 with a 99% confidence interval of (−0.89, −0.59) for Tuesday Lake in 1986 (Cohen & Carpenter 2005).

An important difference between our diagram and the food web of Tuesday Lake was that in this paper one resource – the fungal prey – was incorporated in the detritus at the top of Fig. 1 [with, by definition here, $N = 1$ and log(N) = 0]. We incorporated the soil mycelium into the detritus because the numerical abundance of fungi in the field (seen strictly as taxonomical N – fungus density at

Table 1 Standard deviation and Studentized residuals of the body mass of the soil organisms shown in Fig. 1. The variance around the log–log regression line across trophic levels is constant and independent of the magnitude of *M*

	SD (litterbag *M*)	Studentized residuals (*M* on *N*)
Bacteria (B1)	0.026	2.967
Nematoda (N2)	0.022	−0.860
Nematoda (N4)	0.175	−0.788
Nematoda (N5)	0.242	−0.879
Nematoda (N6)	0.014	−0.517
Nematoda (N7)	0.020	−0.251
Nematoda (N8)	0.023	−0.756
Nematoda (N9)	0.333	−0.337
Nematoda (N10)	0.002	−1.017
Nematoda (N13)	0.023	−0.726
Nematoda (N15)	0.081	−0.272
Nematoda (N17)	0.041	−0.805
Nematoda (N19)	0.581	−0.110
Nematoda (N20)	0.010	0.199
Nematoda (N21)	0.064	−0.182
Nematoda (N22)	0.029	−0.162
Nematoda (N24)	0.353	−0.265
Nematoda (N25)	0.222	−0.367
Acarina (A27)	0.000	−1.551
Acarina (O28)	0.152	−0.132
Acarina (G29)	0.311	−0.551
Acarina (P30)	0.990	−0.682
Acarina (G31)	0.664	−0.296
Enchytraeidae (E33)	0.087	0.427
Enchytraeidae (E34)	0.351	0.836
Collembola (C35)	0.838	0.362
Acarina (U36)	0.058	0.486
Collembola (C37)	0.460	0.894
Collembola (C38)	0.895	1.568
Lumbricidae (L39)	0.090	1.710

The significant direct relationship between the standard deviation of *M* (absolute *M*, not log *M*) for a given taxon and the corresponding average *M* (absolute *M*, not log *M*) for its litterbag-grown individuals exhibits $P = 0.0171$. The prediction of *M* on *N* ($P_{\text{obs-pred}} < 0.0001$) indicates that our linear model explains a highly significant portion of the variation in the soil organisms' *M*. The numbers and letters in brackets refer to the Supplementary material.

species level – and not as hyphal length-derived *N*) was vague due to the destructive soil sampling method and subsequent treatment. Moreover, the inclusion into the organic matter of fungal sporopollenins (biopolymers resistant to strong acids and bases which make up most of the material of the outer layer of the wall of fungal hyphae and spores) was reasonable from the biogeochemical point of view (Mulder *et al.* 2000). The advantage was that two independent regression lines for the lower trophic levels in a detrital soil food web could be made, one for the bacterial channel (the bacterial prey and the bacterivore organisms like nematodes, bacterial-grazing mites and collembolans showed $P = 0.00018$, rejecting the null hypothesis of no correlation) and one for the fungal channel (the detritivores, namely enchytraeids, earthworms, hyphal-feeding nematodes, collembolans and fungal-browsing mites, showed $P < 0.00001$, rejecting the null hypothesis of no correlation). All soil organisms (predators included) in Fig. 1 had $R^2 = 0.715$ ($P < 0.00001$, $n = 30$, again rejecting the null hypothesis of no correlation). With different combinations, including vs. excluding bacteria and including or excluding detritus, the results for the three GLM-selected farms are given in Table 2, along with the regression lines of bacterivore and detritivore organisms under all three management regimes. Notwithstanding the difference of more than one order of magnitude in the bacterial *N* between the organic farm and the intensive farm, the angles vary by only 3%, from 135° to 131°. Excluding the bacterial *N* from our regression analysis for all the investigated farms makes the slopes steeper (Table 2), although it reduces the difference in the slopes of the two extremes in management regime, the organic system (124° with detritus, 127° without detritus) and the intensive system (123° with detritus, 126° without detritus). Bacterial *N* significantly affects the slopes in the nutrient-rich organic farm (640 mg P_2O_5 kg^{-1}), as the 3% variation including bacteria becomes only 0.8% excluding bacteria (Table 2). The exclusion of the bacterial *N* emphasizes the differences between the two other farms and the conventional farm, where the regression shows an angle of 128° with and 132° without detritus.

