

doi:10.1016/j.ecocom.2006.05.004

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## Allometry, biocomplexity, and web topology of hundred agro-environments in The Netherlands

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### Abstract

For almost all soil organisms, the logarithm of numerical abundance ( $N$ ) is inversely related to the logarithm of body mass ( $M$ ). It is helpful to use allometry and food-web topology to condense environmental information. Using mathematical evidence derived from 99 real webs, a hypothesis is formulated to explain how belowground soil organisms become affected by increasing effects of animal manure and this is discussed in relation to soil productivity. As a matter of fact, the intercepts of allometric correlations change in a highly significant way according to aboveground grazing by mammals. Linear regressions of  $\log_{10}(N)$  values fitted against their  $\log_{10}(M)$  averages show allometric unity (slopes equal to  $-1$ ) only in one fourth of the webs. Under different levels of taxonomic aggregation, our intercepts remain directly correlated with macroherbivory. Also after removal of bacteria from these real webs, intercepts of the linear regressions robustly fitted on the eukaryotes'  $M$  and  $N$  reflect the local nitrogen availability from animal manure. Other basic web properties, such as trophic links and structural complexity, display a comparable pattern from nutrient-poor to nutrient-rich ecosystems, in contrast to a rather erratic connectance. Regardless of total soil biodiversity, only in 23 real webs a host of organisms ranging from earthworms and insects to bacterial cells seem to interact in ways beneficial to each other.

### 1. Introduction

"It is clear that whatever phenomena are shown by space should also be more or less paralleled by those shown by size... Very little investigation is required to show that this is indeed the case." John Christopher Willis (1922).

Uncultivated land areas, like permanent grasslands, heaths and forests, have been reduced dramatically. Especially in small European countries like The Netherlands, the general intensification of agriculture has resulted in heavy habitat fragmentation. Changes in extensive agricultural management have severely influenced the diversity and abundance of invertebrates with concomitant effects for – among others – a wide range of farmland birds (Chamberlain et al., 2000, Freemark and Kirk, 2001 and Chust et al., 2003). Only the organic management was reported to increase biodiversity of most agro-environments (Mulder et al., 2003, Mulder et al., 2005a, Mulder et al., 2005b and Bengtsson et al., 2005). Ecological consequences on the ecosystem functioning due to variable agricultural practices (possibly related to differences in

aboveground productivity) were contradictory. We have studied multiple taxonomic groups (earthworms, enchytraeids, nematodes, mites, collembolans, and bacteria) in 99 soil food-webs (hereafter, simply webs) across The Netherlands, looking for the best agreement between land use and real web response.

### **1.1. Singular species do never thrive apart from other occurring species**

If some species enables the system to persist in nominal behavioural states as long as (or longer than) its expected natural longevity, we may describe the features (species, functional processes and ecological limits) as related to sustainable development. As most ecological studies advocate that the distribution, abundance, and dominance of a given taxon under certain environmental conditions reflect both the response of the local population and the extent to which local habitats meet the primary requirements of the taxon itself (review in Breure et al., 2005), it becomes possible to summarize any variation in taxonomic richness by grouping together areas under similar regimes.

Starting point is the observation that animals are not randomly distributed (Ghilarov, 1944 and Ghilarov, 1965) as their body mass and their numerical abundance are not independent (Cohen et al., 1993, Cohen et al., 2003, Makarieva et al., 2004 and Makarieva et al., 2005). The second, obvious step is the observation that most density-dependent trends must be correlated with abiotic properties, a complementary perspective of this well illustrated postulate (Mulder et al., 2005b and Mulder et al., 2005c). The suitability of a specific area is in fact determined by several environmental variables, so combining by linear regression the log-transformed body mass and numerical abundance of the observed species into allometric summary parameters may be a sensible way of classifying ecosystems.

### **1.2. Are allometric patterns related to biodiversity loss?**

Each ecosystem or community exhibits a capacity to incorporate environmental changes. Concrete systems representative in their abiotic and biotic properties as well as their faunal composition for a range of real sites can be defined as group of sites characterized by selected physical, chemical and biological attributes. Thus, even under environmental conditions that are hold constant for a certain time span, the ecosystem functioning is part of a continuous, dynamic process.

Using empirical evidence from field studies, we will investigate the extent to which the demographic response of belowground organisms reacts to incremental changes along an aboveground productivity gradient (i.e., grazing pressure by mammals, often cattle, and consequent animal manure). We wish to show whether community differences in their relationships are large enough to influence the ecosystem functioning of soil systems and make a first attempt to operationalize further our analysis. Our main goals are to identify agro-environments that are most vulnerable to the loss of biodiversity and to evaluate the extent to which the number of species affects the web topology and the allometric intercepts and slopes.

## **2. Materials and methods**

### **2.1. Data**

Spatial patterns of total microbial biomass and soil invertebrates provide a fine-tuned assessment of the basal soil quality in The Netherlands. To achieve this, soil organisms were collected between 1999 and 2004. In this study, we shall investigate 99 sites on Pleistocene sand belonging to low-intensity management (traditional agro-forestry, 19 Scots pine plantations), middle-intensity management (pasture mixed farming, 2 × 11 grasslands under organic regime), high-intensity management (multicropping, 25 fields, intercropping, seven fields, crop rotation, four experimental fields, and alley cropping, two fields), and no management at all (10 mature, nutrient-rich grasslands and 10 dry heathlands). Land use information on animal manure (yearly nitrogen input) was gathered directly by farmer interviews. All locations were set in a regional context by comparison with the characteristic values of farm size, management regime, livestock density, cropping and harvesting.

### **2.2. Microfauna and bacteria**

Nematodes were extracted from 100 g fresh soil using funnel elutriation, sieving and cottonwool extraction (Mulder et al., 2003 and Mulder et al., 2005b). All individuals within two clean 10 ml water suspensions were screened and counted with a stereomicroscope. In two permanent mounts in formaldehyde, 150 soil nematodes were identified at genus level by light microscopy (400–600×) and assigned to feeding habits in consultation with taxonomic experts. Microbiological samples were collected from the same soil samples as for nematodes and stored at a temperature of 12 °C and 50% water holding capacity. Bacterial cells were counted in soil smears by fluorescent staining. Cell number, average cell volume, and frequency of dividing cells were determined by direct co-focal laser scanning microscopy coupled to a fully automatic image analysis system (Bloem et al., 1995). To estimate the bacterial biomass from the cell number we used the measured cell volume average of the entire bacterial population and a biovolume-to-carbon conversion factor of  $3.2 \times 10^{-13}$  g C  $\mu\text{m}^{-3}$  (Bloem et al., 1995 and Mulder et al., 2005a).

