

Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain

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The relative importance of top-down and bottom-up control in setting the equilibrium abundances within trophic levels is examined in a comparative study on the litter-based food chain of a temperate deciduous forest. During two consecutive years, we estimated the abundances of macroinvertebrate detritivores and their predators on a natural gradient of annual litterfall. Detritus-based food chains are thought to be classical examples of donor-controlled systems. Indeed, both trophic levels showed higher abundances on sites with higher annual litterfall. Therefore, they appear to be bottom-up controlled. Using the Errors-in-Variables regression technique, we quantitatively compared our data with the equilibrium predictions of a set of simple trophic chain models including bottom-up effects with different types of functional responses (Beddington-DeAngelis, Hassell-Varley, and ratio-dependent). The model with a Hassell-Varley type functional response yielded the best adjustment to the data, although with a very high value of the mutual interference parameter suggesting the existence of overcompensating density dependence. Several changes to the structure of this model were considered. Their adjustment to the data consistently yielded such high values of the interference parameter.

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Trophic interactions between, and competition within trophic levels influence their relative abundances for a given input at the bottom of a food chain (usually primary production). How these different forces interact to finally determine equilibrium abundances within trophic levels is a capital criterion in the assessment of the relative importance of top-down and bottom-up effects in ecological communities. Although these terms are widely used in the ecological literature, they do not have clear, unambiguous definitions. Bottom-up control of a given population is usually established by demonstrating that its equilibrium abundance increases when its food supply increases. Top-down control is demonstrated by an increase of the population when the pressure of its predators is decreased. We can observe that these two definitions are not mutually exclusive and, indeed, abundances within trophic levels are, in

many cases, sensitive to both changes in their resources and changes in the predation pressure they suffer (e.g., Rosemond et al. 1993).

However, these terms are used sometimes with more extreme meanings. Bottom-up control in a strict sense is a situation in which the abundance of a population is insensitive to changes in the abundance of its predators. We shall call this case of extreme bottom-up control “donor-control” (although this term has also been used with other slightly different meanings: see review in Persson et al. 1996). Conversely, the extreme case of top-down control is that of a population insensitive to changes in the abundance of its resources. For instance, according to the HSS theory (Hairston et al. 1960), herbivores in a three-level chain should be so efficiently preyed upon that any additional unit of biomass they might produce as a result of an increase in available

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plant biomass would be used up by the carnivores. Carnivores, but not herbivores, should increase along a gradient of available plant biomass: herbivores are top-down controlled. Consequently, the plants, relieved from the herbivores' pressure would increase: the effect cascades down the chain. In a two-level plant-herbivore chain, the plants would be top-down controlled by the herbivores.

It is only with the latter strict definitions that top-down and bottom-up controls become mutually exclusive. However, these terms are rarely used with the latter definitions and more often with the former looser ones. Nevertheless, they are often treated as mutually exclusive: demonstration of top-down control is interpreted as an absence of bottom-up control and vice versa. This has led to some confusion. Food chains can be bottom-up controlled because the equilibrium abundances increase when primary productivity increases, and also incorporate top-down control in the sense that the total length of the food chain determines the strength of the positive response of the abundances within trophic levels to a change in productivity (Ginzburg and Akçakaya 1992). Another source of confusion is due to the fact that the population responses mentioned above are supposed to be equilibrium responses. However, many empirical studies have followed the transient dynamics following manipulations of upper or lower trophic levels. While such observations can be interesting, they cannot be interpreted directly in terms of top-down and bottom-up control.

A first type of empirical studies examine the consequences of a change either at the top level of a food chain or in the productivity at the bottom of the chain. In a system of given primary productivity, the addition or deletion of one level at the top of the chain may change the equilibrium abundances of lower trophic levels (e.g., Power 1990, Churchfield et al. 1991, Spiller and Schoener 1994). In such an event, top-down control is usually inferred. However, while this rejects strict donor control, it is not incompatible with the possibility that the trophic level being considered receives both top-down and bottom-up influences.

A second type of studies are comparative. The effect of changes at the bottom of the chain is assessed by comparing trophic level abundances on a gradient of primary productivity, and with a constant chain length. In the strict trophic cascade (HSS) theory, an alternation of positive correlations with zero or negative correlations is expected between the equilibrium abundances of successive trophic levels and the input rate at the bottom of the chain. On the contrary, both in donor-controlled chains and in situations with mixed bottom-up and top-down effects, the equilibrium abundances of all levels are expected to be positively correlated with the input at the bottom of the chain. Several manipulative or comparative studies have tested these opposite

predictions (review in Ponsard 1998), be it by empirical observations (Wardle and Yeates 1993, Bengtsson et al. 1997 and 1998), experimental systems (Hurd et al. 1971, Vince et al. 1981, Arditi and Saïah 1992, Schmitz 1993, Balciunas and Lawler 1995, Davidson and Potter 1995, Warren and Spencer 1996, Bohannan and Lenski 1997, Mikola and Setälä 1997 and 1998, Kaunzinger and Morin 1998, Scheu and Schaefer 1998), or analyses of data from the literature (Arditi and Ginzburg 1989, McNaughton et al. 1989, Arditi et al. 1991, Moen and Oksanen 1991, Cyr and Pace 1993, Akçakaya et al. 1995). Observation of the strictly alternating pattern predicted by the cascading theory demonstrates the presence of strict top-down control. The absence of such strict pattern is evidence for bottom-up effects, not necessarily excluding top-down influences as well. The combined effects of changes at the top and at the bottom of food chains have also been tested in studies examining the consequence of the addition or deletion of the top level on the response of lower levels to a change in primary productivity (e.g., Vanni 1987, Hansson 1992, Rosemond et al. 1993, Schmitz 1994).

The vast majority of all these studies deal with ecosystems in which the major part of the primary production is consumed alive (mainly lakes, and sometimes streams or grasslands). The present work deals with a detritus-based food chain. It examines whether the abundances of the trophic levels of the forest litter macroinvertebrates are positively correlated with the amount of detritus input at the bottom, on a relatively narrow gradient since we compare only temperate mature deciduous forest stands. Despite the fact that in several ecosystems (Begon et al. 1995), including forests (Swift et al. 1979, Schaefer 1990), a major part of the primary production is consumed as detritus, relatively few studies have addressed the question of the mutual regulation of trophic level abundances in detritus-based food chains (Moore et al. 1993). The latter are often considered as typical examples of donor-controlled systems because the detritivores do not affect the renewal rate of their food (Pimm 1982, Begon et al. 1995), although Bengtsson et al. (1996) argued that this view is debatable in the soil fauna if indirect effects, such as enhanced renewal rate of nitrogen through mineralization by fauna, are taken into account. Moreover, donor-control in the detritus-detritivore interaction does not preclude the possibility of top-down effects at higher trophic levels. However, soil communities also have other characteristics such as a high species diversity (e.g., Schaefer 1991), a high proportion of arthropod species, and a high proportion of generalist feeders. Strong (1992) predicts that these characteristics favor a food-web rather than a food-chain structure of the community, which in turn may favor bottom-up over top-down forces (Polis and Strong 1996).

