

How allometric scaling relates to soil abiotics

Christian Mulder, J. Arie Vonk, Henri A. Den Hollander, A. Jan Hendriks and Anton M. Breure

C. Mulder (*christian.mulder@rivm.nl*), H. A. Den Hollander, A. M. Breure and present address for J. A. Vonk, *National Inst. for Public Health and the Environment – POB 1, NL-3720 BA Bilthoven, the Netherlands.* – J. A. Vonk and A. J. Hendriks, *Inst. for Water and Wetland Research, Radboud Univ. – Toernooiveld 1, NL-6525 ED, Nijmegen, the Netherlands.*

For most species, the logarithm of their average body mass is negatively related to the logarithm of their relative population density, i.e. the numerical abundance. In this way, the allometric scaling (both mass–abundance regressions and body–size spectra) becomes useful in ecological theory to build and explain food webs. Using empirical evidence derived from 145 Dutch sites, a hypothesis is formulated to explain how soil microbivores, detritivores and predators react to increasing resource availability. Shifts in size distribution, and subsequently changes in soil food-web structure, are further discussed in the perspective of Holling's sequential interactions between basic system functions. We show that the allometric scaling and the averages of the (log-transformed) prey:predator body-mass ratios are reliable predictors for assessing faunal responses to nutrient availability. We view this work as a first attempt toward an extensive comparison of ecological processes in different soil systems.

Allometric scaling is used for populations to describe mass–abundance (M – N) relationships $N = a_1 \times M^{b_1}$ (Damuth 1981, Cotgreave 1993, Enquist 2002) and for species as metabolic rate $R = a_2 \times M^{b_2}$ (Peters 1983, West et al. 1997, Enquist et al. 2009) where in literature often is assumed that mass exponent $b_1 = -b_2$. Scaling relationships focus on 'bulk properties' of ecosystems that are less affected by local idiosyncrasies (Marquet et al. 1995, Kaspari 2005), like body-mass averages (\bar{M}) and body size. But can those traits not be seen like true local ecosystem properties?

The increasing popularity of functional traits such as body size and body mass together with the pressing need to enhance the usefulness of cost estimates for ecosystem services contribute to a challenging discussion on biodiversity–ecosystem functioning. Among others, which diversity measure seems to be the most appropriate to unravel ecosystem functioning remains an open question (Petchev and Gaston 2002, 2006, Naeem and Wright 2003, Ricotta 2004, Legendre et al. 2005). Seen that in food-web theory a comparable discussion on stability and sustainability is ongoing, we believe that allometry can provide the necessary 'diversity measure': a wide approach which captures multiple and subtle changes in the body-mass distributions in response to external factors (elemental factors, like limiting nutrients, disturbance like fire, liming or pollution, and climatological factors, like temperature or drought) and reflects the ecosystem functioning under environmental pressures, including human management.

For both kind of allometric scaling, i.e. mass–abundance relations and metabolic rate, it appears that many environmental factors influencing the mass exponent are already predicted by ecological and biological stoichiometry (Stern

and Elser 2002, Cruz-Neto and Bozinovic 2004, Etienne et al. 2006). Ecological stoichiometry is an approach to investigate the balance of energy and multiple elemental factors in ongoing ecological interactions (Stern and Elser 2002) and has been extended to evolutionary and functional questions in the form of biological stoichiometry (Elser et al. 2000, 2003, Gillooly et al. 2005). If we see allometric scaling as a currency to link elemental factors to ecology and physiology, we expect a mechanistic correlation with ecological and biological stoichiometry (Fig. 1). Only such an explanation might contribute to solve the debate on the universality of allometric scaling.

The debate on one universal power law has been running for a long time, but no general agreement has been reached (Glazier 2010). Some groups claim there is one universal mass exponent, with a value of either 2/3 (Heusner 1985, 1991, Dodds et al. 2001, White and Seymour 2003) or 3/4 (West et al. 1997, 1999, Brown and West 2000, Brown et al. 2004). Other groups claim there is no universal power law, and the most common exponent in macroecological literature, namely the 3/4 exponent, is sometimes rejected based on statistical assumptions, on model assumptions, and on large meta-analyses (Heusner 1982, 1985, Dodds et al. 2001, Glazier 2005, 2010, Kozłowski and Konarzewski 2005, White et al. 2007, Enquist et al. 2009). Deviations from the 3/4 exponent are expected when resource supply is not constant or bounded (Enquist et al. 1998, Brown and Gillooly 2003, Brown et al. 2004). As mass exponent b covers a range of values that depend on biotic and environmental conditions (Marquet et al. 2005, Mulder and Elser 2009), we have to see b not as universal exponent, but as useful currency for both biological and ecological functioning.