### **2.3. Mesofauna and macrofauna**

Microarthropods were collected in a randomized block design. Their four-fold cores (diameter 5.8 cm × 5 cm) were kept separate until behavioural extraction. Mites and collembolans were extracted from core samples within 15 days with the temperature gradient increasing stepwise from 20 to 60 °C using the Tullgren high-gradient canister method with a low-wattage tungsten filament bulb. Sampled animals were observed at a magnification of 200–1000× with a light microscope and assigned to feeding guilds according to presence or absence of a specific enzymatic activity (secondary decomposers listed in Mulder et al., 2005c). Three carbohydrases have been measured: cellulase, chitinase, and trehalase. As enzyme activity depends on the food components consumed prior to sampling, carbohydrases reflect the feeding guilds of microarthropods. It should be emphasized that a high amount of our knowledge about their diet range has been derived from microcosm studies of selected organisms. Earthworms, in contrast, can be seen as pure detritivores, being their ingestion of bacteria and fungi passively related to their feeding on soil particles. Enchytraeids are relatives of soil earthworms with a much smaller size but a similar diet. Enchytraeids were sampled in six-fold cores (5.8 cm × 15 cm, six rings of 2.5 cm height), extracted

using wet funnels, identified to the lowest taxonomic level possible (Wim Didden, unpublished results), measured, and counted.

#### **2.4. Statistical analyses**

The analysis of variance (ANOVA) and the generalized linear model (GLM) were performed using the SAS 8.02 statistical package. The binary response at species level was rounded up and fitted to continuous abiotic gradients using multiple regressions and smoothing techniques under a generalized additive model (GAM). Although each observed species has a binomial distribution (its probability of occurrence rounded up to either presence or absence), the error distribution is specified to be Poissonian, as at any predictor value both the expected taxonomic diversity as itself (redefined here as difference between predicted and observed species) are integers (Mulder and de Zwart, 2003). We checked our conditional expectation by studying the Studentized residuals (normal distribution) and by verifying the linearity of the observed averages (Mulder et al., 2005a and Mulder et al., 2005b).

#### **2.5. Allometry**

Extracted microarthropods were divided in body size classes to estimate the corresponding dry weight. Worm-like organisms such as nematodes and enchytraeids were extracted, identified, measured for each specimen, and counted, including juveniles and resting stages. We converted their body size (length and width) to body mass by volumetric relationships. In the case of all eukaryotes, the averages of our body mass values ( $M$ ) have been computed at genus level as this taxonomical resolution offers the best available combination of high environmental information and low structural noise. All genera of eukaryotes (and trophic species, see below) were placed in webs on axes with ordinate  $\log_{10}(N)$  and abscissa  $\log_{10}(M)$ . Obviously, the biomass  $B$  of a genus  $i$  is its average body mass  $M$  times its numerical abundance  $N$ , thus:  $\log_{10}(B) = \log_{10}(M) + \log_{10}(N)$ . However, this taxonomical resolution can not reflect the actual distribution of bacterial  $\alpha$ -diversity, for which we lack reliable data. (Only functional and physiological microbial data were available.) To test whether lumping together the observed number of bacterial cells in one highly-aggregated "trophic species" introduces a bias towards small organisms, we estimated the allometric intercepts of the linear regression of the numerical abundance  $\log_{10}(N)$  as a function of the body mass  $\log_{10}(M)$  for 99 complete webs before (including bacteria) and after the removal of bacteria (only with eukaryotes).

#### **2.6. Web topology**

Based on our empirical knowledge of the feeding habits and guilds of the detected invertebrates, the proportion of all possible trophic links ( $I$ ) that are realized in one web of  $S$  taxa (connectance  $C$ , where  $C = I/S^2$ ) is suggested to reflect (Dunne et al., 2002, Dunne, 2005 and Ebenman and Jonsson, 2005) either the dominance of generalists within a web (high  $C$  values) or a skew towards specialists and immature ontogenetic stages (low  $C$  values). The product of the number of genera (or nodes),  $S$ , and the connectance,  $C$ , equals the ratio  $I:S$  (Chen and Cohen, 2000 and Rossberg et al., 2005). All soil organisms were sampled in the same way. Such homogeneous methodologies are supposed to reduce the influence of empirical differences in long-term sampling efforts (Cohen, 1994 and Mulder et al., 2005c).

### 3. Results

Fig. 1 clearly shows that neither the introduction nor the removal of the trophic species “bacterial cells” entails a methodological problem. For each web, intercepts on the  $\log_{10}(N)$ -axis of the whole set (with bacteria) are only slightly higher than those without bacteria ( $3.32 \pm 0.029$  S.E. versus  $3.27 \pm 0.027$  S.E., respectively). The allometric difference on the ordinates between the 99 coupled intercepts is only  $0.048 \pm 0.0044$  S.E. and the correlation between the two different intercepts, calculated by forcing the regression line through the origin, is striking ( $P = 4 \times 10^{-90}$ )! Still, bacteria remain outliers in our webs due to their Studentized residuals, mostly higher than |2|.