The decrease in the bacterial *N* from organic to intensive management is correlated with 11% decrease in the SE of the resulting linear regressions of Table 2 (detritus included or excluded and bacterial-feeding channel). Moreover, the *c.* 5% lower angle of the bacterial feeding channel under intensive management, while associated with a decrease of the bacterial population, remains close to 135°. Even under stressed environmental conditions (as shown by the lower numerical abundance of bacterivore organisms), the total biomass of (specialized) bacterivore consumers approximately equals its resource's biomass (the bacterial prey). If we exchange abscissa and ordinate, the regression coefficient of log(*N*) as function of log(*M*) varies from −0.82 (nutrient-poor conventional system, $qO_2 > qCO_2$) to −0.77 (energy-rich systems, $qCO_2 > qO_2$), approaching −3/4 with highly reduced respirable substrates.

Bacterial diversity displays notable trends (Fig. 2). Not surprisingly, the Shannon–Wiener index (H'), which measures the evenness in DGGE profiles, was positively related to an increasing number of DNA bands, a crude surrogate for 'species richness' (Fig. 2a). The Shannon–Wiener index was based on the number, retention place, and intensities of the DNA bands in DGGE gels. With 63 DNA bands, the

Table 2 Angles and standard error (SE) of the linear regression line of log[*N* per kg soil (Dry Matter)] as a function of log body mass *M* of soil organisms in a bio-organic (Fig. 1), conventional and intensive farm sampled in the late spring of 1999

	Bacteria included		Bacteria excluded		Feeding channels	
Regimes	Detritus included	Detritus excluded	Detritus included	Detritus excluded	Bacteria + bacterivores	Detritus + detritivores
Bio-organic farm	135° (1.6946)	138° (1.3599)	124° (1.4392)	127° (1.1512)	142° (1.5765)	117° (1.3369)
Conventional farm	136° (1.6796)	139° (1.3287)	128° (1.5628)	132° (1.2511)	139° (1.5036)	123° (1.6278)
Intensive farm	131° (1.5255)	134° (1.1525)	123° (1.3198)	126° (0.9739)	135° (1.3629)	117° (1.2657)

Each angle is measured in degrees of counterclockwise rotation from the horizontal *x*-axis, so that a vertical trophic link from a smaller prey to a larger predator, both of equal numerical abundance, exhibits an angle of 90°, a trophic link of slope −1 has 135°, and a horizontal trophic link from a more abundant prey to a less abundant predator, both of the same body mass, exhibits an angle of 180°. The trendlines for bacterial prey and bacterial-feeding organisms (*Bacterivores*) and for detritus and detritivore organisms (*Detritivores*) are provided on the right. From top to bottom, the manure excreted by the cattle in each farm was 24, 33 and 45 $m^3\ ha^{-1}\ year^{-1}$. Within both feeding channels, linear correlations between the log numerical abundance *N* and the log body mass *M* of soil organisms were highly significant ($P \leq 0.0001$). For additional information on the organisms used for regression analysis, see Supplementary material.

organic farm in Fig. 1 had the highest number of DNA bands among the organic farms investigated here (black circle in Fig. 2a). This very high number of DNA bands in a carbon-rich organic farm is remarkable because it is contrary to the inverse correlation between the number of DNA bands and C_{org} ($P = 0.0015$, mean number of DNA bands = 49.98). Yet the spatial variation in DNA profiles from replicate plots at the same location was as large as categorical differences between the intensive, conventional and organic management regimes (ANOVA: $P = 0.0144$).

Thymidine and leucine incorporation rates correlated directly with increasing animal manure ($P = 0.0001$ and 0.0012, respectively). The three grasslands with evident microbial pulses above the dashed line in Fig. 2b (observed C_{bac} > predicted C_{mic}) were nutrient-rich farms with different redox states [i.e. more (less) reduced substrates in intensive (organic) farms]. As C_{mic} is derived from SIR-studies, pulses with $C_{bac}/C_{mic} > 1$ suggest high activities of glucose-responsive microbes. In Fig. 2b, conventional farms were almost always below the regression trendline (no microbial pulses), regardless of the bacterial *N*. In Fig. 2c, conventional farms showed a higher metabolic quotient than on average, whereas the regression slope for the intensive is very close to 1 ($qCO_2 \sim qO_2$). The regression coefficient of qO_2 as function of qCO_2 varies from 1.27 (conventional system) to 0.99 (intensive system) and 0.75 (organic system). The qCO_2 and qO_2 values were highly correlated with some important divergences between the management regimes regarding the redox state and energy content of the respirable substrate (the more reduced the substrate and the higher its energy content), the higher qCO_2. The complete set of grasslands sampled in 1999 showed a regression slope of 1.15.