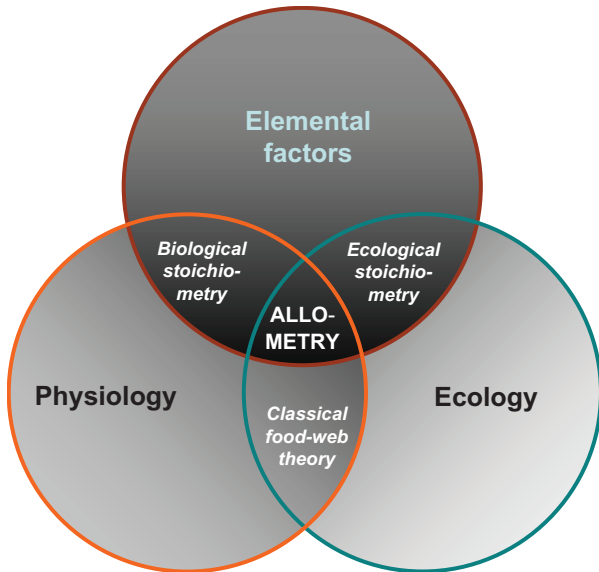


Figure 1. Elemental chemistry, physiology and ecology were combined to form an approach to the evaluation and explanation of allometric scaling. Although this figure is based on correlation, overlapping areas provide examples of causation. The distribution of body-mass averages and numerical abundance for individual species in a community is affected by natural and human-induced processes, from exploitation to species extinctions. Food-web theory, biological and ecological stoichiometry contribute to define the allometric reference for a given ecosystem.

Some proposals for reframing ecology and economy already exist. Holling stated in 1987 that ecosystems behave between four basic functions: exploitation (rapid colonization processes), conservation (slow resource accumulation), release (rapid changes between triggered complex structures), and reorganization/retention (minimal nutrient loss makes nutrient available for the next phase). All the phases from Holling’s sequence are clearly linked to resource quality and availability, in a comparable way to the distribution of organisms with different body-mass averages according to the basic function of the ecosystem they occur therein. Combining the basic functions of Holling’s sequence with our notion that changes in allometric scaling should be seen as dynamic currency, results in an integrated model (Fig. 2).

If true, such an integrated model would have many applications for ecologists and implications for stakeholders. One application would then be the assessment of the ‘ecological status’ of an ecosystem. Environmental and human-induced changes in the exponent b can be seen as quantitative measure of the deviation of entire communities from a reference status, the so-called ‘distance to target’. Allometry is according to us the ideal way to compute the self-organizing ability of complex systems like food webs and their capacity to recover after disturbance (Fig. 2).

Intercepts of mass–abundance relationships (as additional term a in the linear model $\log(N) = b \times \log(\bar{M}) + a$) seem to change as well, like intercepts of body-size distributions which tend to change with disturbances in both aquatic and