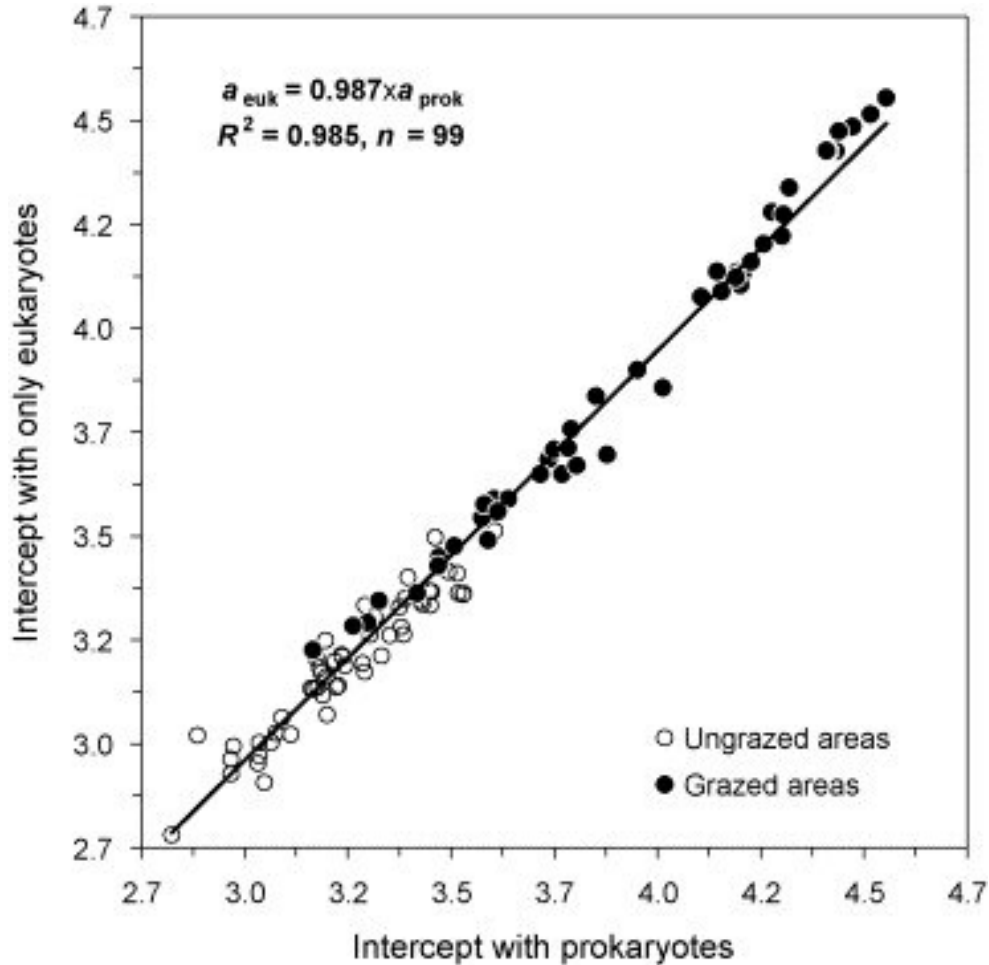


Fig. 1. Comparison between fitted equations in accounting for allometric intercepts ( $a$ ) on the ordinates ( $\log$ -transformed numerical abundances). Both intercepts predicted by imposed linear regressions fitted to the plot of ( $M, N$ ) points of eukaryotes + prokaryotes ( $a_{prok}$ ) and eukaryotes only ( $a_{euk}$ ) explain as much ( $\pm 0.0019$  S.E.). Regardless of the inclusion of bacteria, eukaryotes predict the intercept similarly ( $P < 0.00001$ ). Nutrient-rich mature grasslands and organic grasslands (solid circles) share the highest intercept values, arable fields and pine forests (open circles) share the lowest intercept values ( $P < 0.0001$ ).

The precision of the edge estimates by linear regressions was a tackling question. We have chosen not to merge the aggregated bacterial cells with the high-resolution taxonomic data already available for collembolans, mites, nematodes, enchytraeids and earthworms, notwithstanding that the same microbial data may provide a mechanistic basis for further modelling (Reuman et al., 2006).

### 3.1. Allometric relationships

Many organisms of our soil systems fall near a diagonal where the mean slope of  $\log_{10}(N)$  as function of  $\log_{10}(M)$  approximates the unity ( $R^2 = 0.667$ ,  $F$ -ratio = 530,  $P < 0.0001$ ). Allometric relationships with a slope closer to  $-1$  than to  $-3/4$  are hold in local webs when wide spectra of taxonomic groups are included (Cohen et al., 2003 and Mulder et al., 2005a). Regardless of the biodiversity  $S$  (in our soil systems  $S$  fluctuates between 33 and a 100 genera – excluding the prokaryotes – with a mean of  $56.2 \pm 1.6$  S.E.), all the slopes of the regression lines of the estimates of  $\log_{10}(N)$  as function of  $\log_{10}(M)$  remain extremely significant ( $\pm 0.018$  S.E.). Observed slopes of the regression lines for *complete* webs are also significantly different from each other ( $F = 46$ ,  $P < 0.0001$ ). Twenty-three webs exhibit regression slopes close to  $-1$  ( $\pm 0.014$  S.E.). Slopes close to  $-3/4$  were encountered only three times, twice in grasslands ( $-0.77 \pm 0.09$  S.E. in a pasture under organic management and  $-0.74 \pm 0.63$  S.E. in a mature grassland), and once in an acidic pine forest ( $-0.73 \pm 0.10$  S.E.). Slopes fluctuate strongly according to the inclusion or the exclusion of bacteria. Regression slopes of all 99 *complete* real webs vary from  $-1.23$  to  $-0.70$ , with a mean of  $-0.93$ , whereas the slopes of animal (sub)webs vary from  $-0.94$  to  $-0.12$ , with a mean of  $-0.56$ . In contrast to a reanalysis of 39 terrestrial ecosystems listed by Damuth (1993) in Li et al. (2004), our closed ecosystems (forests) share a significantly less negative slope than our open ecosystems do, varying from  $-1.02$  to  $-0.79$ , with a mean of  $-0.89$  (with bacteria), or from  $-0.68$  to  $-0.12$ , with a mean of  $-0.31$  (without bacteria). Li et al. (2004) argued that closed ecosystems are more stable than the open ecosystems, a hypothesis supported by the fact that simulated tree diversity (Shannon–Wiener indices) seems to increase significantly under a combination of climate change and logging (Chen and Li, 2004), in evident contrast to the response to climate change of open ecosystems (Mulder, 1999 and Mulder and Ellis, 2000). In our study, we suggest that aboveground grazing by mammals as binary predictor explains a larger part of the environmental pressure (stress) on the belowground webs of agro-ecosystems. As a matter of fact, our 46 grazed ecosystems (regardless of the management regime, if any) are, on average, characterized by a significantly more negative slope than our 53 ungrazed (more stable?) ecosystems, such as forests and winter farms ( $P = 0.0002$ ).

A slope exactly equal to  $-1$  between consumer's  $N$  (dependent variable) and consumer's  $M$  (independent variable) implies that one unit of available resource biomass supports a constant (increasing) amount of consumer biomass as the consumer's  $M$  increases. If we consider two coupled taxa, a consumer  $c$  that feeds on a single resource  $r$ , any slope of  $-1$  means that consumer  $c$ ,  $N_c \times M_c$  equals resource  $r$ ,  $N_r \times M_r$  (Cohen et al., 2003). If we consider two taxocenes, such as Rhabditidae (bacterial-feeding nematodes) and bacteria, a (steeper) slope more negative than  $-1$  indicates that the microbial grazer  $c$  has smaller  $B$ , respectively, than the bacterial resource  $r$  itself, assuming that the microbial grazer is below and to the right of the bacteria (as is always the case in our log–log plots; for three downloadable webs see

<http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE704/ELE704sm.htm>). Trophic links whose slopes of log-numerical abundance  $N$  as function of the log-body mass  $M$  fall close to the allometric unity are the most

abundant. According to Reuman and Cohen (2004), we may define the length of a trophic link as the number of orders of magnitude difference between the  $M$  of the predator and that of the prey, plus the number of orders of magnitude difference between the  $N$  of the predator and that of the prey. Given that both the  $N$  as the  $M$  values of all the soil organisms in these 99 real webs span over 12 orders of magnitude, the length (distance) from the smallest organism (bacteria) to the largest invertebrate occurring in our webs (Lumbricidae) was almost 23 orders of magnitude. In contrast to aquatic food-webs (Hall and Raffaelli, 1991 and Cohen et al., 2003), where the distance between top predators (piscivorous fishes) and phytoplankton could be spanned by four links each of length 5 or 6, this distance of length 22.7 is actually *one* exceptionally long link, second only to a link of length 16 between bacterivore mites (*Histiostoma*) and their microbial resource (Mulder et al., 2005a). As soon we take into account only the prey–predator relationships within soil invertebrates, the mean length of food-chains decreased dramatically. For instance, parasite links between nematodes were close to 2 and between microarthropods slightly longer than 3 (cannibalism has always been removed). Feeding on substrate, Lumbricidae may ingest non-parasitic nematodes (Räty and Huhta, 2003); such accidental links are still very long, up to 10 orders of magnitude. Specialized prey–predator links of nematodes were much shorter than those of arthropods: links of nematodes feeding on nematodes share an average length of 0.95, links of mites feeding on nematodes share an average length of 3, comparable to most links of mites feeding on other microarthropods. These short trophic links in detrital soil webs imply that even the longest distance between the averages of (small) nematodes and (larger) enchytraeids is less than 4 orders of magnitude. Therefore, the long trophic link of length 23 could be spanned by at least two “accidental” links each of length 10 or by eight links each of length 3, but never by four links each of length 6. The results of our empirical distribution are comparable to the food-chain length distribution of the constrained imaginable Ythan food-web (Hall and Raffaelli, 1997).