Assessing the relative importance of food and other factors (including predation) in determining detritivore

abundance, and hence detritus consumption rates, is especially useful to better understand nutrient cycles. Some experiments have been conducted to examine the response of several soil taxa to the removal or addition of litter (Arpin et al. 1985, Garay 1988, Judas 1989 and 1990, David et al. 1991, Hövemeyer 1992, Ponge et al. 1993, Chen and Wise 1997) or logging residues (Bengtsson et al. 1997, 1998), or to the addition of food supplies in liquid form (Scheu and Schaefer 1998). Others have studied the top-down effects of vertebrate predators on soil invertebrates by conducting enclosure experiments (Churchfield et al. 1991, Chen and Wise 1998, Wise and Chen 1998, Wyman 1998). Many of these studies did not examine the abundances of trophic levels as such. They are directed at one or several particular taxonomic groups (earthworms, diptera larvae, springtails . . .) and give no data about the other ones, providing only indirect indications on the regulation of the abundance of whole trophic levels. However, even the most comprehensive among these studies reach opposite conclusions. In studies manipulating the input at the bottom of the chain, evidence has been found for both top-down (e.g., Bengtsson et al. 1997) and bottom-up control (e.g., Scheu and Schaefer 1998). In predator enclosure experiments, Churchfield et al. (1991) and Wyman (1998) observed trophic cascade effects, while Wise and Chen (1998) and Chen and Wise (1998) did not. Therefore, it remains an open question whether trophic levels are controlled mainly by top-down or by bottom-up forces in the soil macrofauna.

Our study is based on the abundances of litter macrodetritivores and predators, recorded in mature temperate forest stands on a natural gradient of increasing annual litterfall, during two consecutive years. David et al. (1991) observed that experimental removal of the litter input had consequences on the abundances of most taxa, but only after a delay of one year or more. Therefore, studies on natural gradients are more likely to yield reliable information on equilibrium abundances than short- or middle-term experimental ones. The community of invertebrates that lives on the leaf litter has been found to be relatively – though not completely – isolated from that of the underlying soil layers (Heal and Dighton 1986). The litter invertebrate communities of all study sites are assumed to be at equilibrium. We will examine whether the relationships between equilibrium abundances along the litterfall gradient are closer to that predicted by top-down or by bottom-up food chain models, and, more precisely, which mathematical form of the functional response (amount of prey eaten per predator per unit of time) gives the closest quantitative description of the pattern we observed. This will be done using a statistical tool which has yet rarely been used in ecology, the Errors-in-Variables regression. We will restrict ourselves to equilibrium predictions and to simple food chain models aggregating all species into one single compartment per trophic level.

Litter-based food chain models

In many predator-prey models, the gains of the predator or losses of the prey are represented by the functional response, i.e., the function describing the amount of prey eaten per unit of predator per unit of time (the word “amount” can be understood as a number of individuals or as a biomass). This can be extended to food chain models by defining a functional response for each trophic level, representing the amount of resources from the i -th level eaten per consumer of the $(i + 1)$ -th level. A two-level food chain can then be represented by the following equations:

$$\frac{dN}{dt} = f(N) \cdot N - g(N, P) \cdot P \quad (1a)$$

$$\frac{dP}{dt} = e \cdot g(N, P) \cdot P - \mu \cdot P \quad (1b)$$

where N and P are the abundance of prey and predators, t is the time, $f(N) \cdot N$ is the growth rate of the prey in the absence of predation, e is the conversion efficiency, μ is the mortality of the predators, and $g(N, P)$ is the functional response. If the model is to satisfy the law of mass conservation, the amount subtracted from the prey abundance must correspond to that added to the predator abundance (the numerical response of the predators), modulated by a conversion efficiency factor (Ginzburg 1998 and included references). The functional response appears in both equations, and is thereby the critical link between the abundances of successive trophic levels.

At least 18 different mathematical forms of various complexities and number of parameters have been proposed for the functional response in ecology (list in Michalski et al. 1997), and over 50 in microbiology (Bastin and Dochain 1990). We will examine a few categories of the most simple and the most widely used ones. Among those, one set of functional responses depend only on the amount of prey (“prey-dependent” functions of Lotka-Volterra, or Holling 1959): the amount of prey consumed per predator increases with the amount of prey that are present, but is independent of the amount of predators that share these prey. Food chain models with this kind of functional responses produce the cascading pattern expected in food chains dominated by top-down effects: all levels an even number of levels below the top are positively correlated with resource input, and the levels an odd number of levels below the top are negatively or not correlated at all with resource input.

A second set of functional responses, which also depend on the amount of prey but additionally take into account some “horizontal” interactions in the form of interference between predators (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi

and Ginzburg 1989), produce positive correlations between the input rate and the equilibrium abundances of all trophic levels, i.e., a pattern in which all levels are bottom-up controlled. These functional responses have been called “predator-dependent” (Arditi and Ginzburg 1989).

The food chain we consider here consists of the detritivore and the predator levels (D and P). The litter has no direct effect on its own “reproduction” (or renewal rate). Rather, it flows regularly into the system, and is therefore the analogue of the nutrients, rainfall or light that determine the growth rate of primary producers in photosynthesis-based food chains. Therefore, we do not consider the litter as a trophic level per se but we consider that the litterfall determines the production of the first trophic level, i.e., the detritivores. More precisely, the detritivore production rate is assumed to be proportional to the annual litterfall, L . Following the general mathematical form (1), our food chain can be represented by the following model:

$$\frac{dD}{dt} = \gamma \cdot L - g(D, P) \cdot P \quad (2a)$$

$$\frac{dP}{dt} = e \cdot g(D, P) \cdot P - \mu \cdot P \quad (2b)$$

where γ is a positive constant, e is the conversion efficiency of the predators, μ is their mortality, and $g(D, P)$ is the functional response of the predators.

In prey-dependent (Prey-d) functional response models, g is a growing function of D alone:

$$g(D, P) = g(D) \quad (3)$$

while in the predator-dependent (Pred-d) functional response models, g increases with D and decreases with P . A number of Prey-d functional response models exist, the most commonly used being the Lotka-Volterra model $g(D) = a \cdot D$ and Holling’s “disc equation”:

$$g(D) = \frac{a \cdot D}{1 + a \cdot h \cdot D} \quad (4)$$

where a and h are positive constants. However, we will only study equilibrium properties, and these do not depend on the exact functional form of $g(D)$. It is actually unnecessary to give the explicit formulation of this function when it is prey-dependent.