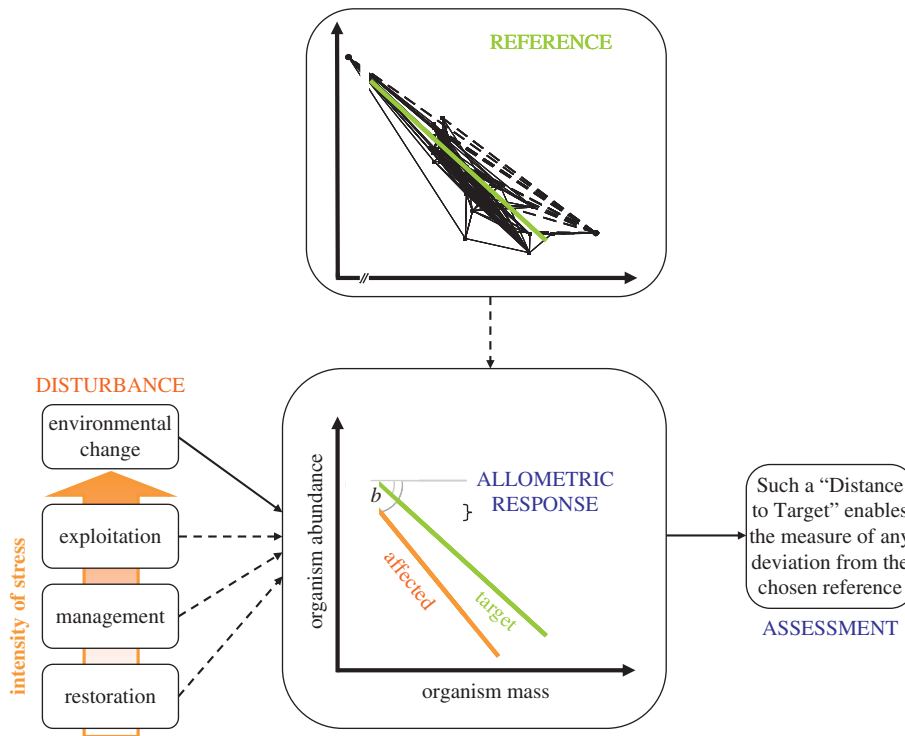


Figure 2. How the scaling and performance of food webs reflects environmental factors. In the upper part of the figure, one reference soil food web is given, with body-mass averages \bar{M} (x-axis) and numerical abundances N (y-axis) of the organisms occurring in the detrital food web of one Dutch grassland under bio-organic management (Mulder et al. 2005, redrawn). The lower circle represents the detritus (organic matter inclusive fungal mycelium and plant roots); detritivore links plotted as broken lines. The upper circle represents the bacterial cells. At the bottom of the figure, redrawn from Petchey and Belgrano (2010), a diagram flow from ecological disturbance to environmental assessment is provided for terrestrial ecosystems.

terrestrial ecosystems (Boudreau and Dickie 1992, Mulder et al. 2006, 2008). In contrast to aquatic food webs, which are strongly size-structured with larger predators eating smaller prey (Sheldon et al. 1972, Dickie et al. 1987), terrestrial food webs are less clearly size-structured, with arthropods utilizing relatively large prey (Cohen 1995). Therefore, besides allometry, we will take the prey:predator body-mass ratios into account as well to identify possible deviations in the soil system.

For most soils, their abiotic conditions largely depend on historical land use. Nutrient availability (manure) and soil pH (liming) are strongly influenced by human activities. We hypothesize that the availability of nutrients in the soil (land-use history) determines the value of the mass exponent b , with collinear effects in the intercept a , and in the energy fluxes across and between trophic levels. We examined this belowground in 145 real soil food webs for which the allometric scaling, trophic levels and (elemental and microbial) nutrients were determined.

Material and methods

In the Netherlands, biological data on faunal assemblages are available for 300 sites selected in a random stratified design comprising stringent combinations of land use and soil type. The majority of these sites are rural, being most of

them dairy and cattle farms selected from the databases of the Dutch Agricultural Economics Research Institute (LEI) and the Louis Bolk Institute (LBI). The resulting database comprises about 500 000 entries for more than 800 records (Rutgers et al. 2009). Sampling methods for bacterial cells (frequency of dividing cells, microbial biomass, microbial carbon content), microfauna (non-parasitic soil nematodes), mesofauna (mites, collembolans and enchytraeids) and macrofauna (lumbricids) are extensively described in Mulder et al. (2005, 2008) and Mulder and Elser (2009). In short, the bacterial biomass was estimated from the total number of cells determined by fluorescent staining and by combined direct microscopy and automatic image analysis, whereas the body sizes of at least 150 free-living nematodes of each species were measured to the nearest 5 μm with an eyepiece micrometer. When possible, microarthropods (mites and collembolans) and oligochaetes (enchytraeids and lumbricids) were weighted individually. Protozoans were not sampled, due to their rarity in Dutch sandy soils and due to the many problems in their taxonomical definition and in their further modelling as 'morphospecies' (Finlay 2004).

Unpublished RIVM chemical data were merged with the aforementioned biological data. Besides two P fractions (the PAL in soil, i.e. P content in ammonium lactate extract [0.1 mol NH_4 lactate \times 0.4 mol CH_3COOH], and the water-extractable fraction P-water) and the total organic and the total bacterial carbon fractions (C_{org} and C_{mic}), chemical

Table 1. Summary of the abiotics. Soil conditions – pH in KCl, organic carbon C_{org} (g kg^{-1}) the P fraction in water (mg P l^{-1}) and the PAL fraction in soil (mg kg^{-1}), the heavy metals Cu, Zn, Pb and Cr (mg kg^{-1}), and colloid percentage (%) –, microbial activity (frequency of dividing cells in weekly percentages, FDC, and microbial carbon ($\mu\text{g C}_{\text{mic}} \text{g}^{-1}$), and cattle manure in dairy farms ($\text{N kg ha}^{-1} \text{ year}^{-1}$) of the investigated sandy soils ranked according to their ecosystem type (bold). SD = standard deviation.