Merging at taxonomic level does not introduce statistical biases: mean weight and standard deviation show the same variation patterns for predatory as for non-predatory species (cf. Griffiths, 1998). A multitrophic analysis of organisms shows a certain temporal invariance in the allometric relationship of decomposer webs (Table 1), testifying to the actual importance of universal scaling in understanding ecological functioning (Marquet, 2000 and Marquet et al., 2005). This is not unexpected, as the body mass of animals remains determinant for spatially-scaled predatory activity and, thus, for the link structure within a web. Changes in numerical abundance across trophic levels depend on the relationships between consumer and resource at the genus level.

Table 1.

Multitrophic analysis of the log-transformed biomass ( $\log_{10} \mu\text{g dry weight m}^{-2}$ ) of the organisms in 99 real webs, listed in order of land use

	Primary decomposers <sup>a</sup>	Secondary decomposers <sup>b</sup>	Predators I	Predators II
Fields				
Alley cropping	6.54 (0.20)	5.54 (0.17)	4.84 (0.13)	3.83 (0.16)
Crop rotation	6.51 (0.32)	5.79 (0.61)	4.50 (0.08)	3.34 (0.16)
Intercropping	6.68 (0.36)	5.49 (0.40)	4.31 (0.39)	3.05 (0.63)
Multicropping	6.64 (0.24)	5.72 (0.28)	4.38 (0.33)	3.23 (0.45)
Pastures				
Organic grasslands	6.87 (0.34)	6.15 (0.26)	4.76 (0.28)	3.65 (0.38)
Agroforestry				
Scots pine plantations	6.28 (0.31) <sup>c</sup>	5.80 (0.27)	4.49 (0.28)	3.19 (0.49)
Nature				
Dry heathlands	5.62 (0.08) <sup>c</sup>	6.90 (0.18)	5.55 (0.33)	3.76 (0.53)
Mature grasslands	7.38 (0.49)	6.38 (0.17)	5.13 (0.22)	4.03 (0.86)

Standard deviations in parentheses.

<sup>a</sup> Including detritivores (primary decomposers) and bacteria (primary consumers).

<sup>b</sup> Feeding on microbes, root exudates and decaying plant tissues (secondary decomposers).

<sup>c</sup> No earthworms recorded.

Table 1 depicts how biomass constantly decreases one order of magnitude across each trophic level, and overall  $B$  spans 6 orders of magnitude at genus level. Still, subtle variations in the soil biocomplexity related to land use are recognizable. For instance, the observed  $B$  values of both predators I + II in grazed ecosystems (i.e., nutrient-rich organic grasslands, undisturbed mature grasslands, or nutrient-poor, acidic dry heathlands) are much higher than expected. On the other hand, observed  $B$  values of primary decomposers (like earthworms) and primary consumers (bacteria) occurring under acidic conditions in the soils of most Scots pine plantations and dry heathlands are remarkably low. Among others, Table 1 shows that non-parasitic soil nematodes contribute clearly to the higher biomass of secondary decomposers in open canopies (grasslands and heathlands), differing up to one order of magnitude from closed ecosystems like forests. *Calluna*-dominated heathlands are rather stable thanks to the high litter contents of phenolics and lignin that result in a low nitrogen availability to other plants, but as soon the nitrogen availability becomes high (for instance due to excessive sheep grazing) they are quite rapidly replaced by *Molinia*- or *Deschampsia*-grasses (Mallik, 1995, Mulder and Janssen, 1999 and Bokdam and



Gleichman, 2000). Soil biochemistry contributes to explain the different responses of soil organisms to a vegetation succession.

### 3.2. Web topology

In the present study, the numerical abundances of organisms in soils under organic agriculture remain usually much higher than those under other management regimes. These results confirm the trends described by Mulder et al., 2003 and Mulder et al., 2005b and reviewed by Bengtsson et al. (2005). The existence of different patterns among and between our webs is in complete agreement with the complementarily action of energy transfer agents versus habitat engineer agents. Microarthropods play a key-role in the structure of the depicted web, as can be seen by the rapid increase of secondary decomposers'  $N$ -values (mostly litter-related invertebrates) in species-rich webs (Scots pine plantations). However, real webs "buffer" most functional shifts among soil invertebrates. This is clearly shown in Table 1, where we recognize a rather constant difference in the dry biomass of soil organisms between four trophic levels: roughly one order of magnitude regardless of the land use (0.4 S.D.), besides in those locations where no earthworms were recorded (heathlands and most grasslands). Seen these constant trends in the total biomass we expect a comparable trend in other web properties known to be robust under trophic aggregation, such as the fraction of all possible trophic links that were realized.

Table 2 shows that  $C$  is not scale-variant, as the connectance values for alley cropping (<5 ha) and organic grasslands (>60 ha) are almost the same. Despite a huge variation of the dry biomass of soil organisms according to aboveground macroherbivory (Table 1; Mulder et al., 2003 and Mulder et al., 2005b),  $C$  is the only topological character that does not show evident differences between grazed and ungrazed sites (Table 3). As lower connectance values suggest higher resilience (cf. Chen and Cohen, 2001), webs of open canopies such as heathlands and semi-natural grasslands (mean  $C = 0.19$ ) are supposed to recover faster than webs of less redundant organic grasslands (Table 2). Besides four webs whose connectance equals 0.21, the topology of most undisturbed webs from "natural habitats" that can be regarded as stable exhibits indeed a very low connectance (Table 2), although the means of  $C$  in 46 grazed and 53 ungrazed sites are not significantly different from each other (Table 3). This finding seems to confirm that the connectance is inadequate to determine stability (Melián and Bascompte, 2004).

Table 2.

Average structural properties of 99 real webs and mean allometric intercept  $a_{\text{euk}}$  as predicted by imposed linear regression fitted to the  $(M, N)$  scatter of eukaryotes, listed in order of land use

	<b>Connectance, <math>C</math> (<math>=I/S^2</math>)</b>	<b>Complexity, <math>SC</math> (<math>=I/S</math>)</b>	<b>Biodiversity, <math>S</math></b>	<b>Intercept, <math>a_{\text{euk}}</math></b>
Fields				
Alley cropping	0.27 (0.03)	14.13 (2.26)	52.50 (2.12)	3.18 (0.04)
Crop rotation	0.24 (0.02)	12.16 (3.10)	49.25 (8.01)	3.29 (0.14)
Intercropping	0.21 (0.02)	9.04 (1.14)	42.29 (5.02)	3.20 (0.14)
Multicropping	0.24 (0.04)	11.96 (3.29)	49.72 (8.44)	3.24 (0.11)
Pastures				
Organic grasslands	0.27 (0.03)	13.69 (2.56)	51.55 (7.48)	3.55 (0.17)
Agroforestry				
Scots pine plantations	0.23 (0.02)	17.46 (2.82)	76.89 (8.81)	3.00 (0.12)
Nature				
Dry heathlands	0.19 (0.02)	7.95 (1.89)	41.80 (6.30)	4.35 (0.11)
Mature grasslands	0.19 (0.02)	11.16 (1.49)	58.40 (4.55)	4.11 (0.06)

$S$ , number of "trophic species" (Eukarya);  $I$ , number of trophic links. ANOVA shows that topological properties are robustly linked to the land use (biodiversity, links, connectance, and complexity share all  $P < 0.0001$ ). Standard deviation in parentheses.

