Human and Environmental Factors Influence Soil Faunal Abundance–Mass Allometry and Structure

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SUMMARY

We examined structural variation in soil faunal communities from 146 agroecosystems in The Netherlands, using a unique database of taxonomically highly resolved soil samples gathered by uniform methods. For each site, data included measurements of average body mass (M) and population density (N) of each detected taxon and environmental and human-use factors. We used three descriptors of soil faunal community structure: abundance–mass slope, which is the slope of the regression line through all faunal taxa in a site plotted on log(N)-versus-log(M) coordinates (all logarithms were base 10); the taxonomic diversity of each community's fauna (number of animal taxa at the finest available level of taxonomic resolution); and the total biomass of all fauna. The goal of the study was to account for variation in these descriptors and to develop causal hypotheses.

These structural descriptors varied systematically. More than half of the variation in each descriptor was explained by external human, environmental, and biotic influences. Few predictors were needed to explain structural variation: above-ground ecosystem type (ET, describing the kind of human management); soil bacterial biomass; and a measure of precipitation. ET was the most important predictor of below-ground faunal community structure.

Abundance–mass slopes ranged from –0.85 to –0.07 with mean –0.51; only four slopes were more negative than –3/4 (i.e., the log(N)-versus-log(M) regression line was steeper than –3/4). Slopes less negative than –1 (respectively, –3/4) indicated that, on average, taxon biomass (respectively, taxon energy consumption) increased with taxon body mass. Abundance–mass slope was more negative in more disturbed sites than in less disturbed sites. Disturbance may have produced this pattern by affecting populations of large-M taxa, which are slower to reproduce, more than small-M taxa. Across some types of site (super-intensive farms and possibly intensive farms), greater soil bacterial biomass was associated with less-negative abundance–mass slope, suggesting top-down control of bacterivorous taxa. ET and soil bacterial biomass were sufficient to explain most of the variation in the whole abundance–mass allometric relationship, including slope and intercept.

Total faunal biomasses were higher in recently fertilized sites. Greater soil bacterial biomass was associated with the same increase in log faunal biomass between sites, on average, for all ET. Taxonomic diversity differed in sites of different ET in a way related to human disturbance. Precipitation was associated oppositely with diversity in sites of different types. Testable mechanistic hypotheses for the patterns observed here are discussed.

I. INTRODUCTION

For decades, studies have examined the influence on food web structure of factors such as environmental variability (Briand, 1983); three- versus two-dimensionality of habitat (Briand and Cohen, 1987); amount of primary productivity (Briand and Cohen, 1987; Vander Zanden et al., 1999); acidification in lakes (Locke and Sprules, 1994); habitat duration patterns in temporary ponds (Schneider, 1997); habitat size (Spencer and Warren, 1996; Vander Zanden et al., 1999); and disturbance or "stress" (Havens, 1994; Jenkins et al., 1992). Differences in food web (henceforth web) structure by habitat type (e.g., pelagic versus terrestrial; Bengtsson, 1994; Cohen, 1994; Havens, 1997) and over time and space using habitats of the same type (Carney et al., 1997; Clarke, 1998; Closs and Lake, 1994; Schoenly and Cohen, 1991) have also been investigated. Differences in web structure have typically been measured with a suite of descriptors based on the binary predation matrix ($P = [p_{ij}]$, where p_{ij} is 1 if taxon j eats taxon i, regardless of how often this occurs, and 0 otherwise), such as: link density; various kinds of connectances (Warren, 1994, gives definitions); proportions of top, intermediate, and basal taxa; and minimum, mean, modal, median, and maximal food-chain length (where the length of a food chain is the number of trophic links that comprise it).

However, web studies have been criticized for using data of poor quality, based on insufficient sampling of ecosystems (Bersier et al., 1999; Cohen et al., 1993; Hall and Raffaelli, 1991; Martinez, 1991; Polis, 1991; Polis and Strong, 1996; Winemiller, 1990). Statistics such as connectance and modal food-chain length depend sensitively on sampling effort (Goldwasser and Roughgarden, 1997; Martinez et al., 1999; Winemiller, 1990). Incomplete sampling limits even modern webs (Woodward et al., 2005, their Figure 3). Descriptors of web structure based on detailed trophic data are especially vulnerable to undersampling because "the detection of trophic links systematically lags behind the detection and inclusion of species, which may render the accurate measurement of many web properties inherently problematic" (Goldwasser and Roughgarden, 1997).

In response to the sensitivity of traditional web descriptors to sampling effort, several authors called for quantitative measures of trophic links, so that the intensity or frequency of each link is used in place of a binary indicator of whether the link occurs (Cohen et al., 1990; Kenny and Loehle, 1991; Martinez, 1991; Paine, 1992; Pimm et al., 1991; Wootton, 1997). Quantitative measurements would better characterize webs for which trophic links have highly uneven magnitude (e.g., many weak links and a few strong ones; Reuman and Cohen, 2005). Bersier et al. (2002) proposed descriptors of web structure that used quantitative link

measurements. Their proposed descriptors, based on information-theoretic concepts, were intended to improve upon, but serve the same conceptual purpose, as classical descriptors such as the proportions of top, intermediate, and basal taxa, and link density. The quantitative-link-based descriptors of Bersier *et al.* (2002) may be less sensitive to undersampling if undersampling affects primarily measurements of weak links. However, the highly detailed web data needed to calculate descriptors such as those of Bersier *et al.* (2002) are difficult to obtain; they include an empirical estimate of the strength of each trophic link. We took the opposite approach here: we used descriptors expected to be more robust to moderate undersampling because they do not use trophic data. Vander Zanden *et al.* (1999) took a similar approach using stable-isotope indicators of web structure that did not require detailed trophic data. We explain how the descriptors we used reflect web structure without using trophic data (Section II). The work of Cyr *et al.* (1997) was similar to ours, but used lakes. Some of their results are comparable to ours.

Most studies of the relationship between population density (N) and average body mass (M) of species (e.g., Damuth, 1981; Peters, 1983; Russo *et al.*, 2003; reviews include Blackburn and Gaston, 2001; Kerr and Dickie, 2001; Leaper and Raffaelli, 1999) focused on species from a single broad taxon or trophic level (e.g., birds or herbivorous mammals). When such data were gathered globally or regionally, $\log(N)$-versus-$\log(M)$ scatter plots often showed a linear relationship and had regression slope (here called *abundance–mass slope*) about $-3/4$ (e.g., Damuth, 1981, 1987; Greenwood *et al.*, 1996; Nee *et al.*, 1991). This macroecological relationship has been explained using metabolic theory (Brown *et al.*, 2004; West *et al.*, 1997) and other mechanisms (e.g., Blackburn and Gaston, 1993). For all taxa in a local web (an ecological context very different from that in which data on only one clade are gathered, be it locally, regionally, or globally), recent studies found that $\log(N)$ was often linearly related to $\log(M)$ but abundance–mass slopes varied widely from web to web (Cohen *et al.*, 2003; Cyr *et al.*, 1997; Jonsson *et al.*, 2005; Leaper and Raffaelli, 1999; Marquet *et al.*, 1990; Mulder *et al.*, 2005a, Reuman *et al.*, this volume; Woodward *et al.*, 2005). The faunal abundance–mass slope of a web was one of the descriptors used in this study. Total biomass of all fauna and taxonomic diversity of all fauna were also used.

This study examined the structural variation in 146 soil agroecosystems in The Netherlands. Our descriptors of soil faunal communities did not use trophic data, but reflected patterns of energy flow through the web and indirectly reflected web structure (Section II). We found that variation in abundance–mass slopes and other descriptors was largely explained in terms of environmental, human-use, and biotic factors. We developed testable hypotheses of mechanisms.

II. SOIL FAUNAL DESCRIPTORS

Names and units of soil faunal community descriptors are listed in Table 1 and explained here.

Table 1 Names, abbreviations (if defined), and units for all variables in four categories: environmental, human-use, and non-faunal biotic variables, and soil faunal descriptors

Name of variable	Units and measurement information
Environmental variables	
Mean daily air temperature	°C, mean over 21 days before sampling
Mean noon air temperature	°C, mean over 21 days before sampling
Mean daily precipitation	mm, mean over 21 days before sampling
Maximum daily precipitation	mm, max over 21 days before sampling
Modified Julian date	a linear function of Julian Day; see text
Phosphate content (after water extraction)	mg P_2O_5/l
Phosphorus content (after acetate–lactate extraction)	mg P_2O_5/kg dry soil
Soil pH	Power of H in KCl
Latitude	m south from Amersfoort
Longitude	m west from Amersfoort
Area of site	Hectares
Human-use variables	
Above-ground ecosystem type (ET)	Forest, pasture, winter farm, organic farm, conventional farm, intensive farm, or super-intensive farm
Standardized livestock density	Animal units that excreted an average of 161 kg N/(ha yr) and 41 kg P/(ha yr)
% of site on which maize grew	%
% of site on which grass grew	%
% of site used for other crops	%
Phosphorus in-flux from manure	kg/(ha y), proportional to livestock density
Carbon resource variables	
Soil bacterial biomass	µg C/g dry soil
Log soil bacterial biomass	log µg C/g dry soil
Soil organic matter	% of dry soil
Bacterial diversity	Band count after DGGE
Shannon–Wiener index of bacterial diversity	Index of DGGE band patterns
Percent bacterial cells dividing	%, measured one week after sampling
Mean bacterial cell length	µm
Soil faunal descriptors	
Faunal diversity	Number of taxa
Total faunal biomass	µg/m^2
Abundance–mass slope	–
Abundance–mass intercept	Individuals/m^2, log scale
Expected log(N) of smallest taxa	Individuals/m^2, log scale

A. Abundance–Mass Slope

The abundance–mass slope of a site is the coefficient b in the linear model

$$\log(N) = b \log(M) + a + \varepsilon \tag{1}$$

fitted by ordinary least squares regression to data on animal taxa in the soil samples from the site. Bacteria were excluded because their level of taxonomic resolution (a single node) was not comparable to that of other taxa. Only the total biomass of fungal mycelia and organic detritus was quantified (Mulder *et al.*, 2005a), so fungal mycelia were excluded from calculations of abundance–mass slopes. Protists were not quantified, but are virtually absent from sandy soils such as those used in this study.