	pH	C_{org}	Manure	P-H ₂ O	PAL	FDC	C_{mic}	Colloids	Cu	Zn	Pb	Cr
Farms												
Conventional												
Average	5.0	50	390	42	486	5.3	82	2.5	9.9	28.0	12.4	21.1
SD	± 0.2	± 17	± 118	± 18	± 121	± 1.6	± 36	± 1.1	± 2.6	± 8.2	± 3.8	± 5.3
Semi-intensive												
Average	5.3	30	488	46	549	7.0	69	2.6	10.7	29.0	11.9	24.4
SD	± 0.4	± 9	± 130	± 20	± 141	± 4.7	± 39	± 1.2	± 2.0	± 7.4	± 2.8	± 6.6
Intensive												
Average	5.1	33	1047	62	732	4.8	68	3.6	14.2	34.1	16.4	20.4
SD	± 0.3	± 7	± 584	± 26	± 177	± 1.0	± 28	± 1.0	± 3.8	± 8.0	± 9.1	± 4.0
Organic												
Average	5.2	45	265	39	475	5.2	85	2.6	11.9	30.9	19.3	22.3
SD	± 0.2	± 16	± 77	± 13	± 126	± 1.0	± 63	± 2.1	± 2.3	± 8.3	± 12.4	± 8.0
Pastures												
Average	4.9	30	199	40	527	4.9	60	2.9	9.6	29.3	26.5	22.9
SD	± 0.6	± 9	± 114	± 15	± 191	± 1.7	± 50	± 1.1	± 2.6	± 6.3	± 15.2	± 4.2
Fields												
Multicropping												
Average	5.0	54	0	64	525	5.1	43	1.5	15.8	28.3	26.4	18.7
SD	± 0.3	± 24	0	± 16	± 144	± 2.0	± 27	± 1.2	± 6.7	± 12.8	± 16.8	± 9.3
Intercropping												
Average	5.4	29	0	67	598	4.5	42	4.3	11.0	30.4	17.0	22.4
SD	± 0.4	± 13	0	± 36	± 145	± 1.9	± 16	± 3.9	± 3.4	± 13.7	± 5.9	± 8.8
Nature												
Meadows												
Average	4.5	54	0	19	27	6.2	10	6.2	10.4	39.6	29.6	30.5
SD	± 0.3	± 24	0	± 25	± 30	± 1.4	± 8	± 7.4	± 4.3	± 37.1	± 29.0	± 17.9
Pine forests												
Average	3.2	34	0	9	32	6.3	24	2.7	3.1	10.6	21.4	14.7
SD	± 0.2	± 15	0	± 7	± 36	± 3.0	± 28	± 0.9	± 2.0	± 12.8	± 16.2	± 7.2

results for colloids (particles < 2 μm) and heavy metals (Cr, Cu, Pb and Zn) were used for the first time. Further, the acidity of oven-dried soil samples measured in 1 mol potassium chloride solution (pH-KCl) and the cattle-excreted nitrogen (N-manure $\text{ha}^{-1} \text{yr}^{-1}$) were kept as predictors for each of these locations. Nine ecosystem types with a different land-use history were selected, for a total of 145 soil food webs. Their distinctive general characteristics are summarized in Table 1.

The faunal assemblage was characterized by allometry (mass–abundance slope, slope across the biomass size spectrum, and relative intercepts), observed taxa (nodes), possible trophic links established for each web by taking the sub-predation matrix determined by the trophic guilds that were present (binary matrix published in Mulder et al. 2009), and the production ratio P at one trophic level i to the next trophic level j , which is a function of the proportion of the consumed prey C_j and the conversion efficiency (Table A1). We used the formula $f_{ij} \propto P_i C_j \propto N_i \bar{M}_i^{3/4} \times N_j \bar{M}_j^{3/4}$ (Peters 1983, Hendriks and Mulder 2008). This energy acquisition, which can become a more efficient energy transfer through elemental-driven resource consumption, is supposed to scale with body mass (Mulder et al. 2008, Mulder and Elser 2009).

We focused on the independent responses of prey and predator, and investigated the ratios between the body-mass values of prey and predator and their frequency distribution (Supplementary material Appendix 1 Table A1, A2). Of all the postulated qualitative links (who eats whom, regardless of what rate), only faunal links (animal prey–animal predator) were taken into account. Clusters were recognizable by choosing the redundancy analysis as linear method. Computations used SAS 9.1.3 (general linear models), CANOCO 4.5 (multivariate analysis: RDA), PASW Statistics 18 (box-plots), GraphPad Prism 4 (linearity and significance tests), and EXCEL Visual Basic optimization toolbox.