In contrast to Prey-d models, the properties of Pred-d models depend on the form of $g(D, P)$. Three such models will be considered. First, we will consider the model proposed by Beddington (1975) and DeAngelis et al. (1975),

$$\text{BDA: } g(D, P) = \frac{a \cdot D}{1 + a \cdot h \cdot D + c \cdot P} \quad (5)$$

where a (the attack rate), h (the handling time) and c are positive constants.

Second, we will consider a generalized form of the model proposed by Hassell and Varley (1969),

$$\text{HV: } g(D, P) = g\left(\frac{D}{P^m}\right) \quad (6)$$

where m is a positive constant known as the parameter of mutual interference ($m = 0$ would yield a Prey-d functional response). Function g is usually taken as Holling’s response (4) in which the argument D is replaced by D/P^m . However, the equilibrium properties are the same for any function of the general form $g(D/P^m)$, and it is unnecessary to give a more explicit formulation of function g .

Third, we will examine the so-called “ratio-dependent” model (Arditi and Ginzburg 1989),

$$\text{RD: } g(D, P) = g\left(\frac{D}{P}\right) \quad (7)$$

where g is a positive increasing function of its single argument D/P , i.e., a special case of the general HV model (6) when $m = 1$. Again, the function g is often taken as an analogue of Holling’s response (4). In this case, this functional response is a limiting case of the BDA model (when $1 \ll a \cdot h \cdot D + c \cdot P$). Again, the equilibrium properties do not depend on the exact functional form of g when it is ratio dependent.

The equilibrium predictions for a two-level trophic chain for each of these functional responses are shown in Fig. 1. Details on the relations between the constants and the parameters are given in Appendix A. Under our assumption that the production rate of detritivores is proportional to annual litterfall, all models considered predict the equilibrium abundance of predators to be proportional to annual litterfall,

$$P^* = k_0 \cdot L \quad (8)$$

where $k_0 = (\gamma \cdot e)/\mu$ is a positive constant.

The Prey-d model predicts that the detritivore equilibrium abundance D^* should be independent of P^* and of L . In contrast, the Pred-d models all predict that detritivores will increase with annual litterfall. However, the exact shape of this increase depends on the functional response. It can be proportional (RD), linear with an intercept (BDA) or exponential (HV).

In the HV model, if the exponent m is larger than one in the relation between P^* and L , then the exponent in the relation between D^* and L , m^{-1} , is smaller than one, and vice versa. In Fig. 1, m was taken smaller than 1 but it can be greater, although this is sometimes

considered biologically unrealistic. Indeed, this parameter is an estimate of the strength of interference between predators. The amount of prey consumed by each predator is $g_{HV}(D/P^m)$. A value $m > 1$ means that the increase in total predation that would be caused by the addition of one predator to the system would be over-compensated by the fact that its presence reduces the per capita consumption of all predators, in such a way that the total predation pressure could decrease when the number of predators increases.

Note that the BDA model predicts a positive intercept for the D^* vs L relationship, and a negative one for the P^* vs D^* relationship. The latter suggests the existence of a threshold value of detritivore abundance below which predators cannot exist. However, the former then implies that detritivores can reach a positive equilibrium value even with zero annual litterfall. This problem is also encountered in the Prey-d model, but neither in the HV nor in the RD model (Fig. 1). It can be explained by the fact that as in most trophic chain models we have made the assumption that predation is the only cause of mortality of the detritivores, and it can easily be corrected, for instance by adding a constant mortality to the detritivores by changing Eq. (2a) to:

$$\frac{dD}{dt} = \gamma \cdot L - d \cdot D - g(D, P) \cdot P \quad (9)$$

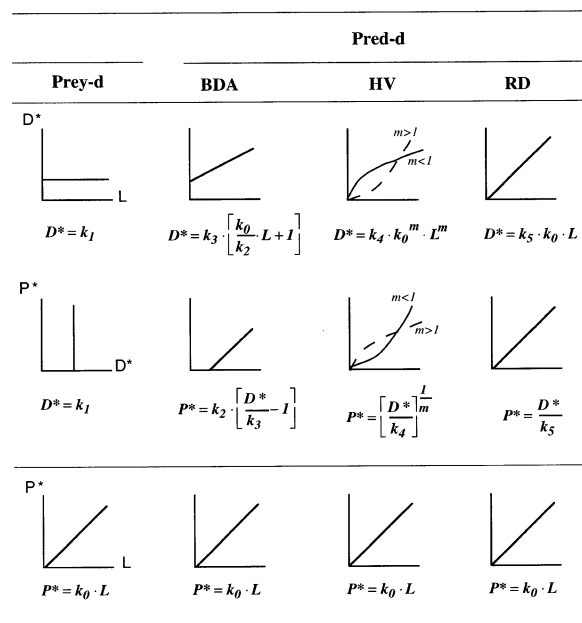


Fig. 1. Predicted relationships between equilibrium abundances in a two-level trophic chain (D^* : equilibrium abundance of the detritivores, P^* : equilibrium abundance of the predators) and input at the bottom of the chain (L : annual litterfall) of four simple models: one prey-dependent, and three predator-dependent ones – BDA (Beddington-DeAngelis), HV (Hassell-Varley) and RD (ratio-dependent). m and k_0 to k_5 are positive constants (see text).

This leads to the extinction of predators below some threshold value of litterfall, L_c . Below L_c , detritivores are the single trophic level and D^* increases proportionally with L , with $D^* = 0$ for $L = 0$. Above L_c , the relation between D^* and L cannot be qualitatively distinguished from that of the original model (2a) with the BDA or the Prey-d models. With the RD model, the prediction of simple proportional relations between all three variables P^* , D^* and L is unchanged. With the HV model, the modification (9) generates more complicated but qualitatively equivalent predictions (see the Discussion). Since predators were present on all our study sites, it was therefore not useful to further consider the more complicated model (9).

Material and methods

Sites

Investigations were made on five forest sites with increasing annual litterfall density, located within 3 km distance on the Orsay University campus (France). Their vegetation is a mixed deciduous mature forest with a sparse understory. Study sites are about 0.5-ha plots, each included in a larger area not obviously different from the study plot. Four sites were studied both in 1995 and 1996, and one additional site in 1996 only.

Annual litterfall (L) was estimated with eight 30×50 cm litter traps per site that were left during the whole litterfall season, from the beginning of September 1996 until the end of December 1996. Wood and branches were sorted out by hand and discarded; the remaining leaves were dried to constant weight at 60°C and weighed. No data are available for earlier years but we assume that the relative proportions of annual litterfall on the five sites remain the same every year. This is reasonable since we are studying mature forest stands of similar tree species composition and similar climate.