Table 3.

Analysis of variance of the structural properties and allometric parameters of 99 real webs according to the existence of macroherbivory by mammals

	<b>Ungrazed (<i>n</i> = 53)</b>	<b>Grazed (<i>n</i> = 46)</b>
Biodiversity, <i>S</i>	58.585 A	50.717 B
Trophic links, <i>l</i>	858.755 A	614.935 B
Web connectance, <i>C</i>	0.23246 A	0.23065 A
Web complexity, <i>SC</i>	13.6255 A	11.7589 B
$\log_{10}(\text{dry biomass}), B_{\text{euk}}$	4.14538 A	5.05102 B
Intercept (on <i>N</i> ), $a_{\text{euk}}$	3.82402 A	3.14467 B
Slope ( <i>N</i> against <i>M</i> ), $\beta$	-0.49283 A	-0.62542 B

Means with the same letter are not significantly different ( $\alpha = 0.05$ ). Only *C* means within the same Tukey grouping.

Possible links per trophic species (*l*:*S*) as a function of biodiversity remain robustly correlated with aboveground grazing (ANOVA single factor,  $P = 6 \times 10^{-63}$ ), especially in organic grasslands sharing a high amount of secondary decomposers. Despite of the different management regimes (if any), all our empirical webs reflect closely a constant relationship between nodes (trophic species) and links (Fig. 2). Although most proportions of links and species are known as sensitive to species aggregation and web sizes (Chen and Cohen, 2000 and Dunne, 2005), our empirical data show that even in soil biota the number of possible trophic links is an extremely robust quadratic property of increasing diversity ( $P = 3 \times 10^{-51}$ ), regardless of the inclusion of basal resource (in our case, bacterial population and fungal mycelium). This log-log relationship is not entirely independent of the scale of a web. The *l*:*S* values fluctuate around a mean of  $12.77 \pm 3.86$ , far away from the ratio of about 2 reported in Cohen and Palka (1990) and closer to the linkage density of 10 calculated by Hall and Raffaelli (1997) for their constrained imaginable Ythan food-web.

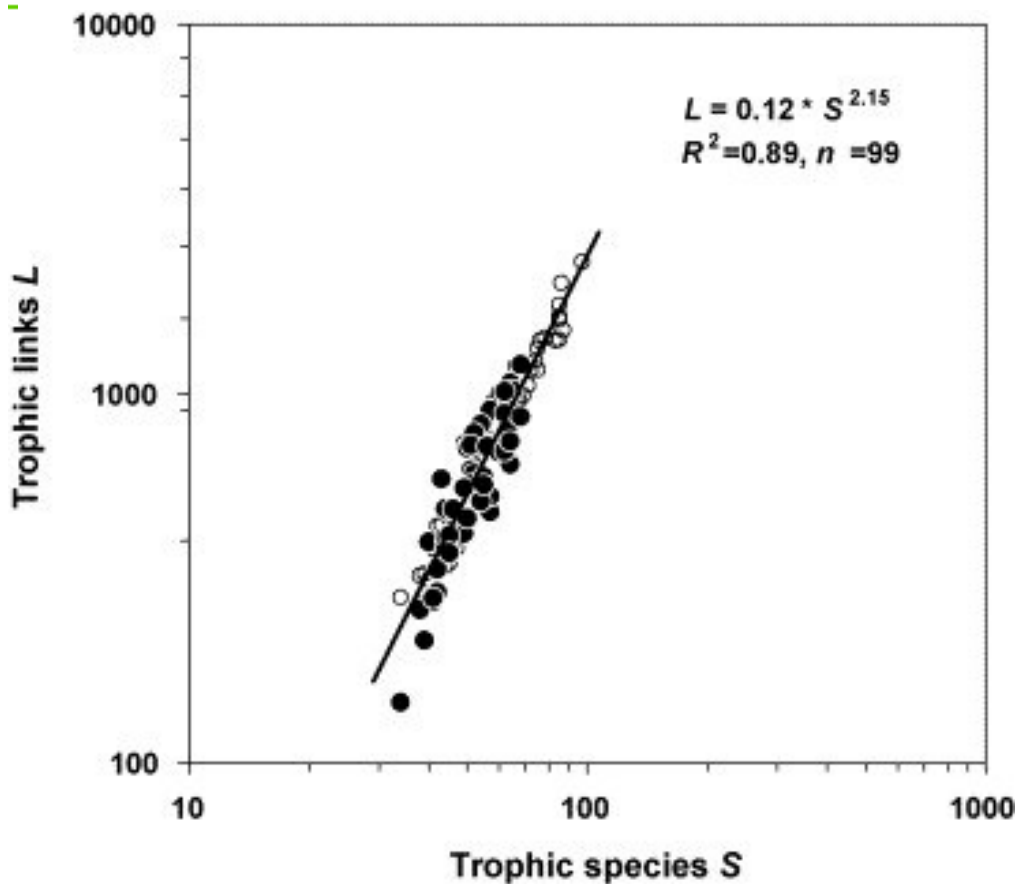
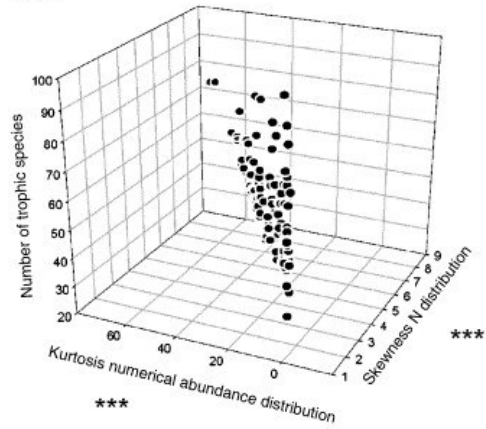


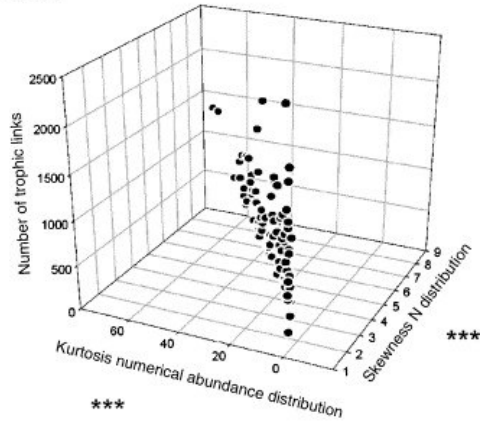
Fig. 2. The close relationship of links to species for webs from a variety of habitats. Grazed habitats are given as black circles, other habitats as open circles. The highest numbers of trophic links and trophic species (genera) are typical for Scots pine forests (see Table 2 for more details).