Results

Restricting the input variables (260 taxa) to the allometric scaling of the soil faunal community enabled a comparison of environmental values with an acceptable number of parameters. The 30 predictors were given in Table 1 (soil characteristics) and in Supplementary material Appendix 1 Table A1 and A2 (allometric scaling and faunal prey:predator body-mass ratios). Most of the webs exhibit significantly linear correlations for both mass–abundance regressions and biomass size spectra (Table 2). Averages of all 30 predictors of the coefficient of variation ($100 \times \text{SD}/\text{mean}$) per ecosystem type were respectively 42.7% (forests), 40.1% (meadows), 33.5% (multicropping), 30.8% (intercropping), 30.6% (pastures), 27.2% (bio-organic farms), 24.7% (semi-intensive farms), 23.9% (conventional farms), and 21.9% (intensive farms). Seen that the soil sampling in cultivated land occurred before tillage, manure applications, and sowing and growth of new crops, the sequence of the coefficient of variation from forests and arable fields to pastures and farms under different management reflects land-use intensity.

A canonical ordination was used to evaluate the recurrence of food webs under similar abiotic conditions in relation to the main landscape units. A redundancy analysis of the allometric and food-web predictors against the abiotic

and microbial characteristics of the soil is provided in Fig. 3. The RDA analysis clearly shows different clusters according to soil quality. Arrows pointing in the same direction, as in the case of basic soil resources like the two fractions of P and microbial C, indicate a strong positive correlation and the arrow lengths are proportional to the steepness of the gradient of each parameter. The relative position of a given location within a cluster points to its degree of correlation with a certain indicator. The linear combination of all the abiotic and microbial characteristics of the soil constraining the relative position of the sites shows three main clusters in Fig. 3: arable fields on the left, grasslands in the middle, up to forests on the right. (These three main clusters were also used for the box plots of Fig. 4). The high significance of the first canonical axis of the RDA was confirmed by a Monte Carlo analysis (F-ratio = 128.89, $p = 0.002$).

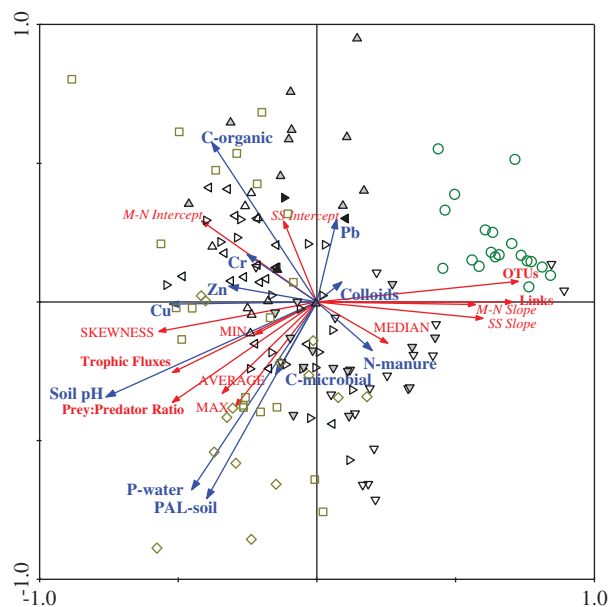


Figure 3. One direct gradient analysis explains the food-web structure (here as red variables) by two ordination axes of a redundancy analysis that are constrained to be linear combinations of soil abiotics (blue variables, environmental basis as given in Table 1). The 145 ecosystems are given as follows: boxes for arable fields, triangles for grasslands and circles for forests. In particular, multicropping as squares, intercropping as diamonds, farms as open triangles (left triangles for conventional regime, up triangles for bio-organic regime, right triangles for semi-intensive regime, and down triangles for intensive regime), pastures as closed down triangles, and meadows as closed up triangles. Three black-filled triangles, one for bio-organic (see top Fig. 2), one for conventional and one for semi-intensive regime, are the farms described as references in Mulder et al. (2005). The variables are OTUs (operational taxonomic units as nodes), Links (faunal links from a quantified resource guild i to a quantified consumer guild j), Trophic fluxes f_{ij} (relative flux f from resource i ('Faunal prey') to consumer j ('Faunal predator') as the amount of biomass of i consumed by j (dry weight) per unit time), Prey:predator (PP) body-mass ratio (mean of PP ratios of faunal resource M_i on faunal consumer M_j), and minimum, median, average, skewness and maximum of the PP ratios of $\log_{10}(M_i)$ on $\log_{10}(M_j)$. We investigated the slope of the mass–abundance (M – N) relationship and vertical intercept (M – N intercept) on the density axis (N), and the slope of the linear regression fitted on the biomass size spectrum (SS) and vertical intercept (SS intercept) on the biomass axis.