No clear relationship between the aggregate respiratory metabolism of all soil microbivores (including facultative microbivores) and their total biomass was observed. However, the metabolic rate of all soil microbivores (respiratory metabolism R_m) correlated closely ($R^2 = 0.79$) with increasing biomass *B* of active bacterial-feeding nematodes and showed a linear regression of $R_m = 2.74$ (*B*) + 0.82 excluding the *dauerlarvae* resting stage (Fig. 2d). The taxonomic diversity of microbivores was enhanced when microbial populations were more abundant. Consequently, the number of bacterial-feeding nematodes identified to species was higher when the ratio of active nematodes to *dauerlarvae* was higher, which implies that the nematodes were grazing more intensely. This trend was detected even in semi-natural grasslands (grey circles in Fig. 2d), suggesting a key role of active bacterial-feeding nematodes in detrital soil food webs.

DISCUSSION

This study indicates, first, that the numerical abundance *N* of bacteria and their derived C_{bac} play a key role in the structure of detrital soil food webs of Dutch farms. Although variation in average bacterial cell volume makes prediction of *M* from *N* difficult (highest Studentized residuals among the taxonomic units considered here), bacteria contribute strongly to the slope of the regression line of log *M* as a function of log *N*. Second, in detrital soil food webs, the numerical abundance *N* of bacterial-feeding nematodes and their aggregate respiratory metabolism provide a better proxy than bacterial activity for microbial pulses that can be ascribed to animal manure ($P < 0.005$ in organic and conventional farms, but $P > 0.1$ in intensive farming systems).

Our results confirm that when species or other taxonomic units of a community food web are plotted on (*N*, *M*) coordinates, the data points approximate a line