Abundance of soil fauna

Soil macrofauna was trapped once a month with pitfall traps from late April 1995 to October 1995 (seven trapping sessions), and twice a month from late April 1996 to November 1996 (14 trapping sessions). During each trapping session, ten pitfall traps per site were left in the field for one week. They were distributed following the same spatial pattern on each site, with a minimum distance of 5 m between traps. The preservative used in the traps was salted water to avoid as much as possible any attraction/repulsion phenomenon due to smell, to prevent the animals from staying alive and eating each other, and from escaping from the traps. The captures were counted and determined with a

taxonomic accuracy at least sufficient to determine whether feeding habits were detritivorous or predaceous. Scavenger species (Silphidae) and individuals less than 3 mm or vertebrates (amphibians, small mammals) were not taken into account.

It has repeatedly been warned against the use of pitfall trapping results as population density indices (Adis 1979, Franke et al. 1988, Topping and Sunderland 1992). Trapping success depends on the ranging behavior of individuals, which may vary with species (Greenslade 1964, Luff 1975), sex (Müller 1984), stage, defensive secretions or sexual pheromones from individuals that are already in the trap (Luff 1986), microclimate (Briggs 1961, Greenslade 1961 as cited in Greenslade 1964), season (Müller 1984), etc. Therefore, pitfall trapping yields activity densities rather than population densities (Kaczmarek 1978). Nevertheless, it has also been recognized that “pitfall traps (...) allow relative comparison between different areas of a habitat within the same sampling period” (Adis 1979), and that, despite its drawbacks, it is the only applicable method for some kinds of studies (Greenslade 1964) since no alternative offering a comparable sample size to sampling effort ratio has been proposed yet (Lövei and Sunderland 1996). For a given sampling period, there is no obvious reason why between-site differences in activity density should not reflect true differences in population densities. Therefore, we hypothesize that the biases mentioned above do not favor any of the predictions we want to test over the alternative ones.

Trophic level abundances

“Detritivore abundance” (D) and “predator abundance” (P) are the mean number of individuals belonging, respectively, to a detritivorous or a predatory species caught per trap on a given site during a given trapping session. The main detritivorous taxa were woodlice, millipedes, Orthoptera, gasteropods, and Dermaptera. The main predatory taxa were spiders, harvestmen, centipedes, and staphylinid and carabid beetles. Most soil invertebrate predators are more or less omnivorous, consuming detritivores, but also other predators (whether or not from the same species) and sometimes detritus, usually in unknown proportions (Blandin et al. 1980, Gunn and Cherrett 1993). None of the predatory soil macroinvertebrates, as far as we know, is clearly specialized on preying on other predators, so that there is probably not more than one trophic level of predators. This was confirmed by the natural abundances of stable isotopes of nitrogen measured in about 50 macroinvertebrate species (Ponsard and Arditi 2000). We therefore aggregated all the predatory species into one single predator level, being aware that there must be a certain degree of intra-level predation. The values of D and P measured during each

trapping session will be considered representative of equilibrium values D^* and P^* (see Discussion).

In 1996, intervals between trapping sessions were two weeks. In order to lower the importance of short-term fluctuations, two-week moving averages of D^* and P^* were used, yielding 13 data sets calculated from the 14 original ones. For 1995, the time interval between consecutive trapping sessions was longer (about one month), and the seven original data sets were used. Therefore, we will examine a total number of 20 data sets, each consisting of the values of L , D and P of four (1995) or five (1996) sites. In addition, we will examine the annual average abundances, calculated on the seven data sets of 1995 and on the 14 data sets of 1996.

Statistical means of comparison

Two questions have to be examined: first, the general validity of the two-level trophic chain approach with assumption of proportionality between instantaneous growth rate of detritivores and L , and, second, the identification of the most appropriate functional response. Both questions were addressed by comparing the equilibrium predictions of the different models with the data, fitting simultaneously L , D^* and P^* . The quality of the adjustment of the predictions of the various models to the data was quantified by their likelihoods, combined with an Errors-in-Variables regression approach. This approach takes uncertainties in measurements of all state variables into account. See Appendix B for a detailed description and implementation.

Regarding the first question (general validity of the approach, irrespective of a particular functional response), we calculated the likelihood of the adjustment of the relation between P^* and L , either for the proportionality relation predicted by the four functional response models (8) or for three simple alternatives:

$$P^* = q \quad (10)$$

$$P^* = r \cdot L + s \quad (11)$$

$$P^* = v \cdot L^w \quad (12)$$

where q , r , s , v , and w are real constants.

Note that the alternatives (10–12) are not predicted by any of the four models. They are intended to examine whether the data agree reasonably well with the common prediction (8). Eq. (8) is nested into Eqs (11) and (12). To compare the likelihood of the Eqs (11) and (12) with that of Eq. (8), we used a likelihood ratio test (Hilborn and Mangel 1997). This test compares $\log(\Lambda_2 - \Lambda_1)^2$ to the χ^2 distribution with $n_2 - n_1$ degrees of freedom, where Λ_1 and Λ_2 are, respectively, the likelihoods of the more complex and the simpler

equations, and n_1 and n_2 are their number of fitted parameters. Eqs (11) and (12) both have two fitted parameters, and Eq. (8) has one. Eq. (10) also has one fitted parameter. Therefore, the adjustment quality of Eq. (10) is compared directly to that of Eq. (8) on the basis of their likelihoods, but the statistical significance of this comparison cannot be tested.

Regarding the second question (selection of the most appropriate functional response), Fig. 1 and Appendix A show how the different functional responses lead to two coupled equations (characteristic for each functional response) that relate D^* , P^* and L to each other. Again, the likelihood combined with Errors-in-Variables was used as an estimate of the quality of the adjustment of each of these systems of coupled equations to the data. Since some of the models to be compared were not nested, the likelihood ratio test could not always be used. Therefore, we compared the likelihoods of the different adjustments on the basis of the Akaike Information Criterion (AIC). The AIC takes into account both the likelihood and the number of fitted parameters p : $AIC = \log(\Lambda) + 2p$ (Hilborn and Mangel 1997). The number of fitted parameters is $p = 3$ for the adjustments of the BDA model (k_0, k_2, k_3) and of the HV model (k_0, k_4, m), and it is $p = 2$ for that of the RD model (k_0 and k_3) and of the Prey-D model (k_0 and k_1). The AIC decreases with increased adjustment quality. It allows the ranking of a series of models according to their adjustment quality and complexity, but does not permit testing to see whether differences in this quality are statistically significant. When the two models with the lowest AIC values were nested, we tested the significance of the difference between their adjustment qualities with a likelihood ratio test.

Results

From the weights of litter (fallen into the eight traps per site), the estimated mean \pm SE annual litterfall values are, respectively, 2.50 ± 0.85 , 2.71 ± 1.07 , 2.85 ± 1.26 , 3.19 ± 0.16 t/ha on the four sites studied in 1995 and 1996, and 3.39 ± 0.88 t/ha on the fifth site studied in 1996.