Abundance–mass slope provides information about how faunal taxon biomass varies with taxon M. Because the biomass B of a taxon is its abundance N times its average body mass M, $B = NM$, the abundance–mass slope plus one indicates how B changes for taxa of increasing body mass (Cohen *et al.*, 2003). If $b = -1$, then the trend is for all taxa to have equal biomass. If the abundance–mass slope is less negative than -1, for example, if $b = -3/4$, then biomass tends to increase with increasing body mass; if the abundance–mass slope is more negative than -1, for example, if $b = -5/4$, then biomass decreases with increasing body mass.

Abundance–mass slope also describes how taxon energy consumption varies with taxon M, reflecting how energy flows through the web. The energetic equivalence hypothesis assumes that taxa absorb energy from the environment in amounts that do not depend systematically on M (Damuth, 1981, 1987). If all taxa absorb energy at constant rate R, then since the metabolic rate E of an individual organism is approximately a power law of its body mass, $E = kM_{\text{indiv}}^{\eta}$ (e.g., Peters, 1983), then (henceforth, neglecting variation of individuals' M_{indiv} from the mean M of their respective taxa) we can write $R = kNM^{\eta}$, so that $N = R/(kM^{\eta})$, and

$$\log(N) = -\eta \log(M) + \log(R/k) \tag{2}$$

Thus the energetic equivalence hypothesis predicts an abundance–mass slope $b = -\eta$. The value of η is often claimed to be close to 3/4 (Brown *et al.*, 2004; Peters, 1983; West *et al.*, 1997). Observing an abundance–mass slope less negative than (respectively, more negative than) $-\eta$ suggests that larger taxa absorb more (respectively, less) energy from the environment than smaller taxa. Departures of abundance–mass slopes from the benchmark value $-3/4$ register departures from energetic equivalence or a failure of the metabolic assumption that all taxa absorb energy at a rate proportional to NM^{η} (Figure 1).

If webs are size-structured so that large taxa eat primarily small ones, then differences between webs in abundance–mass slope reflect differences in how
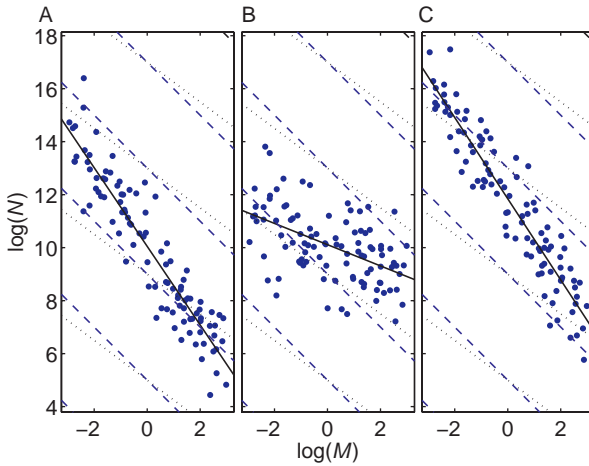
Figure 1 Differences in abundance–mass slope and intercept. Dots are populations of taxa in hypothetical webs; solid lines are ordinary least squares regressions whose slopes are the abundance–mass slopes. The communities in (A, C) have more-negative (steeper) abundance–mass slopes than that in (B). The community in (C) has higher abundance–mass intercept than those in (A, B). Dashed lines have slope –1: two taxa on the same dashed line have the same biomass; taxa on higher dashed lines have more biomass. Dotted lines have slope –3/4: two taxa on the same dotted line consume the same amount of energy; taxa on higher dotted lines consume more energy.

energy filters through trophic links, which is related to web trophic structure. In a two-species food chain, if the population production of the resource r is $kN_rM_r^{\eta}$ and the population production of the consumer, c, of r is $kN_cM_c^{\eta}$, assuming all production of r is consumed by c, then

$$\alpha kN_rM_r^{\eta} = kN_cM_c^{\eta} \tag{3}$$

where α is the efficiency by which c converts what it eats into its own production. Taking logs of this equation and rearranging gives

$$\log(N_c) - \log(N_r) = \log(\alpha) - \eta[\log(M_c) - \log(M_r)] \tag{4}$$

Dividing Eq. 4 by $\log(M_c)$–$\log(M_r)$ shows that the slope of the line connecting r and c on $\log(N)$-versus-$\log(M)$ axes (the abundance–mass slope) is $\log(\alpha)/\log(\beta)$–η, where $\beta = M_c/M_r$ is the consumer-to-resource body mass ratio. Several authors have elaborated this theory to relate aspects of food web structure such as average consumer-to-resource body mass ratio and mass-specific taxonomic diversity to the abundance–mass slope of this study and other types of mass–abundance allometry (Brown *et al.*, 2004, especially their Eq. 13; Damuth, 1994; Jonsson *et al.*, 2005; Reuman *et al.*, 2008, this volume).

B. Faunal Diversity and Total Biomass

Soil faunal taxonomic diversity, or simply faunal diversity, was defined as the number of faunal taxa in each site. For clarity, we emphasize that this count excluded bacteria, fungal mycelia, plant roots, and detritus. Many previous studies used the number of web nodes (often denoted S) to describe or model web structure (e.g., Cohen, 1990; Williams and Martinez, 2000). Other studies examined spatial variation in the diversity of species within a clade such as birds or nematodes (Jetz and Rahbek, 2002; Mulder *et al.*, 2003). Variation of single-clade diversity may be easier to study than variation in whole-web diversity because taxonomic expertise is often specific. However, organisms live in physical sites which include taxa from many clades, so variation in site diversity is also ecologically important, and the local diversity of clades depends in part on the site's entire biotic structure. Thinking of diversity at a site as a vector of the numbers of taxa with one entry for the number of taxa of each major clade is a useful way to combine clade-specific and whole-site or whole-web approaches in future research. The *total faunal biomass* of each site was computed by summing MN over all faunal taxa.

C. Abundance–Mass Intercept and Expected Log Population Density of Smallest Taxa

We defined the *abundance–mass intercept* of a site as the coefficient, a, in Eq. 1, fitted to faunal M and N data from the site. Abundance–mass intercept depends on the units of M because the vertical axis (the $\log(N)$-axis) occurs at $M = 1$ unit ($\log(M) = 0$). The same units for M (micrograms dry mass) were used throughout the study but the abundance–mass intercept is not easy to interpret because $\log(M) = 0$ ($M = 1$ μg) occurred in the middle of the body-mass range.

We used a web descriptor that contained the same information as abundance–mass intercept and was easier to interpret biologically: the *expected log(N) of the smallest taxa*. The smallest faunal taxa in each site were about the same size. The minimum $\log(M)$ occurring in each site had mean value -1.5 ($M = 10^{-1.5} = 0.032$ μg, corresponding to the average body-mass values of soil nematodes such as *Aphelenchoides* and *Metateratocephalus*) and ranged from -1.4 to -1.6. An expected $\log(N)$ of smallest taxa was defined for each site to be the value $\log(N)$ of the best-fitting line Eq. 1 at $\log(M) = -1.5$. Expected $\log(N)$ of smallest taxa has a clear biological interpretation and is independent of the units used to measure M. If units of M were chosen so that the smallest taxa had $M = 1$, then expected $\log(N)$ of smallest taxa would equal abundance–mass intercept. In a size-structured system, expected $\log(N)$ of smallest taxa is directly affected by the energy available to basal species and by their consumers.

III. DATA

All data for this study were gathered between 21 April 1999 and 4 June 2002 from 146 farms, pastures, and forests on Pleistocene sand in The Netherlands. Mulder *et al.* (2003, 2005a,b) gave complete details on how data were gathered. We here describe the nature of the data including definitions and units of measurement. Names, units, and abbreviations of variables are listed in Table 1.

A. Data on Taxonomy, Average Body-Mass, and Population Density

For each site, all soil animals, including nematodes, arthropods (mites, insects, and myriapods), enchytraeids (potworms), and lumbricids (earthworms), were identified to genus or family. Of the 65 nematode, 177 arthropod, and 18 oligochaete taxa identified in any of the 146 sites, 78% of the nematodes, 88% of the microarthropods, and 100% of the oligochaetes were identified to genus; the rest to family. For each taxon, average body mass (M, in micrograms dry mass) and population density (N, in individuals per square meter of soil surface) were measured. The same M was used for all sites where a given taxon occurred. Bacteria, fungal mycelia, plant roots, and detritus were each treated as single "taxa"; of these, M and N were obtained only for bacteria. Protists were ignored.

B. Environmental Data

Modified Julian date started on 17 September with a value of –164 and increased by one each subsequent day until 16 September, where it stopped with a value of 200 in a nonleap year and 201 in a leap year. Both modified Julian date and standard "Julian Day" (Mulder *et al.*, 2003) must start on some day of the year, artificially indicating a difference of 365 or 364 between that day and the previous one (for leap years and nonleap years, respectively). We used modified Julian date because the new discontinuity occurred in the middle of the largest interval with no sampling. Modified Julian date values ranged from –16 to 122, well away from the discontinuity.

The Royal Netherlands Meteorological Institute (www.knmi.nl, De Bilt) supplied air temperature and precipitation data (minima, maxima, and averages for the 21 days before sampling) near each investigated location. The mean of the highest and lowest temperatures on each day were provided, and the mean of these minima and maxima is calculated over the period of 21 days.

Soil phosphorus content was measured using two methods of extraction. Phosphate content after water extraction used aqueous extraction at water-to-soil ratio 60:1 by volume, after 22 h of pre-equilibrating soil with water, and 1 h of gently shaking before filtration (Sissingh, 1971). Phosphate content after water extraction reflects the maximal possible concentration of phosphorus in the soil moisture biofilm, a thin layer of water around soil particles. Phosphorus content after acetate–lactate buffer extraction includes phosphorus occluded in oxides on the surfaces of soil particles and in water-insoluble compounds. Results of the two methods were highly correlated in our 146 sites ($R^2 = 81.4\%$).

Acidity (pH) of oven-dried soil samples was measured in 1 M potassium chloride solution. Latitude and longitude were given in meters, falsely projected south and west, respectively, from Amersfoort (52 °09′22″N, 5 °23′15″E; see Mulder *et al.*, 2005b). This stereographic double-projection on the Bessel spheroid is widely used in The Netherlands.