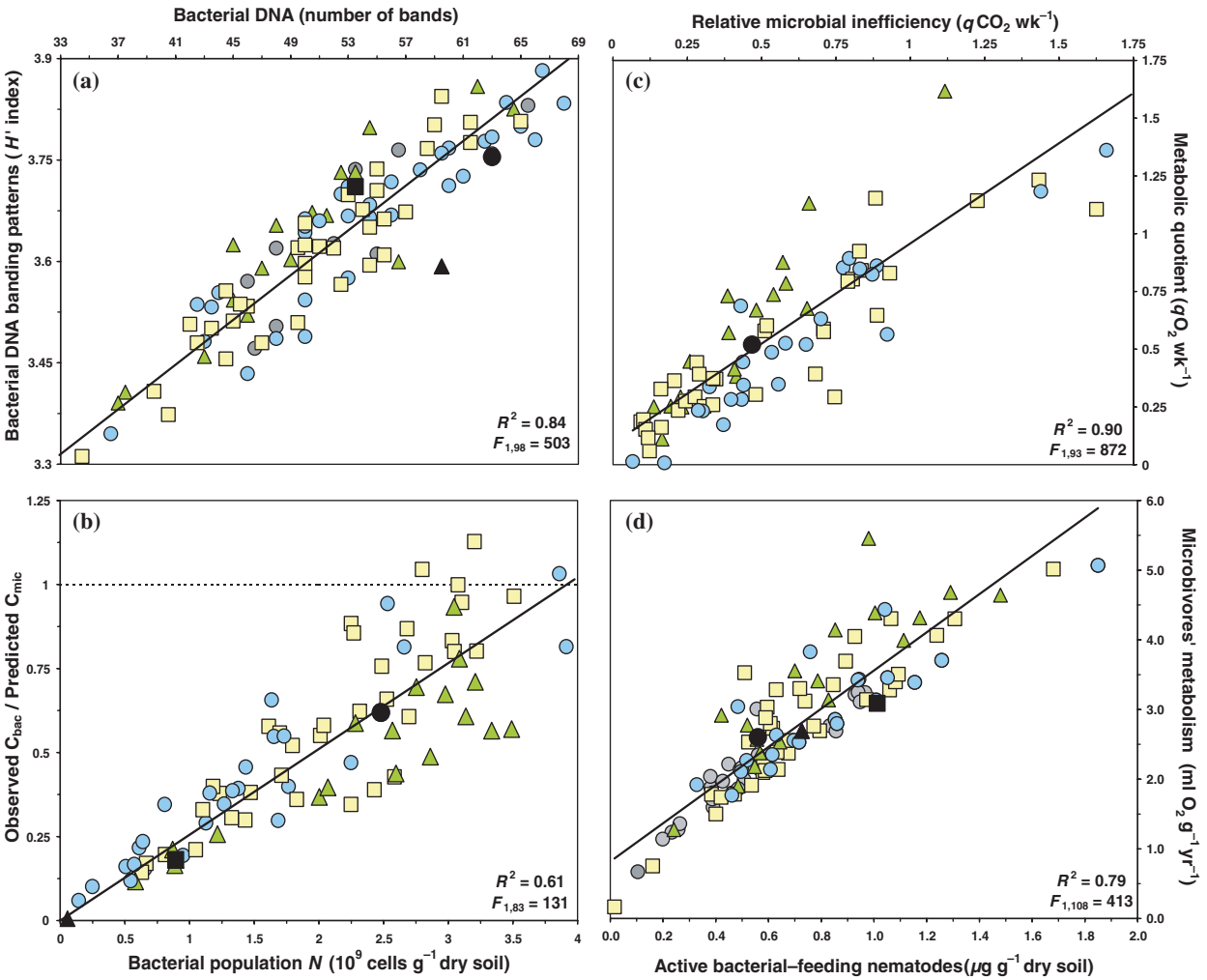

Figure 2 Microecology of bacteria and related consumers in soils of 110 Dutch grasslands. (a) Number of DNA bands (upper *x*-axis) vs. the Shannon–Wiener index of the proportion of the total intensity of the *i*th DNA band (*y*-axis); (b) Billions of bacterial cells (*x*-axis) plotted against the ratio between the bacterial-carbon based microbial quotient (C_{bac}/C_{org}) and the microbial quotient C_{mic}/C_{org} expected in grasslands on sand (*y*-axis, where the horizontal line gives $C_{mic} = C_{bac}$); (c) CO_2-production (qCO_2 per week, upper *x*-axis) and the O_2-consumption (qO_2 per week, right *y*-axis); (d) Biomass of the active bacterial-feeding nematodes (on the *x*-axis, $N \times M$ derived from bacterivores excluding their *dauerlarvae*) and aggregate respiratory metabolism of *all* soil microbivores in both the nematofauna and mesofauna (right *y*-axis, the regression fits on the complete set of 110 grasslands). All given regression lines have slopes significantly different from 0 ($P < 0.0001$). Black circles represent the organic farm shown in Fig. 1, open, blue circles the other organic farms. Unmanaged grasslands are represented by grey circles. The selected conventional farm is represented by a black triangle; the other conventional farms are represented by open triangles in green. The selected intensive farm is represented by a black square; the other intensive farms are represented by open squares in yellow. The other two investigated sites of Table 1 share qCO_2 and $qO_2 > 5$.

with slope *c.* −1; the slope of −1 across all trophic levels is consistent with the biomass exponent of 0 reported by Hendriks (1999) for all body size classes together. On (*M*, *N*) coordinates, the data points approximate a line of slope *c.* −3/4. The regression slopes on both (*N*, *M*) coordinates and (*M*, *N*) coordinates are consistent with estimated slopes for Tuesday Lake, Michigan (Cohen & Carpenter 2005).

Microbes and microbivores

The integration of field data and processes at different spatial scales is a challenge in contemporary ecology. A size-structured food web is likely to contain small and abundant species that operate more locally than larger and less abundant species (cf. Jennings & Mackinson 2003). There is increasing evidence that belowground ecosystems gain a

much higher stability when consumers of different body sizes linked to either the bacterial or the fungal energy channel occur at the same spatial scale (Brose *et al.* 2005). Within a detrital soil food web, increasing diversity in M of soil organisms can force further complementarity in resource use. The existence of different patterns among detrital soil food webs in our grassland soils is in agreement with functional differences at higher trophic levels between species-poor and species-rich ecosystems (Spencer *et al.* 1999) and with the complementarity of energy transfer agents (small organisms with $M < 0.25$ μg) vs. habitat engineers (large organisms with $M > 15$ μg).