Fig. 2 shows the seasonal dynamics of detritivore and predator abundances on the five study sites. A common feature seems to be the existence of two main abundance peaks followed by a relative stability in the autumn. This stable period was characterized by low abundances, especially for detritivores. The data of 1995 are generally similar to those found at the same time of the year in 1996. However, the average predator abundances were generally higher in 1995 than in 1996 (Fig. 3). This difference may be due to an overestimation of the 1995 mean predator abundance compared to the 1996 value, since the predator abundances were

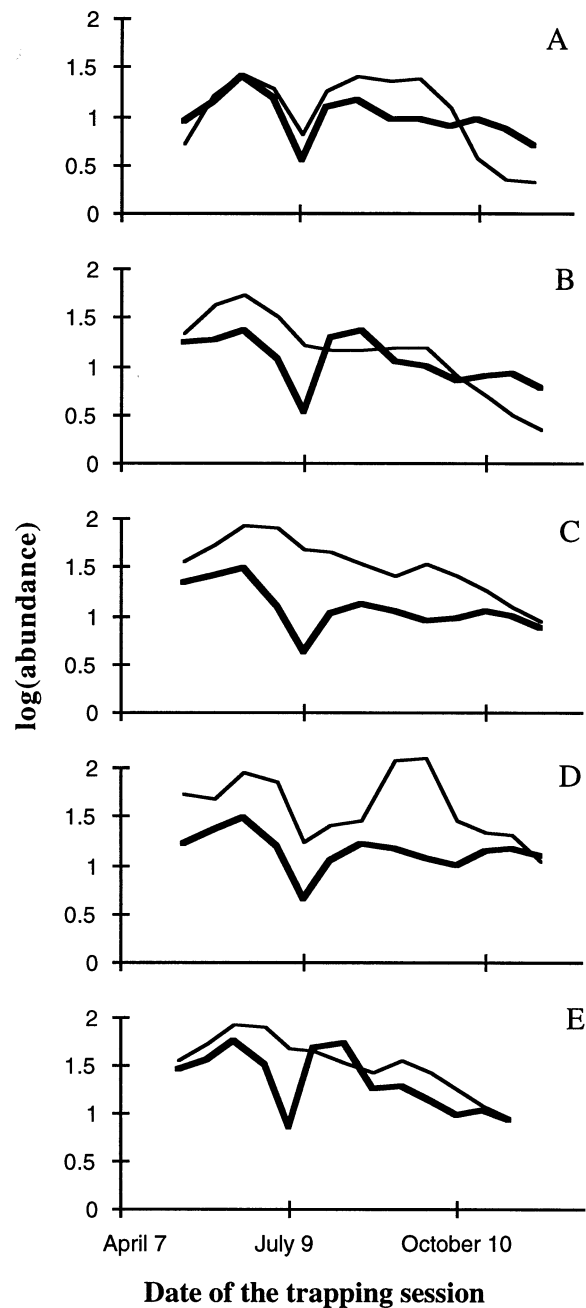


Fig. 2. Seasonal fluctuations of detritivore (thin line) and predator (thick line) abundances on the five study sites (A, B, C, D, E) in 1996. Two-week moving averages of the abundances are plotted against average date of the trapping session.

very low in July 1996 but there was no trapping during the corresponding period in 1995.

For the annual values of both 1995 and 1996, the log-likelihood of the fit was lower for Eq. (8) than for Eq. (10), and the fits of Eqs (11) and (12) were not

significantly better ($P < 0.01$) than that of Eq. (8), meaning that Eq. (8) fitted the data best. In one of the 20 seasonal data sets, the log-likelihood was lower for Eq. (10) than for Eq. (8) and the fit was not significantly better for Eqs (11) and (12). In thirteen cases the log-likelihood was lower for Eq. (8) than for Eq. (10), and the fit of Eqs (11) and (12) was not significantly better than that of Eq. (8). The value estimated for k_0 was always positive, in agreement with the underlying hypotheses of the models. For the six remaining data sets, the log-likelihood was lower for Eq. (8) than for Eq. (10), but the hypothesis of a significantly better fit was accepted for both Eq. (11) and Eq. (12) compared with Eq. (10). In all six cases, the values estimated for n , v and w were positive. This means that P^* and L are positively related, and that the best description of this positive relation is, in general, the simple proportional relation of Eq. (8).

The values obtained for parameters k_1 , k_4 and k_5 obtained by fitting the relationships between L , D^* and P^* predicted by the different models were always positive, in agreement with the predictions. Table 1 shows the estimated values of parameters k_2 , k_3 and m . Estimation of confidence intervals of parameters in non-linear regression is still a subject of debate among statisticians, especially in relatively new techniques such as Errors-in-Variables. We estimated the standard deviation for these parameters by jackknife for the values of 1996 (when there are five data points), and give the estimates for 1995 as indicative values without standard deviation.

In all cases but one, the adjustment of the equations of the BDA model yielded negative values for k_2 and k_3 , which is in contradiction with the assumptions of the model. Only the single compatible case will further be considered. Fig. 4 shows the AIC of the four models. The AIC of the adjustment of the Prey-d model was the lowest in one case out of 20, when all models had AIC values that were very close to each other. This was also the single data set for which the adjustment of the BDA model did not yield parameter values incompatible with the assumptions of the model. In one other case, the RD model yielded the lowest AIC. In all other cases (18 of 20), the AIC of the Prey-d model was the highest, that of the RD model was intermediate, and that of the HV

model was the lowest. The RD and the HV models are nested. Therefore, their adjustment quality can be compared by likelihood ratio tests: in all 18 cases, the adjustment of the HV model was significantly better than that of the RD model ($P < 0.01$). This is also the case for the fits on the annual average values of 1995 and 1996. This means that among the four models considered here, the HV model usually gives the best description of the relation between L , D^* and P^* . In addition, Fig. 3 shows the fit of the HV model to the yearly averages of 1995 and 1996: despite some differences (especially for the predator abundances), the regression curves are almost the same in both years.

The median of the adjusted value of parameter m for the HV model was 6.8, and it was 7.0 and 7.5 for the adjustment of the annual averages of, respectively, 1995 and 1996. This means (Fig. 3) that the typical shape of the relationship between L , D^* and P^* is that predator abundance is directly proportional to annual litterfall, detritivores increase (with an exponent $m > 1$) with annual litterfall and, consequently, predators increase non-linearly (with an exponent $m^{-1} < 1$) with the detritivore abundance. The jackknife estimates of the standard deviation of the estimate of m show that this parameter is significantly greater than 1.