C. Human-Use Data

1. Above-Ground Ecosystem Type

Above-ground ecosystem type (ET) took seven values: forest, winter farm, pasture, organic farm, conventional farm, intensive farm, and super-intensive farm (Mulder *et al.*, 2005a,c, 2006; Schouten *et al.*, 2004). The last five ETs were called *cultivated farms*.

Winter farms were defined to be lands not cultivated or grazed at the time of sampling, but previously and later used for grazing or to grow non-cereal crops. Previous land-use of winter farms included multicropping, intercropping, crop rotation, and alley cropping. Forests were subjected to the low-intensity management of traditional agroforestry; they were typically plantations of Scots pine (*Pinus sylvestris*), but sometimes also included European larch (*Larix decidua*) or naturalized Douglas fir (*Pseudotsuga menziesii*).

Other sites were cultivated actively at the time of sampling. Management regime was the most important factor in defining the other ET values. Organic farms, pastures, and conventional farms were subjected to middle-intensity management; intensive and super-intensive farms were subjected to high-intensity management. Organic farms were certified organic by the Agricultural Economics Research Institute of The Netherlands (LEI-DLO, www.lei.wur.nl). Bio-organic and biodynamic farming techniques were used on organic farms. Compost and farmyard manure were used for fertilization; no biocides were used. Pastures were used for both grazing and farming. They were similar to organic farms, and used specific agronomic practices to enhance nitrogen fixation by the rhizobia of the clovers *Trifolium repens* and

Trifolium pratense. On conventional farms, mineral fertilizers were used to compensate for the much smaller amount of farmyard manure used compared to organic farms.

On intensive and super-intensive farms, both organic and mineral fertilizers were used in substantial amounts. More biocides were used on super-intensive farms than on intensive farms. Biocide and fertilizer use information was gathered through farmer interviews. The Dutch Central Bureau of Statistics (CBS) regularly surveyed the use of chemical pesticides in arable and horticultural farming (www.cbs.nl). Previous surveys were conducted in 1992, 1995, 1998, and 2000. Livestock density also played an important role in site classification, as did farm area, crop mixture, the farming regime used during the 5 years before sampling, and recent harvest or planting (Mulder *et al.*, 2005d,e). The majority of sites of this study were rural (87.0%); the majority of farms were no-tillage (61.4%). Numbers of sites of each ET are listed by Reuman *et al.* (this volume, their Table 4).

2. Other Human-Use Data

Standardized livestock density was measured as the numbers of animal units (cows, calves, pigs, and poultry) per hectare that excreted an average of 161 kg N ha^{-1} yr^{-1} and 41 kg P ha^{-1} yr^{-1} according to the CBS (www.cbs.nl, accessed February 2006). The percentages of each site on which grass, maize, and other crops (mainly potatoes and beets) grew were measured. Phosphorus in-flux from animal manure was assumed to be proportional to standardized livestock density, and was therefore not included as a separate predictor in models.

D. Carbon Resource Data

Carbon resource data describe important carbon pools that support the bottom of the soil faunal food web: soil organic matter and bacteria. Soil bacterial biomass (Mulder *et al.*, 2005a) and its logarithm were predictors in models (see Section IV). Soil organic matter was measured as a percent of dry soil. Genetic diversity of bacteria was determined using Denaturing Gradient Gel Electrophoresis (DGGE; Mulder *et al.*, 2005a,b) after DNA amplification by polymerase chain reaction (PCR) using a general probe for bacterial 16S-ribosomal DNA (Bloem and Breure, 2003). The variable genetic diversity of bacteria used here was the number of bands appearing after electrophoresis at fixed denaturant concentration. Band patterns were analyzed by image analysis using two replicates per site. Bacterial cells were counted in soil smears by fluorescent staining (Paul *et al.*, 1999). Cell numbers, lengths

(in micrometers) and the frequencies of dividing cells (percentages of bacterial cells dividing one week after sampling) were determined by direct confocal laser scanning microscopy coupled to a fully automatic image analysis system (Mulder *et al.*, 2005a).

IV. METHODS

All computations were done in Matlab version 6.5.0.180913a (R13). A statistical significance level of 1% was used.

A. Classification of Variables

Variables classified (in Table 1) as *environmental variables*, *human-use variables*, and *carbon resource variables* were used to predict response variables classified as *soil faunal descriptors*.

B. Stepwise Regression

To analyze variation in soil faunal descriptors and to develop hypotheses about causes of the variation, stepwise linear regression was an appropriate exploratory technique because of its simplicity. We used the stepwise linear regression algorithm of Appendix I. Starting from a model that predicts a soil faunal descriptor by its mean, the algorithm alternately may add predictors for greater explanatory power, and remove them for model simplicity. A backward-only elimination procedure was not used because we wanted simple models. A forward-only procedure was not used because many predictors of this study are related, and a model without redundancy was desired. Our stepwise procedure rarely removed predictors, so a forward-only method might have produced similar results.

C. Testing Assumptions of Linear Models

The standard linear model Eq. 1 makes five principal assumptions about data, listed in most elementary statistics texts and reviewed by Cohen and Carpenter (2005) and Reuman *et al.* (this volume). The validity of four assumptions can be tested statistically with our data. Because 110 of the 146 sites satisfied all four testable assumptions at the 1% level (Reuman *et al.*, this volume), we used abundance–mass slopes and intercepts of all sites for subsequent modeling of these descriptors. Including sites that violated the

regression assumptions was not statistically problematic because we used only the point estimates of b and a, not their confidence intervals. Stepwise regression was also used to construct linear models of b and a using only the 110 sites for which assumptions were satisfied (Appendix III), with similar results.

We also used the general linear model

$$y = Xb + \varepsilon \tag{5}$$

where y is a site descriptor and X encodes predictors. We tested whether data met the assumptions of each general linear model using seven tests, described in Appendix II. Results of these tests are in Appendix III. Typically, assumptions were not violated, or were only mildly violated.

V. RESULTS

A. Models of Soil Faunal Community Structure

Linear models of abundance–mass slope, log faunal biomass, and faunal diversity explained, respectively, 58.0%, 60.7%, and 73.8% of the variation in the three response variables (Table 2). Of the 23 potential predictors (environmental, human-use, and carbon resource variables, Table 1), stepwise regression selected only ET, maximum daily precipitation, soil bacterial biomass, and soil organic matter. Soil organic matter provided only a marginal increase in total R^2, but this may be expected since soil organic matter was uniformly low for sandy soils such as those of this study, and did not vary much among our sites compared to differences in soil organic matter between sandy soils and other types of soil such as clay and peat. A large percentage of observed variation in all soil faunal descriptors was explained. Only a few predictors were needed.

B. Relative Importance of Variables

1. ET was the Most Important Predictor

ET alone explained 51.7%, 56.6%, and 66.0% of the variation in abundance–mass slope, log faunal biomass, and faunal diversity, respectively (Table 2). ET was always the most influential single predictor and was always chosen first in stepwise regression.

ET provides information about soil faunal structure beyond that contained in all other predictors combined. All predictors including ET (but excluding interaction terms) explained significant variation in faunal diversity (69.9%) beyond that explained (57.6%) by all predictors except ET

Table 2 Coefficients of determination (R^2) for linear models of site descriptors (first column)

Response variable	R^2, sole predictor ET (%)	Second predictor	Increment in R^2 (%)	Third predictor	Increment in R^2 (%)	Total R^2 (%)
Abundance–mass slope	51.7	ET × soil bacterial biomass (Figure 3)	6.3	NA	NA	58.0
Log faunal biomass	56.6	Soil bacterial biomass (Figure 4)	4.1	NA	NA	60.7
Faunal diversity	66.0	ET × maximum daily precipitation (Figure 5)	6.3	Soil organic matter	1.6	73.8

Final models never had more than three predictors. Stepwise regression did not include an additional predictor in a model unless inclusion caused a significant increase in R^2 (1% level, F-tests). ET, maximum daily precipitation, soil bacterial biomass and soil organic matter are defined in Table 1. ET × y denoted interaction terms between ET and y. NA = Not Applicable, because no significant third predictor was selected. Total R^2 may differ from sum of component R^2s due to rounding.

($F_{6,111} = 7.6$, $p < 0.0005$). The same was true with marginal significance for abundance–mass slope (61.4% vs. 55.3%, $F_{6,111} = 3.0$, $p = 0.01$), and log faunal biomass (67.9% vs. 62.9%, $F_{6,111} = 2.9$, $p = 0.012$).

2. Human-Use Variables Were More Important Than Environmental Variables

Human-use variables substantially influenced soil faunal descriptors even after controlling for the influence of environmental variables. Environmental effects on descriptors were mediated by human-use factors. In detail, human-use variables explained more variation in each soil faunal descriptor than did environmental variables (faunal diversity: 65.5% vs. 45.0%; abundance–mass slope: 51.4% vs. 34.1%; log faunal biomass: 59.9% vs. 49.5%). Human-use and environmental variables together explained significantly more variation in each soil faunal descriptor than environmental variables alone (F-tests, $p < 0.0005$ for all three), but not significantly more than human-use variables alone (F-tests, $p > 0.042$ for all three).

For the model including all human-use and environmental predictors, R^2 values for each soil faunal descriptor were: for faunal diversity, 67.3%; for abundance–mass slope, 58.8%; for log faunal biomass, 63.2%.

3. Comparison Between Human-Use and Carbon Resource Variables

Human-use variables substantially influenced abundance–mass slope and faunal diversity after controlling for carbon resource variables. The effects of carbon resource variables on abundance–mass slope and faunal diversity were mediated by human-use factors. In detail, human-use variables explained more variation in these two descriptors than did carbon resource variables (abundance–mass slope: 50.7% vs. 37.7%; faunal diversity: 65.4% vs. 33.0%). Human-use and carbon resource variables together explained significantly more variation in each of these two descriptors than carbon resource variables alone (F-tests, $p < 0.0005$), but not significantly more than human-use variables alone (F-tests, $p > 0.113$). For the model including all human-use and carbon resource predictors, R^2 values were 68.4% for faunal diversity and 53.1% for abundance–mass slope.