Faunal communities of the forest cluster are marked by a positive correlation with trophic links, operational taxonomic units (OTUs), and both allometric regression slopes (MNSL and SSSL), and a negative correlation with pH (lower pH, higher acidity) and the aforementioned basic soil resources C (especially microbial carbon) and P (both fractions). Bacteria are clearly more abundant under bio-organic farms: the microbial carbon content of the soils under organic farming is in fact 3.5 times higher than under pine forests (85 ± 63 SD vs 24 ± 28 SD, respectively). Indirectly, shallow slopes suggest that the probability of occurrence of a taxon with bigger body-size increases in open landscapes, i.e. grasslands and fields (Fig. 4). In other words, the cumulative probability of occurrence for larger invertebrates and the probability of occurrence for smaller invertebrates increase in different ways with the number of nodes: in webs with a higher biodiversity, such as in forests, the largest taxa ($\bar{M} > 1 \mu\text{g}$) were the most dominant. The forests had therefore the highest variance in complexity, and the intensively managed farms the least (Supplementary material Appendix 1 Table A1).

The regression slopes of (log-summed) biomass size spectra (SSSL) are a function of the bin centres on a log(\bar{M})-scale and indicate how biomass changes with increasing \bar{M} bins. If we should assume bigger \bar{M} for taxa belonging to a higher trophic level, implying lower prey:predator (PP) body-mass ratios, we would expect a certain degree of colinearity between allometric scaling and the average of the PP body-mass ratio. However, this was not the case (140 DF, GLM $p = 0.013$), although the median of PP body-mass ratios remained related to the intercepts of both the mass–abundance linear regression and the line across the biomass size spectrum (in both cases, 140 DF, GLM $p < 0.002$). These results show the extent to which the frequency distribution of (log-scaled) faunal PP body-mass ratios in soil systems is skewed: the median of all the possible PP-ratios in all the 145 food webs is, on average, -0.323 ± 0.210 SD, whereas the mean of all PP-ratios in all webs is, on average, 1.224 ± 0.294 SD. The median shows a dominance of predators generally bigger than

their possible faunal prey, in contrast to the mean showing predators generally smaller than their possible faunal prey (Supplementary material Appendix 1 Table A2). But variance of a given magnitude should matter less when the median is high (here: clearly positive) than when the median is low (here: slightly negative). These statistical results support the intrinsic complexity of the soil food webs regarding consumer–resource interactions.

The dimensionless (unitless) flux f_{ij} – being the production ratio at one trophic level P_i in function of the proportion of the consumed prey C_j at the next trophic level –, is given in Supplementary material Appendix 1 Table A1 and summarized in Fig. 4. A total of 139 823 possible trophic links between 260 taxa from 145 real community food webs was investigated. On average, f is the highest in our ten bio-organic agroecosystems (14.15 ± 0.34 SD) and the lowest in our 19 forests (12.20 ± 0.44 SD). The average fluxes of ‘open-canopy nature’ – that is, the meadows –, and of our ‘close-canopy nature’ – that is, the aforementioned forests –, differ one order of magnitude (Fig. 4). According to Costanza et al. (1997), we could see these forests as a slowly accumulating ‘capital of biomass’ (comparable to Holling’s basic ‘conservation’ function). If f is indeed an indicator of sustainability, then the flux might open a way to develop more general theories in vegetation succession, conservation biology and restoration ecology.

Discussion

Allometry of soil organisms provides objective metrics for biological soil quality that integrates physical and chemical variables. The specific goal of soil policy is the sustainable use of soil, often seen as deviation from a reference status (Breure et al. 2005). Any definition of reference states comprises three steps: the classification of ecosystem types, the recognition of bioindicators, and their subsequent assignment to ecosystem processes. Despite mutual benefits, these three steps evolved separately, as most field ecologists focused on the biological

Table 2. Allometric scaling in 145 soil food webs. Linear regression slopes significantly different from zero in most cases (goodness-of-fit test, 5% significance). The slope of the mass–abundance regression (MNSL) is more often different from zero than the slope of the biomass size spectrum (SSSL). However, the significance of a linear regression fitted across the biomass size spectrum remains comparable to that of a linear regression fitted in a mass–abundance scatter, i.e. across the (\bar{M} , N) web (SSSLs exhibit an average r^2 of 0.4278 ± 0.1809 , undistinguishable from the average r^2 of 0.3952 ± 0.1467 of the MNSLs). Details in Supplementary material Appendix 1.