Discussion

Seasonal fluctuations are not due to predator-prey dynamics

Both detritivore and predator abundances appear to fluctuate during the year, showing two periods of relatively high and stationary abundances in the spring and the summer, separated by a sharp fall in early July (a feature also found, e.g., in Ausmus et al. 1976), and ended by a period of high predator abundance and declining detritivore abundance during the autumn. This pattern is reminiscent of the one found in temperate lakes for phytoplankton and zooplankton densities and usually interpreted in terms of predator-prey dynamics (Sommer et al. 1986). However, the seasonal fluctuations observed in the present study are unlikely to reflect a predator-prey dynamics comparable to that

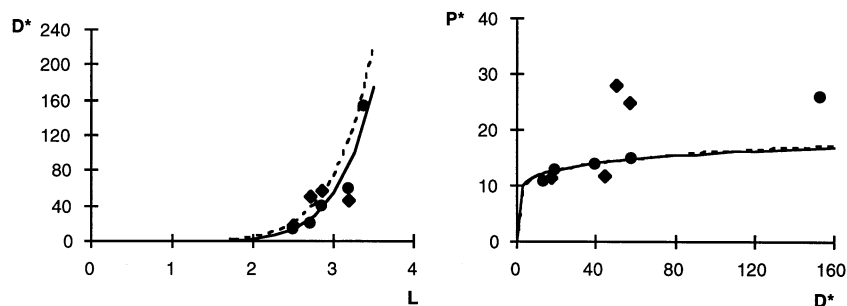


Fig. 3. Adjustments of the best fitting model (HV) to the annual litterfall L and the annual means of detritivore (D^*) and predator (P^*) abundances in 1995 (diamonds and dashed line) and in 1996 (circles and solid line).

Table 1. Estimation of the parameters of the predictions of the BDA and HV models. Parameter values in italics violate the assumptions of the model. k_2 , k_3 and \dot{m} are the values obtained by fitting all the data, \bar{k}_2 , \bar{k}_3 , \bar{m} and their respective SD are the means and standard deviation of the same parameters obtained by jackknife.

	BDA				HV	
	k_2		k_3		m	
	\hat{k}_2	$\bar{k}_2 \pm \text{SD}$	\hat{k}_3	$\bar{k}_3 \pm \text{SD}$	\dot{m}	$\bar{m} \pm \text{SD}$
30/4/95	<i>-14.4</i>		<i>-88.6</i>		6.5	
13/5/5	<i>-8.8</i>		<i>-100.4</i>		5.9	
1/6/95	<i>-11.6</i>		<i>-58.5</i>		3.5	
21/6/95	<i>-15.0</i>		<i>-1134.7</i>		24.1	
5/8/95	79.0		48.7		0.7	
28/9/95	<i>-6.4</i>		<i>-53.2</i>		4.9	
26/10/95	<i>-11.0</i>		<i>-73.0</i>		9.0	
1995 annual values	<i>-11.6</i>		<i>-195.5</i>		7.0	
9/5/96	<i>-13.2</i>	<i>-13.3 ± 2.2</i>	<i>-250.6</i>	<i>-252.5 ± 111.4</i>	6.9	7.0 ± 0.3
24/5/96	<i>-16.6</i>	<i>-16.6 ± 1.5</i>	<i>-244.4</i>	<i>-236.6 ± 59.9</i>	5.4	5.4 ± 0.6
8/6/96	<i>-22.7</i>	<i>-22.2 ± 1.9</i>	<i>-406.6</i>	<i>-372.9 ± 112.3</i>	5.8	5.7 ± 1.1
25/6/96	<i>-13.0</i>	<i>-13.0 ± 0.7</i>	<i>-805.6</i>	<i>-757.7 ± 200.3</i>	8.9	9.2 ± 1.2
9/7/96	<i>-4.0</i>	<i>-4.0 ± 0.2</i>	<i>-367.8</i>	<i>-373.8 ± 44.3</i>	10.1	10.8 ± 3.0
22/7/96	<i>-10.9</i>	<i>-10.9 ± 0.9</i>	<i>-598.2</i>	<i>-550.3 ± 169.4</i>	8.8	9.2 ± 1.2
8/8/96	<i>-13.7</i>	<i>-13.6 ± 1.0</i>	<i>-713.4</i>	<i>-643.5 ± 217.1</i>	8.5	8.5 ± 0.9
25/8/96	<i>-10.4</i>	<i>-10.4 ± 0.3</i>	<i>-527.9</i>	<i>-505.7 ± 83.8</i>	7.6	7.5 ± 0.7
9/9/96	<i>-9.0</i>	<i>-9.1 ± 0.5</i>	<i>-452.5</i>	<i>-427.8 ± 48.1</i>	6.6	6.8 ± 1.0
25/9/96	<i>-7.5</i>	<i>-7.4 ± 0.7</i>	<i>-188.6</i>	<i>-179.9 ± 69.6</i>	6.3	6.1 ± 0.7
9/10/96	<i>-8.3</i>	<i>-8.3 ± 0.4</i>	<i>-86.1</i>	<i>-83.6 ± 22.2</i>	8.4	8.2 ± 1.5
24/10/96	<i>-8.1</i>	<i>-8.1 ± 0.3</i>	<i>-76.1</i>	<i>-75.7 ± 22.7</i>	8.3	8.1 ± 0.7
7/11/96	<i>-5.5</i>	<i>-5.5 ± 0.4</i>	<i>-34.2</i>	<i>-35.2 ± 7.4</i>	6.0	6.0 ± 0.5
1996 annual values	<i>-12.2</i>	<i>-12.1 ± 0.9</i>	<i>-348.5</i>	<i>-339.6 ± 116.9</i>	7.5	7.4 ± 0.4

found in lakes. First, there is no recognizable delay between the changes in detritivore and predator abundances. They appear instead to be synchronized. Second, most species of soil macroinvertebrates have generation times that are much longer (from several months to one or several years) than those of planktonic organisms (several days to several weeks).

At least two factors could account for the seasonal fluctuations among litter macroinvertebrates: activity rates and succession of life-history stages. Activity rates vary with climatic conditions. These are likely to affect both detritivores and predators in a similar way, which could explain their synchronized fluctuations. Drought could explain the general decline in the number of trapped individuals in early July. Cold temperatures probably cause a general decrease in the animals' activity during the autumn. However, only the number of trapped detritivores decreased in autumn, while on most sites the number of trapped predators did not. A high proportion of male spiders was found among them during this period, which could be due to an increased ranging related to their mating activities. The succession of life-history stages can also cause seasonal fluctuations in population indices, even in a stationary population (i.e., with no long-term trend to increase or decrease), especially when reproduction or mortality are strongly synchronized, and when a high number of

juveniles is produced. This can result in seasonal fluctuations in the abundance indices of whole trophic levels if the peaks due to different species tend to occur simultaneously – as is the case, for instance, among carabid beetles that are either spring or autumn breeders (Lövei and Sunderland 1996) – or if some of these peaks are of particularly large amplitude, as is the case, among the detritivores, for isopods.

We therefore assume that the detritivores and predators observed in undisturbed mature forest sites are in an equilibrium, and that the fluctuations we observed were mainly due to variations of the activity rate and to the life-history succession of the different species, rather than to true population dynamics.