For log faunal biomass, models using both human-use and carbon resource predictors explained significantly or marginally significantly more variation in both descriptors than models with human-use predictors alone ($R^2 = 58.7\%$ vs. 63.7%, $F_{7,124} = 2.4$, $p = 0.022$), and also more variation than models with carbon resource predictors alone ($R^2 = 38.4\%$ vs. 63.7%, $F_{10,124} = 8.7$, $p < 0.0005$).

4. Human-Use Predictors Were Essential

Human-use variables explained significant additional variation in all soil faunal descriptors beyond that explained by all other predictors (i.e., environmental and carbon resource) combined (faunal diversity: 69.9% vs. 51.1%; abundance–mass slope: 61.4% vs. 44.8%; log faunal biomass: 67.9% vs. 56.0%; F-tests, $p < 0.0005$ for all).

C. Interpreting Variation in Structure

Since ET was an important predictor of soil faunal descriptors, we summarize the mean values of each descriptor by ET, and give ranks and statistical ranks of the ET for each descriptor (Table 3). By computing mean abundance–mass slope (Table 3) and intercept and mean expected $\log(N)$ of smallest taxa by ET, we found the mean abundance–mass allometry line for each ET (Figure 2). Forests, the most nutrient-limited and possibly the least disturbed ET, had the least negative mean abundance–mass slope (–0.30), the lowest average soil faunal biomass, and the highest mean faunal diversity. Forests had, on average, the most rapid increase of taxon biomass and energy consumption with taxon M. Winter farms had the most negative mean abundance–mass slope (–0.61), the lowest average faunal biomass

Table 3 Mean values of soil faunal descriptors by above-ground ecosystem type (ET)

	Abundance–mass slope	Log faunal biomass	Faunal diversity
Forests	–0.30 (1[a])	5.88 (7[b])	76.9 (1[a])
Organic farms	–0.52 (4[b])	6.56 (4[a])	52.1 (4[c])
Pastures	–0.48 (3[b])	6.66 (2[a])	61.9 (2[b])
Conventional farms	–0.56 (6[b])	6.57 (3[a])	44.9 (7[c])
Intensive farms	–0.54 (5[b])	6.48 (5[a])	46.3 (6[c])
Super-intensive farms	–0.48 (2[b])	6.71 (1[a])	61.6 (3[b])
Winter farms	–0.61 (7[c])	5.90 (6[b])	48.4 (5[c])
p-Values	5.8%	27.7%	3.8%

Numbers in parentheses are ranks of the mean values by ET. Superscript letters indicate a statistical rank: a linear model in which the sole predictor was a categorical variable with categories given by the letters was not statistically significantly different from the model with sole predictor ET (F-tests, p-values given in the last row). For example, in predicting abundance–mass slope, a model with three categories (a) forests, (b) organic farms, pastures, conventional farms, intensive farms, and super intensive farms, and (c) winter farms, was not statistically different from the model with sole predictor ET.
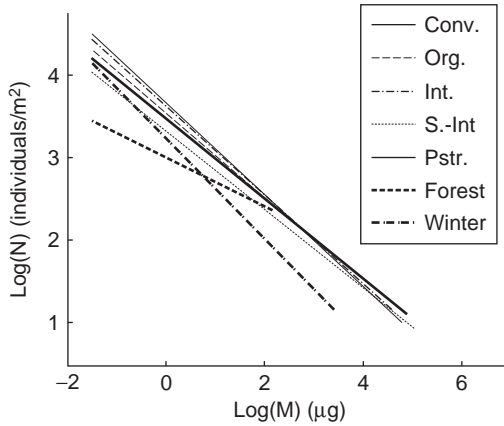
Figure 2 Mean abundance–mass allometric relationships for each ecosystem type (ET). For each ET, mean abundance–mass slopes and intercepts were computed. Resulting average allometry lines were plotted from mean $\log(M)$ of smallest taxa to mean $\log(M)$ of largest taxa for each ET: conventional (Conv.), organic (Org.), intensive (Int.), and super-intensive (S.–Int.) farms, pastures (Pstr.), forests (Forest), and winter farms (Winter).

(statistically tied with forests), and the lowest mean faunal diversity. Winter farms had, on average, the slowest increase of taxon biomass and energy consumption with taxon M. Cultivated farms were intermediate between forests and winter farms in many respects.

1. Explaining Abundance–Mass Slope: Disturbance and Top-Down Effects

Several possible mechanisms (e.g., disturbance and fertilization) could account for the dominant influence of ET on soil faunal structure. Winter farms may have been most disturbed by humans and environmental factors: they were sampled during winter and had been cleared of most crops at last harvest. Forests may have been least disturbed: they were not actively managed. Cultivated farms may have suffered an intermediate level of human and environmental pressure. Increasing disturbance (here only speculatively assessed) from forests (no grazing or tillage) to cultivated farms (grazing, no tillage) to winter farms (winter conditions, tillage, no grazing) may have had a more detrimental impact on present large-bodied animals, which are slower to reproduce, causing the corresponding decrease (steepening) in slope (Table 3). We hypothesize that disturbance is one of the mechanisms (see Section VI) responsible for the variation in abundance–mass slopes. Our results do not suggest that disturbance can explain the presence or

absence of specific small versus large taxa, but only that disturbance may help explain relative abundances of taxa that are present. Lumbricids, which encompass the largest-M taxa in any of our sites, were absent in both relatively undisturbed sites (forests) and in relatively disturbed sites (winter farms), but were present in sites hypothesized to have intermediate levels of disturbance.

Increasing soil bacterial biomass was associated with increasing (less steep) abundance–mass slope for super-intensive and possibly intensive farms (Figure 3). The increase in abundance–mass slope with increasing soil bacterial biomass may have reflected top-down control of faunal populations in super-intensive and intensive farms: as the bacterial resource available to low-M,

ET		Slope	99% Conf.		Intercept	99% Conf.	
Conv.	*	3.86e-5	−7.01e-4	7.79e-4	−0.563	−0.7	−0.427
Org.	×	−7.02e-5	−5.76e-4	4.35e-4	−0.508	−0.591	−0.426
Int.	○	4.91e-4	−1.58e-4	1.14e-3	−0.61	−0.716	−0.505
S.-Int.	+	1.20e-3	2.17e-4	2.18e-3	−0.643	−0.79	−0.496
Pstr.	△	3.18e-5	−6.84e-4	7.48e-4	−0.489	−0.62	−0.358
Forest	✱	−8.05e-4	−1.76e-3	1.54e-4	−0.26	−0.332	−0.189
Winter	□	−2.88e-4	−1.12e-3	5.42e-4	−0.587	−0.668	−0.506
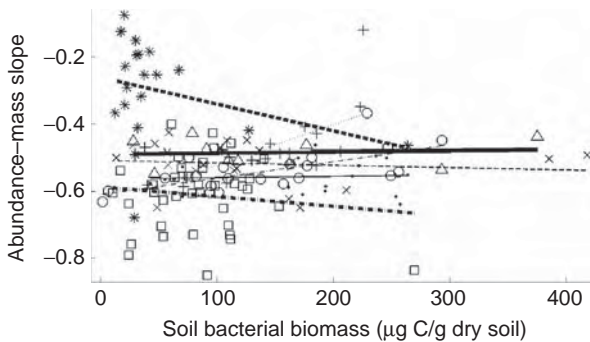
Figure 3 Linear model of abundance–mass slope as a function of above-ground ecosystem type (ET) and soil bacterial biomass. Line styles correspond to ET as in Figure 2. The model that constrained to 0 all model slopes except that for super-intensive farms (so that all lines on the figure except the one for super-intensive farms would be forced to be flat) explained 54.9% of the variation, not significantly less than the model that estimated all ET slopes independently ($F_{6,132} = 1.6$, $p = 14.7\%$). Although the general-linear-model confidence intervals for intensive farms included 0, when abundance–mass slope was regressed against soil bacterial biomass for intensive farms only (ordinary linear regression), the slope was significantly positive ($p = 0.1\%$): abundance–mass slope may have increased with increasing soil bacterial biomass for intensive farms, as well as for super-intensive farms.

bacterivorous faunal taxa increased, abundances of high-M consumers of these animals apparently increased faster than the abundances of the low-M taxa themselves, suggesting that the high-M taxa were partly responsible for keeping populations of their prey in check (cf. Wardle *et al.*, 1998).

2. Explaining Abundance–Mass Allometry

A model with sole predictor ET explained 71.1% of the variation in expected $\log(N)$ of smallest taxa ($F_{6,139} = 56.9$, $p < 0.0005$). Forests had the lowest mean expected $\log(N)$ of smallest taxa ($= 3.44$; $N = 10^{3.44} = 2754.3$ individuals/m^2). Other ETs, including winter farms (mean $= 4.15$), had similar mean expected $\log(N)$ of smallest taxa, ranging from mean $= 4.04$ (super-intensive farms) to mean $= 4.50$ (conventional farms). Forests had rare smallest faunal taxa relative to other sites, whereas in winter farms the abundance of the smallest faunal taxa was comparable to that of cultivated farms. The largest taxa occurring in forests were about as abundant as similar-sized taxa in cultivated farms and the largest taxa in winter farms were much less abundant than similar-sized taxa in other sites (Figure 2).

ET and soil bacterial biomass sufficed to predict the allometric relationship Eq. 1 in its entirety (both slope and intercept or expected $\log(N)$ of smallest taxa). The sole predictor ET explained most of the variation in the intercept ($R^2 = 74.4\%$; $p < 0.0005$), and in expected $\log(N)$ of smallest taxa. ET and the interaction ET $\times$ soil bacterial biomass predicted the slope b (Table 2, Figure 3). ET and soil bacterial biomass were also sufficient to predict log faunal biomass (next section and Table 2). Faunal biomass was related to abundance–mass slope and intercept: shifting all taxa up by the same amount on $\log(N)$-versus-$\log(M)$ axes corresponds to multiplying all faunal N values by the same factor, and would increase both log faunal biomass and abundance–mass intercept by the log of that factor.

3. Explaining Faunal Biomass: Fertilization and Disturbance

Mean log faunal biomasses of forests and winter farms were statistically indistinguishable and smaller than those of the other ETs; mean log faunal biomasses for other ETs were also indistinguishable from each other ($F_{5,139} = 1.3$, $p = 0.277$; Table 3). Winter farms and forests were not recently heavily fertilized, whereas other sites were. We hypothesize that recent fertilization contributed to increased soil faunal biomass. Livestock density provides only a partial measure of fertilization because cattle manure is only one form of fertilization. Forests and winter farms had no livestock. Disturbance may also have contributed to low faunal biomass for winter

farms if winter farms can be considered greatly disturbed and if disturbance preferentially affected large organisms like earthworms.