In addition, the impact of allochthonous inputs on the microflora plays a crucial role at the ecosystem level (Clegg *et al.* 2003). Most soil-ecological studies have focused on 'soil engineers' like lumbricids, as they modify the structure of the soil in which the energy is transferred. A neglected feature in the spatial distribution of resources is the extent to which the mixture of food particles (including microbial biomass) may be linked to the wide range of organisms efficiently involved in food consumption and horizontal dispersal (Gange 1993; Jørgensen *et al.* 2003; Rantalainen *et al.* 2004). Notwithstanding the possible interactions with animals of the largest body size class, the resulting net demographic responses of the microflora to abiotic factors and land-use in the upper 10 cm soil provide reliable explanations of the traits of specialized microbivores in the investigated food web. Moreover, high variability in the bacterial ecophysiological traits contributes to deviations of bacterial M from the linear log–log regression on N (cf. Table 1).

We may exclude possible biases in the methods used because grassland bacteria survive better in storage than bacteria sampled in other agroecosystems like arable soils (cf. Filser *et al.* 2002). The disappearance of dominating genotypes and the subsequent development of a more uniform DNA band pattern as decomposition proceeded in managed grasslands can be interpreted as follows: *r*-strategists (opportunists) that prevailed on litter were replaced by *K* strategists (persisters) related to resistant organic matter and humic acids (Dilly *et al.* 2004). However, not only does the genetic diversity increase at larger spatial scales (the average area of an organic farm is three times that of intensive farms), but so does the physical diversity of the soil texture/structure. In the regression model of Oberholzer & Höper (2000), the significant weight given to very fine sediment supports an important physical role of the clay fraction (among others) in the protection of bacteria from protozoa. Considering that the most abundant pores in Dutch sandy soils have a diameter between 6 and 30 μm (Chenu *et al.* 2001), we may expect that under higher soil compaction the amount of macropores filled by particles with diameter < 2 μm increases. In particular, the metabolic quotient is positively correlated with this clay fraction ($P = 0.0012$). As the incorporation rate of leucine in proteins exhibits a highly significant correlation with management regime ($P = 0.0003$, testing the null hypothesis of no difference in leucine incorporation rates between farming types), we expect a positive relationship between bacterial specific activity (*q*Leucine) and protozoan activity in the field. This hypothesis was described by Ekelund & Rønn (1994) as a possible explanation of the lower bacterial abundance under grazing. The slower rate of carbon turnover of bacteria located in small pores in comparison with bacteria located in pores with diameters between 3 and 6 μm further highlights the possible spatial compartmentalization in detrital soil food webs (Killham *et al.* 1993; Chenu *et al.* 2001; Bonkowski 2004). Regardless of the body sizes of microbivores, clay-filled macropores protect the bacterial population from overgrazing effects by halting protozoan activity.

Estimating the variation in numerical abundance

Primary decomposers have functionally divergent properties giving rise to two different energy-nutrient channels. The rate and magnitude of decomposer–driven processes is highly variable. For instance, in their microcosm experiment Setälä & McLean (2004) showed that decomposition activity (measured as CO_2 production) was only weakly related to the (manipulated) taxonomic richness of soil saprophytic fungi. On the contrary, manipulating the microbivores by adding hyphal-feeding nematodes to microcosms with bacterial-feeding nematodes resulted (Laakso & Setälä 1999) in a much higher NH_4–N mobilization compared to the control (no hyphal-feeders). In the field, taxonomic richness is rather unpredictable due to variable observation efforts or local habitat variability influencing metapopulation dynamics in space and time (for instance, affecting prey carrying capacity, see Takimoto *et al.* 2002). The relative scales of different sources of disturbance can significantly affect population persistence (Orland 2003). Schoenly & Cohen (1991) reviewed temporal changes in terrestrial and aquatic food webs that resulted from differences in species sampled on different sampling occasions.