	Sites (no.)	Mass–abundance regression			Biomass size spectrum		
		MNSL $\neq 0$	Linearity	Goodness	SSSL $\neq 0$	Linearity	Goodness
Farms							
Conventional	19	100%	100%	<0.001	100%	100%	0.010
Semi-intens.	21	100%	100%	<0.001	95.2%	95.2%	0.014
Intensive	19	100%	94.7%	0.003	100%	95.2%	0.001
Organic	10	100%	100%	<0.001	90%	100%	0.002
Pastures	13	100%	100%	<0.001	77%	100%	0.006
Fields							
Multicropping	20	100%	100%	<0.001	65%	85%	>0.15
Intercropping	14	100%	100%	<0.001	92.9%	92.9%	0.018
Nature							
Meadows	10	100%	100%	<0.001	100%	90%	0.006
Pine forests	19	94.7%	31.6%	0.025	100%	100%	0.002

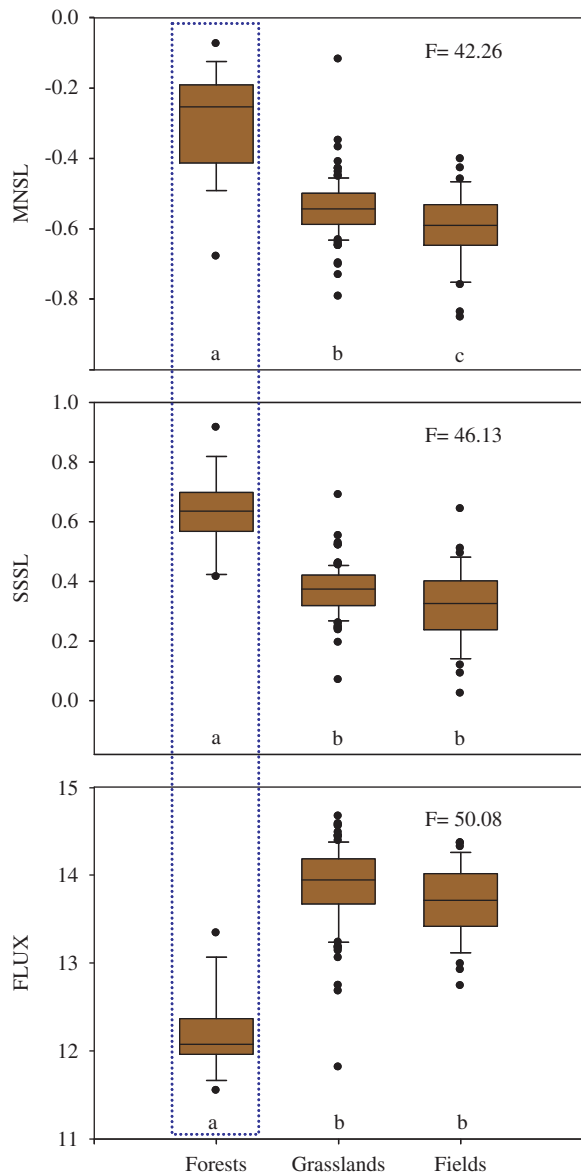


Figure 4. Boxplots for mass–abundance slopes (MNSL), slopes of the regression fitted on the biomass size spectrum (SSSL) and trophic fluxes f_{ij} (see Supplementary material Appendix Table S1 for more details). Different superscripts (a, b, c) indicate significant differences between ecosystem types by the Kruskal–Wallis ANOVA ($p < 0.001$). The boxplot lengths are a function of the coefficient of variation. The joint changes in numerical abundances and body-mass averages of the soil organisms that occur in our ‘Forests’ make these soil systems very close to Holling’s conservation phase of complex structures, whereas the ‘Grasslands’ (farms and meadows of Table 1 were lumped together) and ‘Fields’ are examples of the release of stored capital of biomass and nutrients. Both kind of allometric slopes provide quantitative tools to assess ecosystem functioning.

classification of sites in communities, geneticists paid attention to the identification of effective proxies, and theoretical biologists developed mathematical models. As a direct consequence, the correlation and extrapolation of these three steps may appear difficult. However, if we consider the ecosystem behaviour as the sequential interaction of Holling (1987), allometric scaling clearly provides a dynamic, valuable and quantitative tool to interconnect these three steps.