Increasing soil bacterial biomass was associated with the same rate of increase in log faunal biomass for all ET (Figure 4). This effect was of secondary importance to the effect of ET (Table 2).

4. Explaining Faunal Diversity: Disturbance

Mean faunal diversity distinguished three groups of ET: (1) forests had highest diversity; (2) super-intensive farms and pastures had intermediate diversity; and (3) winter, conventional, organic, and intensive farms had lowest diversity (Table 3). Comparing winter farms and forests suggests that disturbance may have been one factor decreasing faunal diversity. However, because super-intensive farms had higher diversity than intensive

ET		Intercept	99% Conf.		Slope	99% Conf.	
Conv.	*	6.352	6.121	6.583	0.001	0.0004	0.002
Org.	×	6.398	6.195	6.601			
Int.	○	6.296	6.086	6.506			
S.-Int.	+	6.533	6.318	6.748			
Pstr.	△	6.470	6.182	6.757			
Forest	✳	5.819	5.638	6.001			
Winter	□	5.789	5.643	5.935			
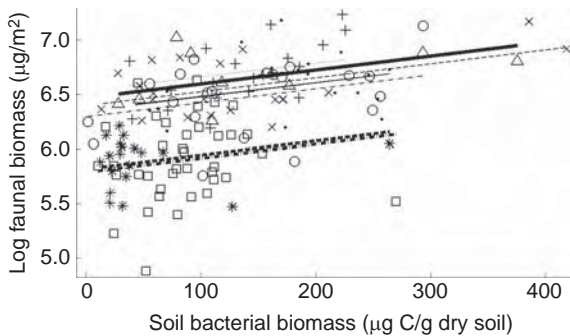
Figure 4 Linear model of log faunal biomass as a function of above-ground ecosystem type (ET) and soil bacterial biomass. Line styles correspond to ET as in Figure 2. A model that constrained the y-intercepts for the winter farm and forest lines to take a single value, and the y-intercepts of all the other lines to take a single value (possibly different from the single value for winter farms and forests) explained 58.5% of the variation in the response variable, not significantly less than the model that estimated all y-intercepts independently ($F_{5,138} = 1.52$, $p = 18.8\%$). Similar results were obtained by regressing log faunal biomass against ET and log soil bacterial biomass (Figure S1).

farms, other factors were likely also operative, or disturbance operated in several ways (next section).

Increasing maximum daily precipitation increased diversity significantly (1% level) for winter farms and significantly decreased diversity for pastures (Figure 5). For intensive farms, the mean of daily precipitation over the 21 days before sampling (mean daily precipitation) was positively associated with diversity ($R^2 = 35.5\%$, $F_{1,144} = 10.5$, $p = 0.004$). Thus, precipitation affected diversity oppositely in sites of different types. Soil organic matter was also included as a predictor in the model of faunal diversity selected by stepwise regression, but soil organic matter increased total R^2 by only 1.6%.

D. Testing for Artifacts

As noted above (Section III.A), ~78% of nematodes, 88% of microarthropods, and 100% of oligochaetes were genera and the rest were families. Thus, taxonomic resolution was slightly higher for larger-M taxa, as expected from

ET		Slope	99% Conf.		Intercept	99% Conf.	
Conv.	*	−0.205	−1.09	0.68	48.4	32.9	63.8
Org.	×	−0.0631	−0.757	0.631	52.9	43.7	62.1
Int.	○	0.553	−0.188	1.29	37.1	24.1	50.1
S.-Int.	+	0.0947	−0.544	0.734	60.3	50.2	70.4
Pstr.	△	−1.26	−2.39	−0.13	86.1	63.5	109
Forest	∗	−0.152	−0.465	0.161	80	72.3	87.7
Winter	□	0.636	0.21	1.06	39	32.1	46
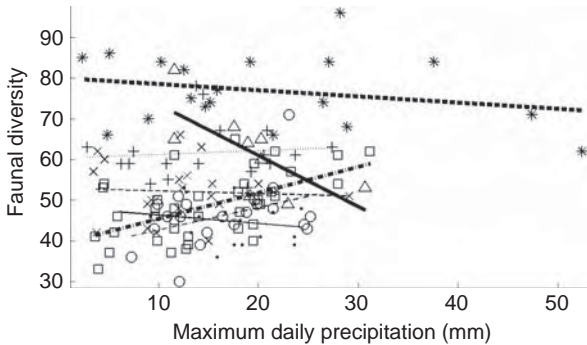
Figure 5 Linear model of faunal diversity (number of faunal taxa) as a function of above-ground ecosystem type (ET) and maximum daily precipitation during the 21 days prior to sampling. Line styles correspond to ET as in Figure 2. The model that constrained to 0 all slopes except those for pastures and winter farms explained 71.0% of the variation, not significantly less than the model that estimated all slopes independently ($F_{5,132} = 1.2$, $p = 31.4\%$).

the many physiological traits and comprehensive classification keys available for soil mesofauna and macrofauna in comparison to the few traits used for the terrestrial nematofauna. Although there was some overlap in $\log(M)$ at the extremes of the size distributions of nematodes, arthropods, and enchytraeids (Figure 6; lumbricids are off the abscissa to the right), most arthropods were larger than most nematodes and most enchytraeids and all lumbricids were larger than most arthropods. Because smaller taxa were less well resolved, average abundance–mass slope may have been less than (steeper than) it would have been if all taxa were genera. Still, lumping did not explain observed variation in abundance–mass slope. Neither the proportion of nematode taxa that were genera (PN) nor the proportion of arthropod taxa that were genera (PA), nor both of these predictors together explained significant variation in abundance–mass slope (F-tests, $p > 0.092$). Neither the model with predictors ET and ET $\times$ PN nor the model with predictors ET, ET $\times$ PN, and ET $\times$ PA explained significantly more variation in slope than the model with sole predictor ET (F-tests, $p > 0.114$). The model with predictors ET and ET $\times$ PA explained marginally significantly more variation than the model with sole predictor ET ($F_{7,132} = 2.7$, $p = 0.011$), but the only significant (1% level) slope coefficient in this model was the coefficient for winter farms. Plotting abundance–mass slope against PA for only winter farms revealed four high-leverage sites with PA $= 1$; when these were removed, PA had no significant association with abundance–mass slope ($p = 0.237$).

Total faunal biomass could not have been affected by lumping since the mathematical operation of computing total faunal biomass is not affected by lumping. PN did not explain significant variation in log total faunal biomass ($p = 0.537$). PA explained a small but significant amount of variation ($R^2 = 10.5\%$, $p < 0.0005$), but this was attributable to joint variation by ET in both PA and log total faunal biomass: the model with predictors ET and PA explained significantly more variation in log total faunal biomass than the model with sole predictor PA ($F_{6,138} = 24.5$, $p < 0.0005$), but not significantly more than the model with sole predictor ET ($F_{1,138} = 0.1$, $p = 0.756$). The model with predictors ET and ET $\times$ PA did not explain significantly more variation than the model with sole predictor ET ($F_{7,132} = 1.9$, $p = 0.074$), so log total faunal biomass was not associated with PA within ETs even though some ETs had sites spanning a wide range of PA. Neither the model with predictors ET and ET $\times$ PN nor the model with predictors ET, ET $\times$ PN, and ET $\times$ PA explained significantly more than the model with sole predictor ET (F-tests, $p = 0.113$ and 0.034, respectively).

Faunal diversity was not significantly associated with PN ($p = 0.282$), but was significantly positively associated with PA ($p < 0.0005$). This positive association may have affected the ranking (Table 3) of ET by mean faunal diversity. Forests, which had the highest mean diversity, and winter farms,
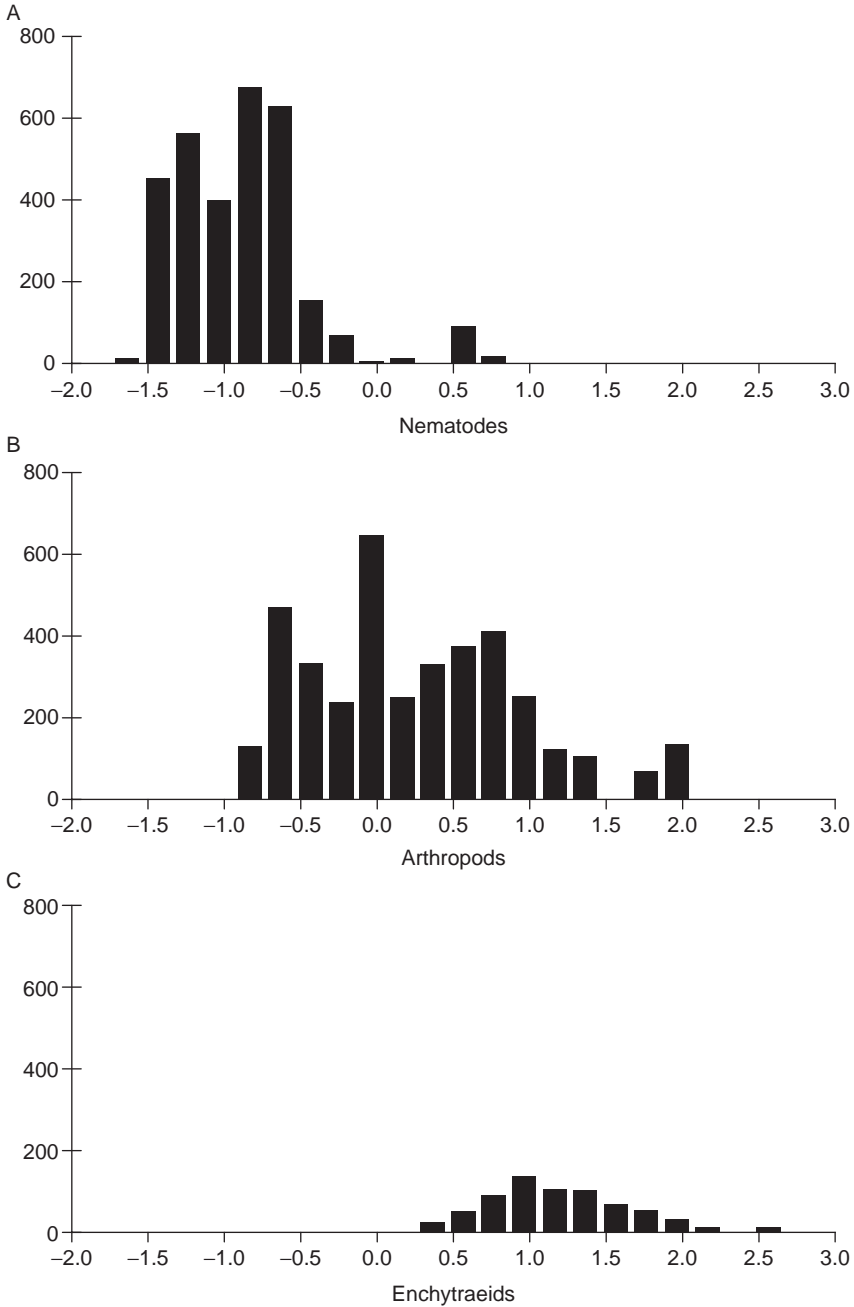
Figure 6 Frequency distribution of the $\log_{10}(M$, micrograms) values in all 146 soil food webs for nematodes (A), arthropods (B), and enchytraeids (C). Lumbricids were not plotted.