However, allometric relationships between body mass and numerical abundance provide a fine tool even at lower taxonomic resolution than species. The scaling of metabolic rate as the three-fourth power of body size is very widespread (Gillooly *et al.* 2001; Ernest *et al.* 2003). So we can easily predict the cumulative temperature-dependent respiratory rate for multiple soil organisms within the fungal and bacterial energy pathways by using metabolic scaling theory. The mean body mass of one bacterial-feeding nematode ($M = 0.032$ μg) is higher than that of one hyphal-feeding nematode ($M = 0.020$ μg). In sandy top-soils,

bacterial-feeding nematodes have, on average, 1.56×10^6 individuals m^{-2} while hyphal-feeding nematodes have 1.62×10^5 individuals m^{-2}. Hence, the aggregate respiratory metabolism of bacterial- and hyphal-feeding nematodes is almost entirely driven by bacterial-feeding nematodes (Fig. 2d and Table S1).

Although bacterial-feeding nematodes represent 57% of the total nematofauna abundance (counting individuals, not species), bacterial-feeding nematodes are 50% of biomass abundance because of the huge individual body mass of the (rare) nematode predators (for example, the omnivore/carnivore *Eudorylaimus* has $M = 0.237$ μg but $N = 35$, only 0.9% of the complete nematofauna). The body mass of these heavier predatory nematodes varies more than those of bacterial-feeding nematodes: the SD of carnivorous nematode body masses equals 0.222 and exceeds by one order of magnitude the average of the SDs of the body masses of bacterial-, hyphal-, and plant-feeders and omnivores. Most differences in the body mass measurements of a given (microbivore) nematode genus can be ascribed to their sex (males vs. females) and stage of life history (adults vs. juveniles). From this point of view, the body mass of larger predators consuming smaller nematodes may change during the year according to the increasing body size of the much more abundant prey individuals, and the prey may have more generations than predators.

Of the 278 trophic links of the three farms of Table 2 (cf. Table S1), 73% show animals preying on organisms with a smaller body mass (prey M up to 11 orders of magnitude smaller than predator M), 20% show animals preying on organisms with the same or larger body mass (up to four orders of magnitude larger in M), and 7% show microorganisms feeding on soil detritus, fungi and plant roots (with up to 12 orders of magnitude of difference in M between the smallest producer/decomposer and the largest decomposer). The nutrient-rich organic farm had the highest proportion of individuals of predatory species of the three farms (respectively, organic farm 12%, intensive farm 10% and conventional farm 4% of all the animals sampled in 1 kg soil). Under the three treatment regimes, all predators together exhibit the most significant population density-body mass relationships (cf. Cohen *et al.* 1993, 2003) compared with the detritivore and bacterivore species. The substantially higher occurrence of predators in organic and intensive farms had an effect on the slope of the regression line similar to that of excluding the bacteria (Table 2). However, the numerical abundance of the predators of the conventional farm ($N = 4585$ individuals m^{-2}) was comparable with that of the intensive farm ($N = 4440$ individuals m^{-2}) and likewise for the non-predators of the organic farm ($N = 39\,561$ individuals m^{-2}) and the intensive farm ($N = 41\,703$ individuals m^{-2}). These results confirm widespread population density-body size relationships for species which span a large range of body mass (here, predators) and bottom-up effects of the food web resources (bacterial N and detritus) on the distribution of non-predatory soil organisms. Both the numerical abundance and the body mass of the mesofauna confirm the relation between body size (weights or lengths) and food web structure suggested by Tuesday Lake data (Cohen *et al.* 2003).

The patchy occurrence of bacteria, fungi and nematodes in space and time is an important difference between terrestrial and aquatic food webs. In contrast to most food web models, which assume all species to occur everywhere in the habitat (e.g. Cohen & Briand 1984), in farm soils the abundance of organisms varies spatially (in response to abiotic conditions and land management) and temporally (in response to seasonality of temperature and precipitation and variation in sampling efforts). Although microbial links and ecosystem functioning in soil appear to be different from those in aquatic systems, the relationships between the numerical abundance of organisms and the average body mass were strikingly similar, even if some ecophysiological traits of the bacteria pointed to environmental stress (like the extremely high qCO_2 and qO_2 in the conventional and intensive farms of Table 2, not plotted in Fig. 2c). While the activity and functional diversity of soil bacteria increase with increasing heterogeneity of soil structure and texture, increasing organic matter and low-pressure management regimes (Table 2), the effects of organic and intensive management are more similar than expected. This finding may be novel and may become operational for the evaluation of different management regimes and food web dynamics.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE704/ELE704sm.htm

Table S1 Average body mass *M*, numerical abundance *N* and trophic links of the genera in the detrital soil food web of Fig. 1

Table S2 Environmental conditions and GLM-predictors of the three selected farms of Table 1

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