Analysis of 99 real webs belonging to different land uses (Table 2) are shown in Fig. 3, Fig. 4 and Fig. 5. Our webs range in size from 33 to 96 genera, connectance ( $S^{-2}$ ) ranges from 0.14 to 0.33, links per species range from 4.56 to 23.49, and the allometric intercept ranges from 2.7 to 4.5 (differing almost two orders of magnitude). The web with the lowest connectance ( $C = 0.14$ , a dry heathland) displays the lowest  $l:S$  value ( $SC = 4.56$ ), but a rather high intercept ( $a_{euk} = 4.03$ ). In contrast, the web with the highest connectance ( $C = 0.33$ , a mesic organic grassland) displays an intermediate  $l:S$  value ( $SC = 14$ ,  $a_{euk} = 3.65$ ). The most species-rich web ( $S = 96$ ,  $SC = 22.98$ ) has intermediate connectance ( $C = 0.25$ ) but a low intercept ( $a_{euk} = 3.25$ ).

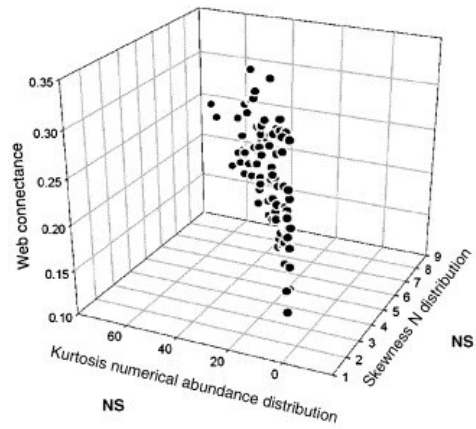
**TAXA**



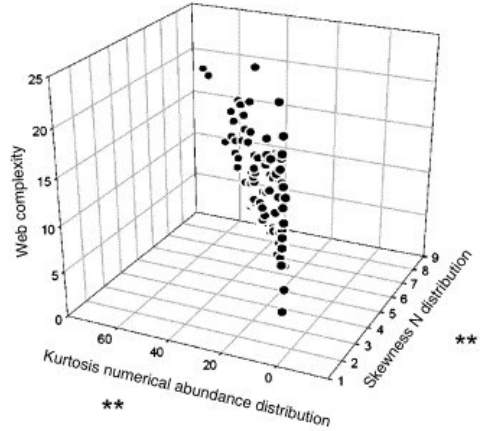
**LINKS**



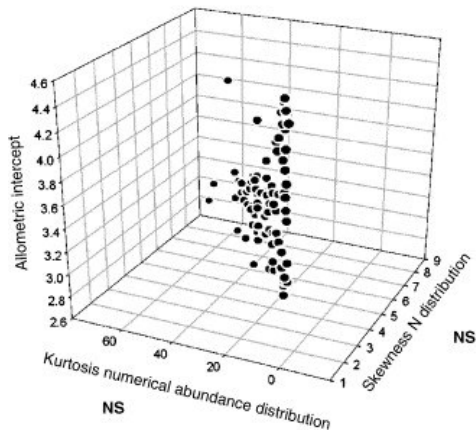
**CONNECTANCE**



**COMPLEXITY**



**INTERCEPT**



**SLOPE**

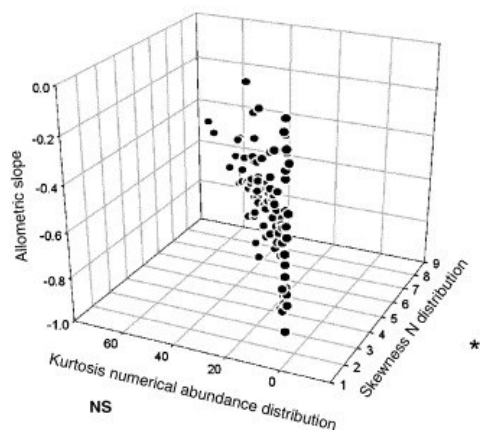


Fig. 3. Comparison of the skewness and kurtosis of the distribution of the numerical abundance of all organisms occurring in the 99 webs (horizontal plane) and allometric and topological characters (vertical axes). \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