which had among the lowest (Table 3), had very similar mean PAs. Super-intensive farms and pastures, which had mean diversity intermediate between forests and winter farms, also had mean PAs similar to forests and winter farms. Because these ETs had similar mean PAs, their mean diversity values were directly comparable. In contrast, conventional, intensive, and organic farms had lower mean PAs, and had mean diversity similar to winter farms (Table 3). If conventional, intensive, and organic farms were as well resolved taxonomically as other sites, mean diversity of each of these ETs may have been intermediate between mean diversities of forests and winter farms, supporting the hypothesis that decreased taxonomic diversity was related to disturbance in the sites of this study.

Within ET, neither PN nor PA affected faunal diversity: none of the three models with predictors ET and ET $\times$ PN, or with predictors ET and ET $\times$ PA, or with predictors ET, ET $\times$ PN and ET $\times$ PA explained significantly more variation in faunal diversity than the model with sole predictor ET (F-tests, $p > 0.086$). Therefore, the effects of precipitation on faunal diversity (Figure 5), observed to occur within ETs, are not confounded by the overall dependence of diversity on PA.

VI. DISCUSSION

We summarize our main findings in the context of prior work. First, our data demonstrated that variation in abundance–mass slope, total faunal biomass, and faunal diversity is systematic, and can be partially explained in terms of external influences. Cyr *et al.* (1997) demonstrated systematic variation in the abundance–mass slopes of lakes. By necessity, they systematically excluded rare species, so their slopes may have been more like the slopes of the upper bounds of $\log(N)$-versus-$\log(M)$ relationships, as calculated by Blackburn *et al.* (1992). Our results and those of Cyr *et al.* demonstrate that abundance–mass slope is a useful descriptor, capable of registering the effects of anthropogenic and other influences on biologically important aspects of multiclade community structure.

Several studies investigated the effects of specific kinds of disturbance on traditional descriptors of web structure. Havens (1991, 1993) and Locke and Sprules (1994) found that acidification in lakes was associated with decreases in taxonomic diversity and measures of web complexity such as connectance and link density. Havens (1994) showed that chemical stress decreased species richness and web complexity in freshwater plankton webs in laboratory mesocosms. Our hypothesis that disturbance was partly responsible for decreases in faunal diversity from forests to winter farms is aligned with these results.

Wardle (1995) argued that tillage in agroecosystems, a form of disturbance, is more harmful to populations of larger taxa than to populations of smaller ones. Wardle's results were based on a literature survey of the effects of tillage on broad functional groups such as collembolans. If populations of larger taxa decrease more than populations of smaller taxa under tillage and other forms of disturbance, then abundance–mass slope will become more negative (steeper). Thus, Wardle's results are consistent with our hypothesis that disturbance can decrease (steepen) the abundance–mass slope. Variation in the abundance–mass slopes of the lakes of Cyr et al. (1997) was positively associated with the population of the largest human settlement within 100 km of the lake. These results conflict with our results and those of Wardle (1995) if human population density can be regarded as an index of disturbance.

A second main result of this study was that only a few predictors (aboveground ET, soil bacterial biomass, and a measure of precipitation) sufficed to explain a majority of variation in soil faunal structure. ET and soil bacterial biomass were sufficient to explain most of the variation in the slope and intercept of the abundance–mass allometric relationship. Cyr et al. (1997) also used only a few predictors to explain abundance–mass slopes in their lakes. One of these, annual lake primary production, may be analogous to soil bacterial biomass because both variables represent the availability of a basal resource. These encouraging results suggest that only a few variables are needed to predict important aspects of faunal community structure.

A. Food Web Descriptors

Our soil faunal descriptors have advantages and disadvantages.

1. Abundance–Mass Slope

Abundance–mass slope describes a site's biomass and energy-use patterns without using trophic data. Only a few individuals suffice to demonstrate a species' presence in a site and to estimate its M, and 10–20 individuals are sufficient for an approximate estimate of N. In contrast, the much greater difficulty of obtaining trophic data was illustrated by Woodward et al. (2005) for the benthic system of Broadstone Stream in southeast England. They created yield–effort curves plotting both the number of species discovered in the system as a function of sampling effort, and the number of prey items identified for each of nine common predators as a function of the number of predator guts dissected. Even after dissecting 200–300 guts of each predator species, Woodward et al. were still discovering new trophic links. Their species-discovery yield–effort curves reached an asymptote after reasonable sampling effort, but trophic link yield–effort curves never did. Woodward et al.

estimated that only 63% of trophic links were detected. Highly resolved trophic data in soil are even harder to get since visual gut content analysis is difficult. Trophic links in the soil also vary spatially: the same species eat different food at different soil depths (e.g., Ponge, 2000). Because abundance–mass slope does not use trophic data, we expect that slope will be less sensitive to undersampling than indices such as connectance.

2. Faunal Diversity and Total Faunal Biomass

Undersampling will cause underestimates of faunal diversity, S. If many rare taxa exist, underestimation could be substantial. If species of low biomass (MN) are less likely to be detected than species of high biomass, then total biomass will be less sensitive to sampling effort than faunal diversity S: in that case, undetected species are more likely to have low biomass, and therefore to contribute little to total biomass, while contributing just as much to S as any other species (namely, 1). If modern webs do not seriously underestimate S, then this is not a big advantage. Faunal diversity generally also depends on taxonomic lumping (Section V.D).

B. Relative Importance of Variables

Environmental effects on soil faunal descriptors were mediated by human-use influences: it was statistically possible to neglect direct environmental effects on soil faunal structure if all human-use predictors were included (Results, Section V.B.2). Environmental factors indirectly influenced soil faunal descriptors by affecting patterns of human use. In agricultural soil systems heavily influenced by humans, farmers make management decisions based partly on environmental factors. This pattern of causation may be special to agriculture, but may become more widespread as human influence on ecosystems increases.

It was also statistically possible to neglect direct influences of carbon resource factors on some descriptors if all human-use predictors were included (Section V.B.3). Human use substantially influenced soil faunal structure even after controlling for the influence of environmental and carbon resource variables (Section V.B.4).

C. Limitations of This Study

1. Limitations of the Data

As noted above, variation in taxonomic resolution across the $\log(M)$ range may have caused average abundance–mass slopes to be less than (steeper than) they would have been if all taxa were genera; but variation in slope and

the causes of this variation were not likely affected (Section V.D). Faunal diversity values were also less than they would have been if all taxa were genera. This may have obscured the ranking of ETs by faunal diversity and the relationship between disturbance and diversity (Section V.D). Faunal biomass was probably not much affected by taxonomic resolution.

Fungi, plant roots, and detritus were not incorporated into any of the variables of this study. Mulder *et al.* (2005a) quantified the total biomass of fungi, plant roots, and detritus, but that information was not used here because N and M could not be quantified separately. In Mulder *et al.* (2005a), the fungi were incorporated into the detritus due to the destructive soil sampling method and subsequent treatment; specifically, the detritus was taken to include all sporopollenins reasonable from the biogeochemical point of view. Effective ways to include N, M, or biomass data for fungi, plant roots, and detritus should be further explored. It may be appropriate to split bacteria into more than one taxon (Reuman *et al.*, this volume). The data of this study did not include sampling records, so it was impossible for us to form yield–effort curves and thereby estimate the completeness of sampling.

2. Limitations of the Models

All models of this study are nonmechanistic, exploratory models. They show that it is possible to predict part of the variation in soil faunal community structure from variation in external variables. These models should be replaced with mechanistic models if possible. Models constructed using stepwise regression can have artificially inflated R^2. Some data mildly violated assumptions of the standard linear model (Appendix III); p-values for models where the data violated assumptions should be considered approximate.

D. Future Directions

1. Descriptors and Predictors

Additional environmental, human-use, and biotic predictors may be needed to explain some of the unexplained variation in the descriptors of this study.

Reuman *et al.* (this volume) showed that most but not all local sites have approximately linear log(N)-versus-log(M) scatterplots. The coefficient c in the best-fitting quadratic model

$$\log(N) = c \log(M)^2 + b \log(M) + a + \varepsilon \qquad (6)$$

is one way to capture nonlinearity. This descriptor requires no trophic data but is purely phenomenological. A mechanistically motivated replacement for c would be useful.

All descriptors should be directly tested for sensitivity to sampling effort using data that include sampling records. Descriptors should also be tested directly for sensitivity to lumping of taxa.

2. Testing the New Hypotheses

To test the hypothesis that disturbance decreases (steepens) abundance–mass slopes in soil fauna, measurements of disturbance are necessary. Disturbances that affect agricultural soils include harvest of plant material, decreased bulk density and mixing of soil horizons by plowing, and compaction of soils by equipment and livestock. Measuring these variables on farms with highly resolved taxonomic, M and N data would permit observational evaluation of the hypothesis. A controlled, replicated experiment in which different types of disturbance are applied to different plots would also be useful, with taxonomic, M and N data gathered for each plot at various fixed times after disturbance. Factorial designs would permit exploration of the effects of combinations of disturbance, including possible interactions among different disturbances. The contrast between the results of Cyr *et al.* (1997) and the findings of Wardle (1995) and this study accentuate the need to measure specific types of disturbance.