Model selection under the assumptions made in this study

Although the gradient of annual litterfall we measured is relatively narrow, it covers nearly half of the 2–4 t/ha range of values usually considered as typical for mature stands of temperate deciduous forests. As emphasized by McQueen and Post (1986), for a given observation error, it is all the less likely to find a significant relation between two variables as the gradient over which they are measured is narrow. However, the abundances of

both detritivores and predators were found to increase with annual litterfall.

For both annual data sets, and in the majority of the seasonal data sets, the increase of predator abundance with annual litterfall was not described better by Eq. (11) or (12) than by the simple proportional relation of Eq. (8). The common prediction of both Prey-d and Pred-d two-level models under the assumption of proportionality between detritivore production and annual litterfall is therefore met.

Regarding the relations between D^* and L and between P^* and D^* , the Pred-d models showed a better adjustment to the data than the Prey-d model for both annual data sets, and in 19 out of 20 seasonal data sets. The abundance of the detritivores and that of the predators were positively correlated among them and with annual litterfall, contrarily to the prediction of the purely Prey-d model. This model must therefore be rejected.

The agreement of the data with the three alternate Pred-d models can be assessed with the help of Table 1 and Fig. 4. Table 1 shows that the estimates of k_2 and k_3 in the BDA model are negative in almost all cases (yearly average values and seasonal data sets), which

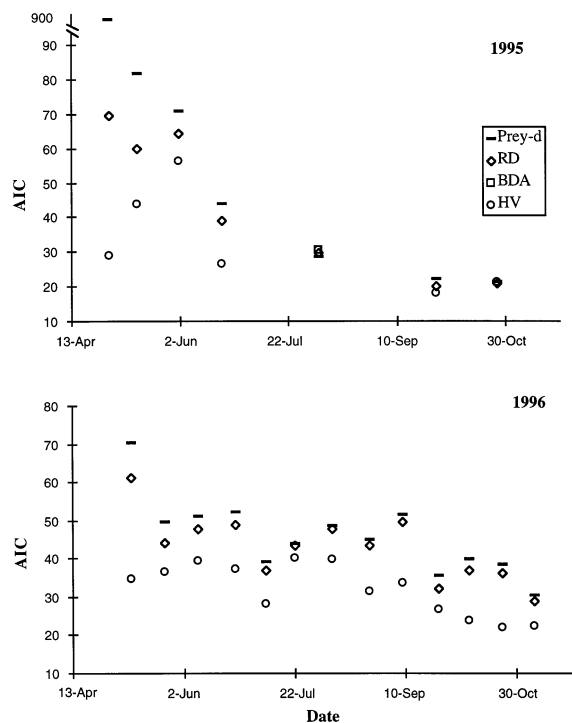


Fig. 4. Quality of the adjustment of the equilibrium predictions of four main models to the data, estimated by the Akaike Information Criterion (AIC). The lower the AIC, the better the adjustment. The BDA model is represented in the single occurrence when the adjustments yielded parameter values compatible with its underlying assumptions (see Table 1). Except in two cases in 1995, the adjustment of the HV model was significantly better than that of the RD model (likelihood ratio test, $P < 0.01$).

violates the assumptions of this model. Parameter k_2 is the negative intercept between P^* and D^* . Parameter k_3 represents the intercept of the relationship between D^* and L , and should be positive for this model to be valid (Fig. 1). The BDA model must therefore be rejected. The two best adjustments to the annual averages were obtained for the HV and the RD models, but the fit of the HV model was significantly better than that of the RD model. Fig. 4 further shows that this trend was consistently observed during the year, despite some fluctuations in the AIC values (i.e., in the adjustment qualities) of all models. For most seasonal data sets, the exponential form of the relationship between equilibrium detritivore abundance and annual litterfall, predicted by the HV model, was the best descriptor of the data, and likelihood ratio tests showed that the difference of adjustment quality of the HV and RD models was highly significant. This means that the additional parameter of the HV model is worth being introduced given the amount of additional accuracy it gives to the predictions. However, the choice of a particular functional response also depends on the purpose of the model. If only qualitative predictions are of interest, one may want to keep the number of parameters of the model low by using the RD functional response. Nevertheless, according to the likelihood ratio test, this will be at the expense of a significant loss in the quantitative accuracy of the predictions.

Although the HV model seems to be the best choice, a striking feature is that we always found the estimated value of m to be much greater than 1. In a two-level trophic chain, m represents the strength of interference between the predators. A value $m > 1$ corresponds to a situation of overcompensation, i.e., a situation in which the share of each predator decreases faster than the number of competitors increases. This is often considered unrealistic in natural conditions. Indeed, the values of m in 24 field and laboratory studies gathered by Hassell (1978) (mainly on host-parasitoid systems) range from 0 to 1.13, those estimated by Arditi and Akçakaya (1990) for 15 predator-prey studies found in the literature range from 0.33 to 1.14 (never significantly greater than 1), and those of field studies of birds preying on mussels are 0.10 and 0.35 (Sutherland and Koene 1982) and 0 to 0.28 (Dolman 1995). Stow et al. (1995) found a substantially larger estimate ($m = 2.8$) in a manipulative experiment on phytoplankton and zooplankton, but they suggested that this could be due to the fact that the zooplankton biomasses in their mesocosms were exceptionally high.

Alternative assumptions

The surprisingly high estimates found for m suggest that it might be necessary to envisage some complications of the model. We have examined the consequences of four main changes to the HV-based food chain

Table 2. Exponents ($\alpha_1, \alpha_2, \alpha_3$) predicted in the relations between P^* , D^* and L (Eq. 13) under the assumptions made in the present study and under four alternative assumptions (a, b, c and d see text).

	Present study	Alternative a	Alternative b	Alternative c	Alternative d
	simple two-level chain	detritivore vulnerability decreases with L: $a = a \cdot L^{-n}$	three-level chain	density-dependent predator mortality $\mu = \mu_0 \cdot P^\beta$	non-proportional production of D with L: $L_N = k_N \cdot L^v$
α_1	m	$m+n$	$1-m_2 \cdot (1-m_1)$	$\frac{\beta+m}{\beta+1}$	$m \cdot (1+v)$
α_2	$\frac{1}{m}$	$\frac{1}{m+n}$	$\frac{1}{\frac{1}{m_2} + m_1 - 1}$	$\frac{1}{\beta+m}$	$\frac{1}{m}$
α_3	1	1	m_2	$\frac{1}{\beta+1}$	$1+v$

model: (a) detritivore vulnerability to predation decreasing with increasing annual litterfall, (b) presence of one or several trophic levels above the invertebrate predators, (c) density-dependent mortality of the invertebrate predators, and (d) non-proportional production of detritivores with the litterfall L .

(a) The vulnerability of detritivores to predation could decrease along the annual litterfall gradient (J. Bengtsson pers. comm.). At least two mechanisms could make such a change possible. First, a higher abundance of predators in the more productive sites might cause a gradual shift of detritivore species composition towards a higher representation of the less vulnerable species. Another possibility would be that the detritivore community composition remains the same, but that individuals need to forage less to get their food in the more productive sites. This lower foraging could make them less vulnerable to predation.