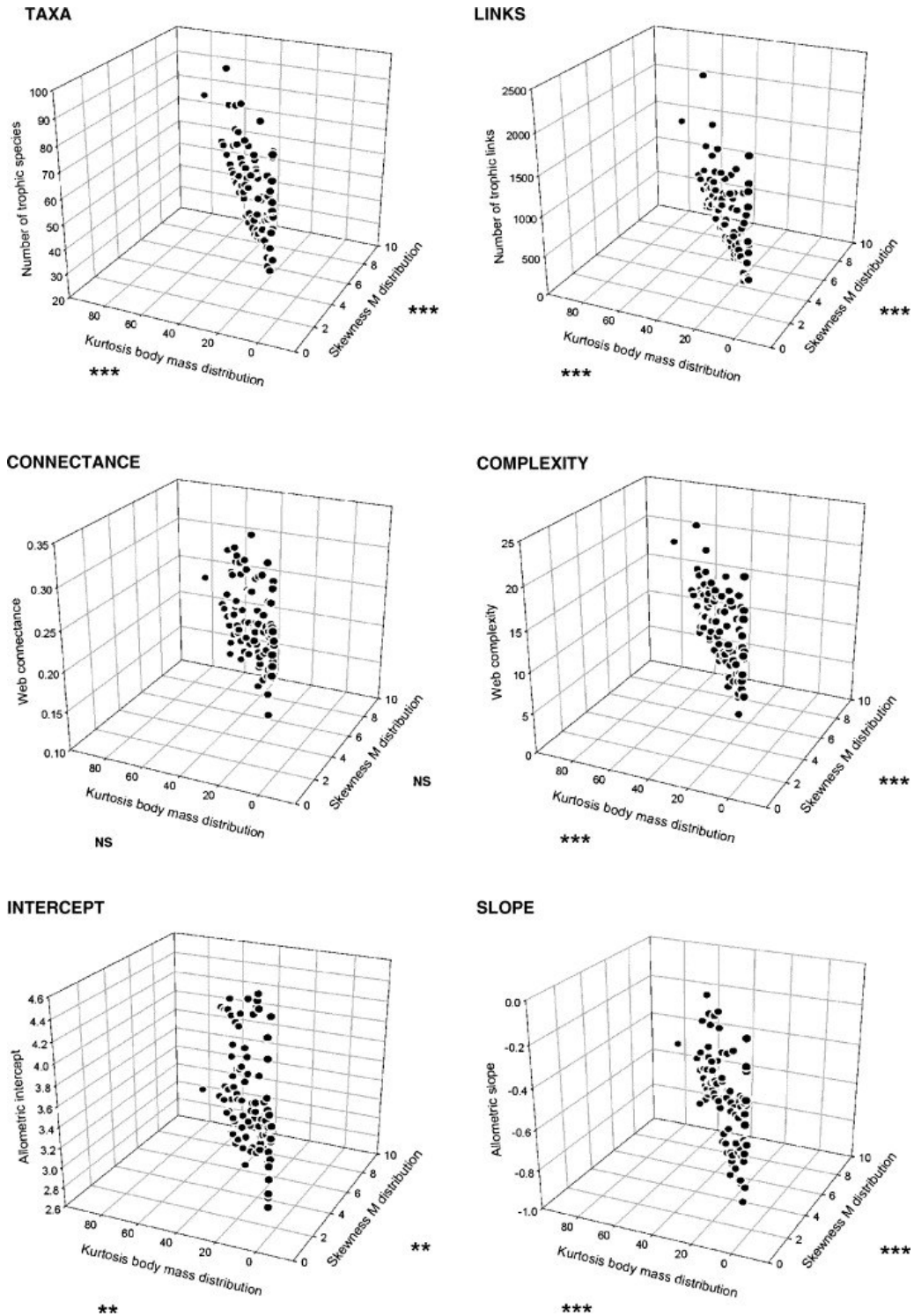


Fig. 4. Comparison of the skewness and kurtosis of the distribution of the average body mass of all organisms occurring in the 99 webs (horizontal plane) and allometric and topological characters (vertical axes). \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

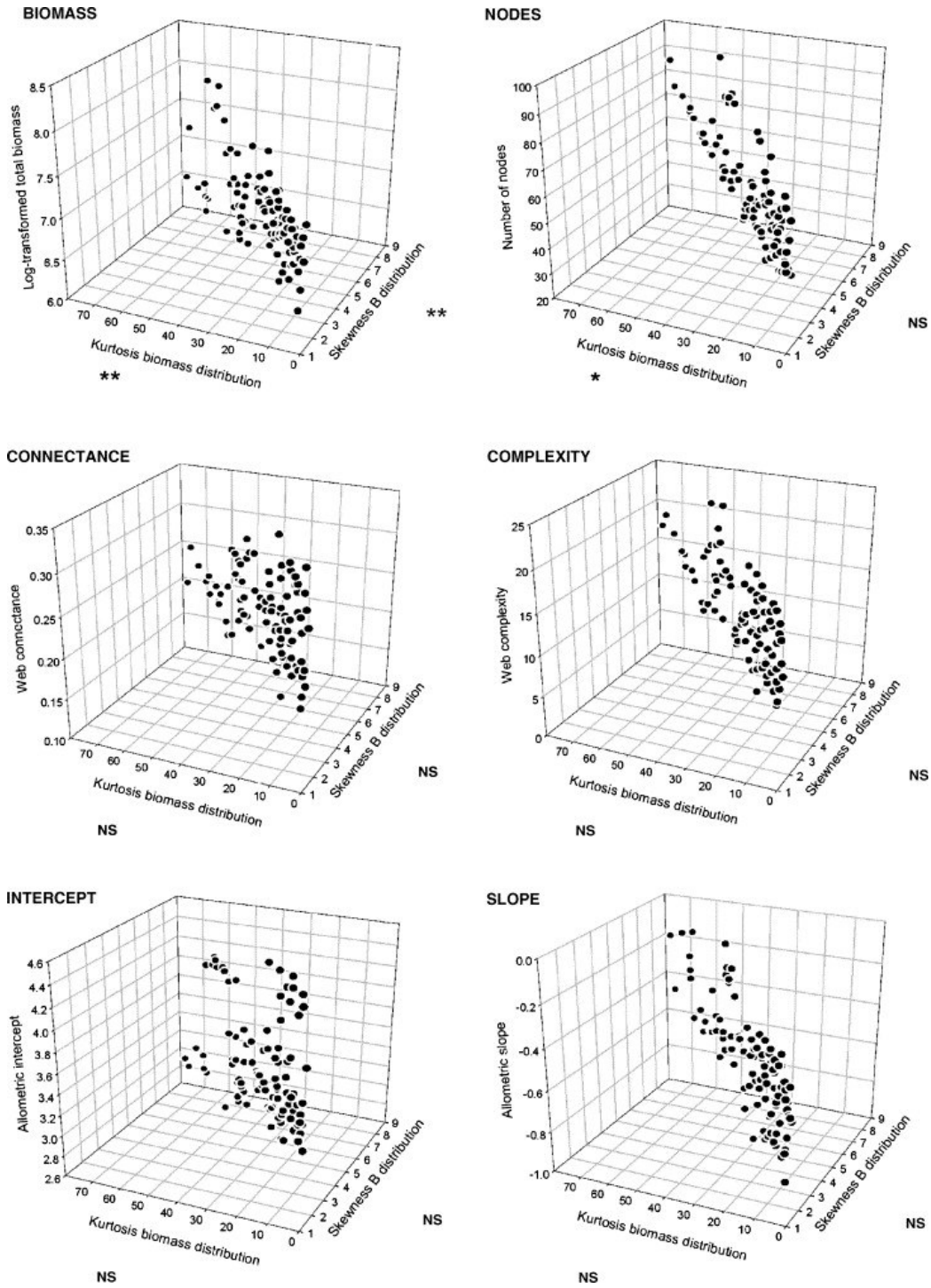


Fig. 5. Comparison of the skewness and kurtosis of the distribution of the biomass at trophic species level of occurring eukaryotes (horizontal plane) and the *total* biomass, the allometric and the topological characters (vertical axes). \*  $P < 0.05$ , \*\*  $P < 0.01$ .

The exact frequency distributions of the numerical abundance  $N$  (eukaryotes per square meter), the average body mass  $M$  ( $\mu\text{g}$  dry weight) and the resulting biomass ( $B = N \times M$ ) of each trophic species in a given web (counting each species once) were described mathematically by three moments: mean (central tendency), skewness (asymmetric distribution) and kurtosis (relative peakedness). The skewness and the kurtosis of the frequency distribution of  $N$  (Fig. 3),  $M$  (Fig. 4) and  $B$  (Fig. 5) were used as predictors of the previously described topological and allometric characters. As expected, the skewness value of 0, typical for a normal distribution, was never encountered (Kolmogorov–Smirnov goodness-of-fit tests always show  $P < 0.010$ ). All frequency distributions were right-skewed, with their (positive) distribution considerably longer to the right than to the left 'tail'; contrasting aspects of centeredness with markedly different metrics were not detected. The lowest kurtosis encountered was 1, indicating much more species around the mean. Biodiversity values were always well predicted by different kurtoses (taxa estimated by  $N$  and  $M$  kurtoses exhibit  $P < 0.0001$ , taxa estimated by  $B$  kurtosis  $P = 0.011$ ); trophic links are easy predictable due to their close correlation with  $S$  (compare Fig. 2 with Fig. 3 and Fig. 4). Seen the thin (leptokurtic)  $M$ -distribution at higher  $S$  and  $I$  values, we can see at least two ecological implications of this trend: (i) the biodiversity-increase in the mesofauna (mites, collembolans, enchytraeids) is higher than in the microfauna (nematodes); and (ii) larger animals (arthropods, enchytraeids) are more often omnivore (generalists) than smaller animals. Complexity, strongly correlated to  $S$  and  $I$ , shares the same strong leptokurtic distributions (Fig. 3 and Fig. 4). In contrast to the structural complexity, connectance  $C$  does not reflect the frequency distribution of  $N$ ,  $M$  or  $B$  values. Also allometric parameters are easy predictable by the  $M$ -distribution (Fig. 4).