On farms, fertilization includes compost, manure, and mineral fertilizers. Fertilization timing, amount, and type should be measured along with highly resolved taxonomic, M and N data. Studies investigating the effects of fertilization on soil community structure and vice versa are common (e.g., Coleman *et al.*, 1983; Ingham *et al.*, 1985; Matson *et al.*, 1997; Okada and Harada, 2007; Verschoor *et al.*, 2001; Wardle, 2002), but have not used the descriptors of this study. Controlled, replicated experiments to investigate the effects of specific fertilization regimes on the descriptors of this study are desirable.

Soils in agroecosystems provide excellent opportunities for observational and experimental tests of the effects of external factors on community structure, because soil systems can be studied in large numbers, and replicated experiments are common (e.g., Wardle, 1995 and references therein, Sanchez-Moreno and Ferris, 2007; Wardle *et al.*, 1995). However, to our knowledge, most studies of variation in soil community structure have focused on soil faunal components (such as the component consisting of all nematodes, or microflora) and interactions among these components, rather than on descriptors of the detailed structure of highly resolved faunal communities. Descriptors such as connectance, common in the literature of web

ecologists, have been used less often for soil webs, partly because trophic data in the soil are often not well resolved (Wardle, 1995). We hope the methods and results of this study will inspire further mutually beneficial collaboration between soil ecologists and web ecologists.

An open question is to what extent our findings from soil agroecosystems may apply to ecological communities with lesser or different kinds of human influence or other sources of disturbance. Do more disturbed communities have more negative (steeper) abundance–mass slopes? Do sites with greater carbon resources for basal taxa have less negative (shallower) abundance–mass slopes? What are similarities in the allometric patterns we have studied between soil agroecosystems and other types of communities such as rainforests, coral reefs, or wetlands?

ACKNOWLEDGMENTS

APPENDIX I. STEPWISE REGRESSION

Design matrices for the general linear models of this study were constructed as follows:

(1) A column of 1s was always included, representing a constant term in the models.
(2) For models including predictor ET, a column was included for each ET value, e, containing 1 for sites of type e and 0 for other sites. There were seven such columns.
(3) For models containing a continuous predictor variable x, a single column with the values of x was included.
(4) For models including the interaction terms ET $\times$ x, a column was included for each ET value, e, containing the values of x for sites of type e and 0 for other sites. There were seven such columns.

Higher-order and other interaction terms were not considered. Design matrices constructed in this way were not full-rank; *F*-tests were performed either by eliminating redundant columns or using the methods on pp. 120–121 of Seber (1977).

Our customized stepwise regression procedure constructed a linear model for a response variable y starting from the model that predicted y with its mean.

(1) At the first step:

  (a) The predictor variables that, by themselves, explained significant variation in y were determined (*F*-test, 1% level).
  (b) Of these predictors, the one that gave the greatest reduction in the corrected Akaike Information Criterion (AIC$_c$; Burnham and Anderson, 2002) was included in the model.

(2) Each subsequent step began by considering the possibility of removing predictors from the model:

  (a) The possibility of removing each of the following predictors was considered:

    (i) Any single continuous predictor for which interaction terms with ET were not also included in the model.
    (ii) ET itself if no interaction terms between ET and other predictors were included in the model.
    (iii) ET $\times$ x for another predictor, x. In this case, both the possibility of removing the interaction terms and x itself, and the possibility of replacing the interaction terms with x were considered.

  (b) From among the options that led to an insignificant reduction in the explained variation in y (*F*-test, 1% level), the one leading to the smallest increase in the AIC$_c$ was selected.
  (c) If a predictor was removed, the algorithm continued from (2); if not, it continued from (3).

(3) The possibility of adding a new predictor to the model was considered:

  (a) The possibility of adding each of the following combinations of predictors to the model was considered:

    (i) Any single continuous predictor not already included in the model.
    (ii) ET if ET was not already included in the model.
    (iii) ET $\times$ x for any single continuous predictor x if ET was already included in the model. Interaction terms could be added even if x

was not already included. Adding ET $\times$ x made x redundant if it was present. Therefore x was deleted if the interaction terms ET $\times$ x were added.

(b) From among the options that explained a significant amount of additional variation in y (F-test, 1% level), the option that gave the greatest reduction in the AIC_c was selected.

(c) The procedure terminated if none of the options explained significant additional variation (F-test, 1% level). The procedure always terminated for the data of this study; a similar algorithm has been proven mathematically to terminate always (Miller, 1996).

At each step, the choice of predictors to add to or remove from the model was based on the AIC_c instead of the coefficient of determination (R^2) because not all predictors were encoded in the design matrix using the same number of columns. Change in AIC_c with the addition of a predictor took into account not only the benefits obtained by adding the predictor (increase in the R^2 of the model), but also the "costs" incurred (more columns in the design matrix). The F-test p-value for adding a predictor to a model also took into account both the benefits and costs of adding the predictor. We did not make fine comparisons between F-test p-values associated with the addition of different predictors to a model because the data of this study did not always meet the assumptions of linear models (Appendix II); F-test p-values were considered reliable enough only for rough comparison to the benchmark value 1%.

The six sites with ID numbers 180, 202, 223, 224, 226, and 238 were missing point estimates of one or more predictors. For example, the area of site ID 202 was preceded by $>$ and the percent of Site ID 180 on which grass grew was preceded by $<$. In all cases, unknown values fell within known ranges. Sites missing point estimates for a given predictor were omitted for fitting and evaluating models that used that predictor. To compare nested linear models, only sites were considered for which all data used by either model were present.

APPENDIX II. TESTING ASSUMPTIONS OF LINEAR MODELS

Linearity of $E(y|X)$ was tested using the "quadratic coefficient F-test with squared prediction." The prediction $\hat{y}$ and residuals $r = y - \hat{y}$ of the best fitting linear model $y = Xb$ were computed. We fitted the quadratic model

$$r = \gamma\hat{y}^2 + \beta\hat{y} + \alpha + \varepsilon \qquad (S1)$$

and did an F-test to see whether the quadratic and linear terms of the model explained significant variation in r. Unless the F-test rejected the null hypothesis that $\gamma = \beta = 0$ with 1% significance, data passed this test.

Linearity of $E(y|X)$ was also tested using the "quadratic coefficient F-test with squared predictors." An augmented design matrix X' was constructed that included all columns of X and additional columns. For each column in X that represented a continuous predictor variable x, a column was added to X' representing x^2. If X included columns for ET $\times x$, then columns for ET $\times x^2$ were added to X'. If X' explained significantly more variation in y than X did (F-test, 1% level), data were said to have failed the quadratic coefficient F-test with squared predictors. The quadratic coefficient F-tests were also tests of the assumption of homoskedasticity of residuals (Reuman *et al.*, this volume). For models with sole predictor ET, the augmented design matrix X' was the same as X; the quadratic coefficient F-test with squared predictors was not performed for these models.

Normality of the residuals r from the best-fitting linear model $y = Xb$ was tested in two ways: using the Jarque–Bera test (Jarque and Bera, 1987) and the Lilliefors test (Lilliefors, 1967). Both are composite tests of normality of unknown mean and variance. The two tests are implemented in Matlab by the functions "jbtest" and "lillietest."

Homoskedasticity of the absolute residuals $|r|$ of data from the best-fitting linear model $\hat{y} = Xb$ was tested using the "absolute residuals F-test with squared prediction." The prediction $\hat{y}$ and residuals r of the best fitting linear model $y = Xb$ were computed. We fitted the quadratic model

$$|r| = \gamma\hat{y}^2 + \beta\hat{y} + \alpha + \varepsilon \qquad (S2)$$

and did an F-test to see whether the quadratic and linear terms of the model explained significant variation in $|r|$. Unless the F-test rejected the null hypothesis that $\gamma = \beta = 0$ with 1% significance, data passed this test.

Homoskedasticity was also tested using the "absolute residuals F-test with squared predictors." The augmented design matrix X' of the quadratic coefficient F-test with squared predictors was used. If X' explained significant variation in $|r|$, data were said to have failed the absolute residuals F-test with squared predictors. For models with sole predictor ET, the augmented design matrix X' was the same as X; the test was not performed for these models.

Following Cohen and Carpenter (2005) and Reuman *et al.* (this volume), we tested the serial independence of the residuals using the Durbin–Watson test, as implemented in Matlab by Kanzler (2005). Residuals were sorted by $\hat{y}$ and then passed to the Durbin–Watson code.

Biological interpretations of values of the coefficients of a linear model $y = Xb$ may not be reliable if X failed the "collinearity test." For this test, if X

contained a column of 1s, it was removed. If columns were included for the predictor ET, one of these columns was removed. We arbitrarily removed the column for forests. If X contained a column for a continuous predictor x and columns for ET $\times$ x, the column for x was removed (it was redundant anyway). If X contained a column for x, it was replaced with a column for $x - \text{mean}(x)$. If X contained columns for ET $\times$ x, these columns were replaced with interaction terms between $x - \text{mean}(x)$ and ET. Each column of the modified matrix X was regressed against the other columns and a column of ones; R^2 values were computed. The maximum of these R^2 values was the collinearity test result. If this result was high (80% is often used as a benchmark value), the columns of X may have been too collinear for model coefficients to be interpreted reliably. Coefficients of a model with highly collinear columns can change drastically if the model is refitted with a few data omitted. This collinearity test is related to the Variance Inflation Factor of Stuart and Ord (1991, p. 1066). The interpretations of model coefficients used in this study were approximate; we only looked at the sign of coefficients, attributing no importance to their magnitudes. For these purposes, even fairly collinear X are acceptable.

APPENDIX III. DETAILED STATISTICAL RESULTS

A. Abundance–Mass Slope

ET alone explained 51.7% of the variation in abundance–mass slope ($F_{6,139} = 24.8$, $p < 0.0005$). A lumped ET model that assigned cultivated farms to a single category, with forests and winter farms making two additional categories explained 48.4% of the variation in abundance–mass slope, not significantly less than the unlumped ET model ($F_{4,139} = 2.3$, $p = 0.058$).