Somehow, soil organisms seem to react (and to adapt themselves) to abiotic conditions. In intensive farms, biodiversity declines, and in the case of bacterial-feeding invertebrates, the number of nodes decreases with increasing land pressure. Compensating shifts between small but abundant free-living nematodes (paucispecific populations linked to microbial resource pulses that might be ascribed to cattle nitrogen as manure) and greater but scarce microarthropods (many small populations belonging to different taxa) are a plausible mechanism to explain these changes in allometric scaling.

In contrast to pelagic ecosystems, in soil systems \bar{M} is not negatively correlated with either trophicity or biomass. An increase in aboveground nutrients (cattle manure) is positively correlated with the number of taxa belonging to the meso- and the macrofauna, whereas the belowground nutrient availability (as depicted by soil acidity and both fractions of phosphorus) is positively correlated with taxa belonging to the microfauna. Summarizing, the log-summed biomasses for collembolans, enchytraeids and lumbricids increase with \bar{M} but their trophic level decrease. The steeper the allometric scaling – the total log-summed contribution of the mesofauna to the entire faunal assemblage becomes greater relative to that of the microfauna –, the higher the soil nutrient availability. Thus, invertebrates react in different ways to abiotic conditions and their independent effects on soil ecological services contribute to a further shift in their own habitat–response relationships. Clearly, the allometric scaling changes according to separate factors (Fig. 1). Possible components comprise the environment (which can be characterized by the soil abiotic conditions), the ecology (which defines, among others, the trophic level and the community traits of the investigated organisms), and the physiology (which assesses the response traits of the investigated organisms).

Soil abiotic conditions clearly explain the extent to which the structure of soil food webs change. In our opinion, the ongoing debate on whether metabolic rate scales as $M^{3/4}$ or $M^{2/3}$ should become addressed only in such a wide framework. Although quarter-power scaling is pervasive and seems physically universal (sensu West and Brown 2004), at local scales like those of our soil systems, exponents change according to the environment, the community ecology and the physiology of the occurring organisms. A recent question point arising from macroecological issues is the actual relationship between gradients in allometric scaling (including gradients in numerical abundance) and ecosystem functioning. Processes generating gradients of numerical abundance are a key focus in the global changes in productivity, since abundance reflects both the habitat–response relationship of the investigated taxa and the physiological optimum of the higher taxon (node) they belong to.

Our results become even more interesting if seen in the dynamic framework of interspecific models. Chakraborty and Li (2010) investigated the success of invasive species after greater than average time-dependent fluctuations in resource supply. In their model, Chakraborty and Li (2010) assumed that species were competing for one (uniformly distributed) limiting resource, resulting in a resource-dependent colonization. In these soil systems, uniform rates of resource supply are absent, making the estimation of interspecific resource competition difficult.

However, the different sensitivity to the elemental resources of organisms with different body size allows to understand better population dynamics and to increase the realism of trait-based interspecies extrapolations. Main implication for soil systems is that elementary factors like carbon and phosphorus, and possibly micronutrients such as copper, are important in: (1) constraining the activity of individuals, (2) determining the population density, (3) defining the belowground consumer–resource interactions, and (4) driving the food-web organization (Allen and Gillooly 2009, Mulder and Elser 2009, Reiss et al. 2009, Mulder 2010).

The Netherlands have a long tradition of biological soil monitoring and ecological applications, starting with De Ruiter et al. (1993, 1994, 1995), Brussaard et al. (1996) and Korthals et al. (2001). We are not aware of other countries with such a wide range of soil biological parameters included in monitoring programs running for so many years. The goal of this paper is to propose simple graphical and quantitative indicators of soil community composition, and to illustrate the extent to which these allometric indicators show effects of land use. These indicators are useful to show how faunal communities respond to farming practices and to soil abiotics.

We find that allometric indicators are superior to previous indicators of ecosystem functioning in the following respects:

- 1) the slopes and the intercepts provide a currency to measure ecosystem functioning;
- 2) a characterization of the fluctuating states of Holling's sequence becomes possible.

Overall, this overview for belowground faunal communities under different management practices shows strong variability in the allometric scaling. We believe, therefore, that our structural approach contributes towards an extensive comparison of ecosystem types and management practices. Our data may allow, among others, an improved management of phosphorus in agro-ecosystems to combat leaching and pollution and to keep ecosystem services.

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Supplementary material (available as Appendix O18869 at www.oikosoffice.lu.se/appendix). Appendix 1.