The topological variance seems erratic in comparison with allometric trends along a gradient of increasing nitrogen availability. In contrast to topological variance ( $C$  in Table 3), the yearly supply of animal manure (here (log-transformed) nitrogen concentration per ha) and the calculated allometric intercept ( $a_{\text{euk}}$ ) are shown to be directly correlated ( $F = 82.7$ ,  $P = 10^{-11}$ ). As Dunne (2005) pointed out in her review, if a regression can be reasonably fit to all these data, it produces a power law of the form  $I = aS^b$  (see also Briand, 1983). In the case of constant connectance,  $b$  equals 2, which means that  $I$  is proportional to  $S^2$ , and thus  $I/S^2$  equals  $a$ . In conclusion, if the web connectance is constant ( $b \approx 2$ , see Fig. 2), the mean connectance is quantified by the value of  $a$ , which is 0.2623 (S.D. = 0.033) for the webs of our 26 livestock-grazed habitats, 0.2356 (S.D. = 0.041) for the webs of our 34 habitats without macroherbivory, and 0.2077 (S.D. = 0.027) for our other 39 habitats (ungrazed forests, or heathlands and grasslands with only a partial lack of grazing). This indicates that approximately one fourth (23%) of all possible feeding links are realized in our 99 webs, with significant differences in web topology occurring either between habitats within managed areas ( $F = 25.8$ ,  $P < 0.0001$ ) or between managed and unmanaged areas ( $F = 29.4$ ,  $P < 0.0001$ ). Grazing mammals clearly affect topological characters of soil food-webs.



#### **4. Discussion**

The extent to which results obtained for soil animals can be transferred to more complex terrestrial webs (top predators of complex webs gain dynamic stability from switching between compartments) remains to be demonstrated. These implications include that: (1) soil organisms necessitate a certain soil structure; (2) species operate at different spatial scales; (3) some species, like predators of large body size, are likely to be distributed across (and temporally integrate) local webs. Differences between potential webs (all nodes linked together) and realized webs imply that the web structure in soil patches reflects spatial population dynamics. Seen the increasing anthropogenic pressure on soil biodiversity, we may expect in our future increasing phase shifts. In such a scenario, shift rapidity may be seen as the result of soil systems with inherently flat unimodal ( $N$ ,  $M$ ) frequency distribution (Fig. 3 and Fig. 4).

Declines in species which are characterizing strong interactions between trophic levels result obviously in trophic-level dysfunction. Nematodes share such strong interactions between trophic levels. Despite the huge numerical abundance and species richness of soil organisms, animals with a body size less than 20  $\mu\text{m}$  are underrepresented, even in many simulated webs. To date, very few terrestrial studies include data from the entire community size spectrum. Twenty years after the call for better microbial data by Fitter et al. (1985), a seminal paper pointed out a remarkable bias against small organisms (Fitter, 2005). Being any web linked to an arbitrary spatial definition, the monitoring of smaller organisms can deeply affect the definition (and subsequently, the evaluation) of soil biota.

Similar conclusions are supported by previous models of Cousins, 1980 and Cousins, 1987. He argued that it is the variation in body size (and related territory of either a consumer or a predator) the key parameter for any organism within a web, not its fixed taxonomy. Many authors have had strong criticism on taxonomy, although most of them did not consider that nomenclature relies on the same morphological character states that they use to define the functional ecology within their models. For instance, Linné (1784) used the structure and the smell of the flower to describe (and provide a name to) plant species, whereas exactly the same attractors determine plant–pollinator interactions. This integrated approach caused an overlap among disciplines.

##### **4.1. Can a universal law become a tool?**

Applied ecology provides fascinating insights into the ecosystem functioning, although possible modelling ambiguities can lead to some exaggerations in agro-environments, especially as soil resources vary. By contrast, the incorporation into ecological studies of spatially explicit allometric attributes like the aforementioned intercepts can greatly expand our actual understanding of the factors driving biotic patterns under different agricultural practices. We believe that this integration of numerical abundance and body mass in one diagram provides at the same time the possibility to link together the character states of the investigated soil organisms to their prey, to the total belowground biomass, and finally to the relative energy use regardless of major horizontal fluctuations (cf. Makarieva et al., 2004, p. 157).

In our soil systems, the buffered switch that seems to occur between the mesofauna and the microfauna is related, to a certain extent, to the body masses of the consumers/predators. Soil pore size plays a key-role in defining the web topology and numerical abundance of organisms. Therefore, the spatial structure of the environment remains determinant for soil communities and populations.

Soil texture does this by limiting (vertical) movements and access of some larger-sized heterotrophs, by enhancing all or part of the bacterial prey, as well as by supplying living space acting as refuges from predators for other animal groups or life stages (Mulder et al., 2005a).

From this perspective, it becomes evident that the highly diverse spatial structure of forest soil profiles offers much more refuges and potential resources to soil decomposers embedded in complex multitrophic interactions than the rhizosphere of open grasslands can do. The physical importance of the spatial structure of the soil system for the possible recovery from stress of soil and litter invertebrates is striking if compared with the weak relationships between faunal recovery and environmental disturbance observed in many laboratory microcosm experiments.

#### **4.2. Concluding remarks**

Ecological modelling suggests that a strong, selective pressure is acting on most taxa. We sought explicitly to test for allometric relationships between the absolute numerical abundance  $N$  of soil organisms (bacteria, nematodes, mites, collembolans, enchytraeids and lumbricids) and their average body mass  $M$  (and the related biomass  $B$ ) under different land use. Decreasing population rates within different trophic groups were sufficiently robust to encompass management regimes and landscape units (Table 1). These results enable us to show the consistent response of terrestrial fauna to the increasing (man-induced) nitrogen availability from animal manure. More resources (faster turn-over) contribute to a significantly higher intercept. Regression lines whose slopes are consistent with unity may suggest "steady states" of some webs, i.e. a dynamic equilibrium between the consumers (primary and secondary decomposers) and their predators. The goal of this paper is to propose some simple graphical and quantitative indicators of community composition and ecosystem functioning, and to illustrate the application of these indicators to real webs. Some topological properties such as web complexity (structure) are useful to show how the soil biocomplexity responds to different forms of environmental pressure or to specific farming practices. But it is the allometric approach itself that seems reliable for the assessment of ecological limits to sustainable development and for possible recovery from environmental stress. We find that allometric indicators are superior to previous indicators of ecosystem functioning as they provide a common currency to understand governing processes by a comparison between different ecosystem components and enable us to express feedbacks at community level.

#### **Acknowledgements**

We thank J.E. Cohen, W. A.M. Didden (1950–2005), W.J. Dimmers, G.A.J.M. Jagers op Akkerhuis, H. Keidel, D.G. Raffaelli, D.C. Reuman, and H. Setälä for long, encouraging discussions and support.

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