Data violated the assumptions of both the model with sole predictor ET and the model with predictors ET and ET $\times$ soil bacterial biomass (Table 2): homoskedasticity, both absolute residuals F-tests, $p < 0.01$; normality of the distribution of residuals, Jarque–Bera test, $p < 0.01$. But the residuals appeared symmetrically distributed and only mildly heteroskedastic for both models. The collinearity test result for the latter model was 78.8%.

When only the 110 soil faunal communities satisfying the assumptions of the linear model Eq. 1 were included, stepwise regression selected a model with sole predictor ET that explained 48.5% of the variation in abundance–mass slope ($F_{6,103} = 16.7$, $p < 0.0005$). The assumptions of homoskedasticity (both absolute residuals F-tests, $p < 0.01$) and normality of the distribution of residuals (Jarque–Bera Test, $p < 0.01$) were not met; but residuals appeared symmetrically distributed and only mildly heteroskedastic. Forests had the least-negative mean slope (–0.30) across the 110 faunal communities,

followed by super-intensive farms (–0.47), pastures (–0.48), organic farms (–0.54), intensive farms (–0.54), conventional farms (–0.55), and winter farms (–0.60). A lumped ET model that assigned cultivated farms to a single category, with forests and winter farms making two additional categories, explained 43.9% of the variation in abundance–mass slope, not significantly less than the un-lumped ET model ($F_{4,103} = 2.3$, $p = 0.064$). Thus, using only the 110 soil faunal communities that satisfied the assumptions of the linear model gave mean abundance–mass slope values for each ET that were substantially indistinguishable from those obtained using all communities.
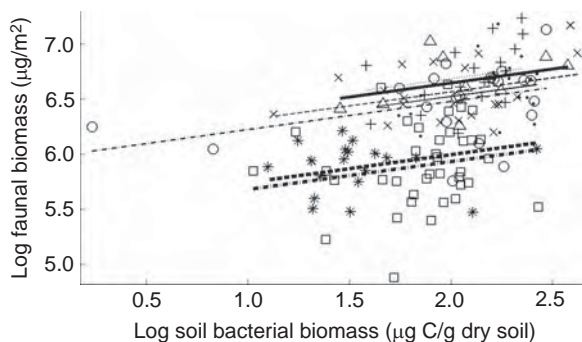
B. Log Faunal Biomass

ET alone explained 56.6% of the variation in log faunal biomass ($F_{6,139} = 24.8$, $p < 0.0005$). A lumped ET model that assigned forests and winter farms to one category, and all other sites to another category explained 54.6% of the variation on log faunal biomass, not significantly less than the unlumped ET model ($F_{5,139} = 1.3$, $p = 0.277$). Data satisfied all seven tests of the assumptions of the model with sole predictor ET and the model with predictors ET and soil bacterial biomass (Table 2). The collinearity test result for the latter model was 55.9%. The model with predictors ET and log soil bacterial biomass (Figure S1) explained 60.0% of the variation in log faunal biomass ($F_{7,138} = 29.57$, $p < 0.0005$) and data passed all seven tests of the assumptions of that model. The collinearity test result was 58.2%.

C. Faunal Diversity

ET alone explained 66.0% of the variation in faunal diversity ($F_{6,139} = 44.9$, $p < 0.0005$). A lumped ET model that assigned pastures and super-intensive farms to a single category; conventional farms, organic farms, intensive farms and winter farms to another category; and forests to a third category explained 63.4% of the variation in faunal diversity, not significantly less than the unlumped ET model ($F_{4,139} = 2.6$, $p = 0.038$).

Stepwise regression selected a model of faunal diversity with predictor variables ET, soil organic matter, and ET × maximum daily precipitation. The collinearity test result was 58.9%. Faunal diversity was negatively influenced by soil organic matter in this model. The influence of increasing maximum daily precipitation on faunal diversity was significantly positive for winter farms, significantly negative for pastures, and not significantly different from 0 for other ET (1% level). The collinearity test result for the model of faunal diversity with predictor variables ET and ET × maximum daily precipitation (Figure 5) was 58.7%. Data satisfied all assumptions of the

ET		Intercept	99% Conf.		Slope	99% Conf.	
Conv.	*	6.016	5.557	6.475	0.254	0.0594	0.449
Org.	×	6.058	5.635	6.480			
Int.	O	5.970	5.545	6.395			
S.-Int.	+	6.177	5.731	6.624			
Pstr.	△	6.138	5.663	6.613			
Forest	✳	5.488	5.138	5.838			
Winter	□	5.425	5.040	5.809			

Figure S1 Linear model of log faunal biomass as a function of above-ground ecosystem type (ET) and log soil bacterial biomass. Line styles correspond to ET as in Figure 2. A model that constrained the y-intercepts for the winter farm and forest lines to take a single value, and the y-intercepts of all the other lines to take another value explained 58.1% of the variation in the response variable, not significantly less than the unconstrained model ($F_{5,138} = 1.29$, $p = 27.1\%$).

three models of faunal diversity that used predictors ET; ET, soil organic matter, and ET × maximum daily precipitation; and ET and ET × maximum daily precipitation.

For intensive farms, the mean of daily precipitation over the 21 days before sampling was positively associated with faunal diversity ($R^2 = 35.5\%$, $F_{1,144} = 10.5$, $p = 0.004$).

D. Abundance–Mass Intercept and Expected Log Population Density of Smallest Taxa

ET alone explained 74.7% of the variation in abundance–mass intercept ($F_{6,139} = 68.4$, $p < 0.0005$). Data satisfied all the testable assumptions of this linear model except normality of the distribution of residuals (Jarque–Bera Test, $p < 0.01$), but the residuals appeared symmetrically distributed except for one outlier. Forests had the smallest mean intercept (3.00),

followed by winter farms (3.23), super-intensive farms (3.32), pastures (3.46), organic farms (3.54), intensive farms (3.62), and conventional farms (3.67). A lumped ET model that assigned pastures and organic farms to one category, intensive and conventional farms to another category, and the three remaining ET values to three more categories explained 74.1% of the variation, not significantly less than the un-lumped ET model ($F_{2,139} = 1.7$, $p = 0.187$).

The model selected by our stepwise regression procedure used predictor variables ET, percent bacterial cells dividing (PBD), and interaction terms between ET and modified Julian date. It explained 80.4% of the variation in abundance–mass intercept ($F_{14,131} = 38.4$, $p < 0.0005$); data passed all seven tests of the assumptions of the model. The collinearity test result was 90.5%, so model coefficient values should be interpreted with caution.

The model with predictor variables ET and ET $\times$ modified Julian date explained 79.3% of the variation in abundance–mass intercept ($F_{13,132} = 38.9$, $p < 0.0005$); data satisfied all seven tests of the assumptions of this model. Collinearity test results were 90.3%, so model coefficient values should be interpreted with caution.

Restricting to the 110 soil faunal communities for which the assumptions of the linear model Eq. 1 were satisfied, the predictor variable ET alone explained 77.4% of the variation in abundance–mass intercept ($F_{6,103} = 58.9$, $p < 0.0005$); no variables or interaction terms explained a significant amount of additional variation in the presence of ET. All testable assumptions of linear models were satisfied except the assumption of normality of the distribution of residuals (Jarque–Bera Test, $p < 0.01$); but residuals appeared symmetrically distributed except for one outlier. Forests had the smallest mean intercept (3.03) across the 110 faunal communities, followed by winter farms (3.24), super-intensive farms (3.34), pastures (3.47), intensive farms (3.65), conventional farms (3.67), and organic farms (3.69). The lumped ET model that assigned organic farms and pastures to one category, conventional farms and intensive farms to another category, and the three remaining site types to three more categories explained 75.4% of the variation, not significantly less than the unlumped ET model ($F_{2,103} = 4.7$, $p = 0.011$).

For the model of expected log(N) of smallest taxa with sole predictor ET, data passed all the tests of the assumptions of this linear model except the Jarque–Bera test. The residual distribution appeared approximately symmetric. The collinearity test result was 54.9%. The stepwise regression procedure selected a model of expected log(N) of smallest taxa with predictors ET, and the interaction terms ET $\times$ modified Julian date and ET $\times$ longitude, and explained 78.9% of the variation in expected log(N) of smallest taxa ($F_{20,125} = 23.3$, $p < 0.0005$). The model with predictors ET and ET $\times$ modified Julian date explained 75.5% of the variation in expected log(N) of smallest taxa ($F_{7,132} = 3.45$, $p = 0.002$).

E. Log Faunal Population Density

ET alone explained 56.8% of the variation in log faunal population density ($F_{6,139} = 30.4$, $p < 0.0005$). Data satisfied all the testable assumptions of this linear model except normality of the distribution of residuals (Jarque–Bera Test, $p < 0.01$), but the residuals appeared symmetrically distributed except for one outlier. Forests had the smallest mean log faunal population density (5.46), followed by winter farms (5.96), super-intensive farms (5.99), intensive farms (6.06), pastures (6.11), conventional farms (6.14), and organic farms (6.17). Forests had, on geometric average, $10^{5.46} = 288{,}403$ animal individuals per square meter of soil surface; organic farms had 1,479,108. A lumped ET model that assigned winter farms, super-intensive farms and intensive farms to one category; pastures, conventional farms, and organic farms to another; and forests to a third category explained 55.2% of the variation in log faunal population density, not significantly less than the unlumped model ($F_{4,139} = 1.26$, $p = 0.289$).

The model selected by our stepwise regression procedure used predictor variables ET, soil organic matter, and standardized livestock density; it explained 62.6% of the variation in log faunal population density ($F_{8,137} = 28.7$, $p < 0.0005$). The same model with standardized livestock density removed explained a significant but small amount (2.2%) less variation ($F_{1,137} = 8.05$, $p = 0.005$). Data passed all seven tests of the assumptions of both linear models except the Jarque–Bera test; residuals appeared approximately symmetrically distributed. For the model with predictors ET, soil organic matter and standardized livestock density, the influence of increasing either continuous predictor on log faunal population density was significantly positive (1% level). That model had collinearity test result 77.0%. For the model with predictors ET and soil organic matter, the influence of increasing soil organic matter on log faunal population density was significantly positive (1% level). That model had collinearity test result 55.7%.

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