(b) Although their abundances are not known, various vertebrate species that prey on invertebrate predators (blackbirds, shrews, foxes, owls, amphibians, cats, dogs) have been recorded on all the study sites (pers. obs.). These animals are not specialized on preying on soil invertebrate predators: they may also consume detritivorous invertebrates, invertebrates belonging to the grazer food chain, plant material, or even prey on one another. If their influence on the mortality of the invertebrate predators is weak enough, the assumption made in the present study that invertebrate predators are top predators holds in the sense that their mortality is essentially constant, even if they are occasionally preyed upon. However, if the vertebrate predation pressure is strong, and if the abundance of these predators increases with increasing invertebrate abundance, then they have to be taken into account as an additional trophic level. In a food chain longer than two, and in which the functional responses of all trophic levels are

of the HV type but with different interference parameters, the relation between the equilibrium abundances of the first two trophic levels is exponential, as in a two-level chain. However, the exponent of this relationship not only depends on the interference parameter of the second trophic level, but also on those of the levels above. This was shown by Sarnelle (1994) and generalized by McCarthy et al. (1995) for four-level chains. Following this idea, we have calculated the expected relation between P^* , D^* and L if P and D are the first two trophic levels of a three-level chain (see below). (c) In a two-level trophic chain with a Prey-d functional response, Gatto (1991) showed that the equilibrium abundances of the two trophic levels became positively correlated with the input at the bottom of the chain if the mortality of the predator was density dependent. Among litter invertebrates, a density-dependent mortality due to cannibalism has, for instance, been reported for cursorial spiders (Wagner and Wise 1996).

(d) We have also examined the possibility that detritivore production might not be determined by the amount of annual litterfall as such, but by some component of the litter, i.e., nitrogen, which is normally limiting at the plant-animal trophic transition because of the difference of the C:N ratios (Scriber and Slansky 1981). For instance, Vince et al. (1981) applied different levels of nitrogen fertilization to salt marsh plots. They found that both grass and herbivorous insect biomasses increased as a result of fertilization, but that insect responses were greater when not only grass standing crop, but also grass nitrogen content increased, i.e., for the highest fertilization levels.

The relations between L , D^* and P^* predicted under these alternative assumptions are in all four cases of the general form:

$$D^* = A_1 \cdot L^{\alpha_1} \tag{13a}$$

$$P^* = A_2 \cdot D^{*\alpha_2} \quad (13b)$$

$$P^* = A_3 \cdot L^{\alpha_3} \quad (13c)$$

where A_1 , A_2 and A_3 are positive constants given in Appendix C, and the exponents α_1 , α_2 and α_3 are given in Table 2. The coefficients A_1 , A_2 , and A_3 are still linked by a relation that allows estimating only two of them to find the third ($A_3 = A_2 \cdot A_1^{\alpha_2}$).

Alternative (a) appears to be a possible explanation for the relation we found between P^* , D^* and L . It amounts to partitioning parameter α_1 into mutual interference among the predators (m) on one hand, and dependence of detritivore vulnerability to predation on annual litterfall (n) on the other hand. This hypothesis would deserve further investigation. Observing the pattern of equilibrium abundances on a gradient of productivity does not allow estimating m and n separately, and gives no information on how a change in annual litterfall might change detritivore vulnerability to predation. Comparing the detritivore communities in sites of different productivities would allow the examination of the hypothesis of a change in species composition. The taxonomical resolution in our data is not sufficient to make any detailed comparison. However, we did not notice any obvious changes in species composition between the study sites. Behavioral observations testing whether the vulnerability of individuals of a given species decreases with annual litterfall (e.g., because of reduced detritivore foraging, or via any other mechanism) may be a more promising direction for further research.

Regarding alternatives (b), (c) and (d), the exponents are linked by the relation $\alpha_1 \cdot \alpha_2 = \alpha_3$, but α_3 may be different from 1, contrary to our earlier model of Eq. (8). We fitted the relations of Eq. (13) by Errors-in-Variables regression as we did for the earlier models, but since one additional parameter had to be fitted (i.e., four instead of three), we only used the data sets of 1996 (5 sites). The median estimates of the exponents were $\alpha_1 = 9.2$, $\alpha_2 = 0.3$ and $\alpha_3 = 2.4$. A value $\alpha_3 > 1$ tends to discard alternative (b) (see Table 2) because it would mean that $\beta < 0$, i.e., that the mortality of the predators decreases when their abundance increases. In alternative (a), $\alpha_1 > 1$ and $\alpha_3 > 1$ would mean that both parameters of mutual interference, m_1 and m_2 , are higher than 1. A high value of α_3 is compatible with alternative (c). However, the value $\alpha_2 < 1$ would in this case imply that m is still larger than 1. Therefore, none of the three alternatives (b), (c) and (d) can explain the surprisingly high value found for m . The model proposed in Eq. (9), adding a constant mortality rate of the detritivores, cannot explain it either. Indeed, compared to the model in Eq. (2) with a HV functional response, it predicts a faster increase of D^* with L and a slower increase of P^* with D^* for a given value of m because a constant death rate is added to the mortality of the detritivores due to predation (Appendix

C). Therefore, fitting the predictions of this model to our data set would yield even higher estimates for m .

Note also that the data show clear positive relations between P^* , D^* and L . The purely Prey-d models never predict a positive relationship between two consecutive trophic levels, whatever the food chain length (Arditi and Ginzburg 1989). Therefore, the rejection of the purely Prey-d model holds even if macroinvertebrate predators are not top predators. It also holds for alternative (c) and model (9), but alternative (b) would make Prey-d and Pred-d models impossible to distinguish on the basis of the qualitative relation between P^* , D^* and L .

Conclusion

It has been shown that abiotic factors, such as pH, strongly influence the species composition of soil animal communities, which in turn influences the decomposition rate of the litter (e.g., Schaefer 1991). Drought or extreme temperatures can make some of the soil micro- and mesofauna taxa inactive (Whitford 1989). Other authors have emphasized the importance of mutualism, since the soil is a very constraining environment (Lavelle et al. 1995). It could therefore seem that trophic interactions do not play a key role in determining population densities in such systems. This may be true over a large gradient of abiotic factors. However, our study shows that, within a narrow range of variation of these factors, some patterns emerge when trophic interactions are considered between groups defined on trophic criteria.

Neither predator nor detritivore equilibrium abundances were found to be strictly top-down controlled since both increased on a gradient of annual litterfall. Whatever the actual length of the food chain, our results therefore argue for at least some degree of bottom-up control on soil macroinvertebrate abundances. To find the most adequate description of the shape of the relations between the variables, rather than testing the quality of adjustment of a single model chosen a priori, we considered a set of the simplest available food chain models and selected the one showing the best adjustment. The model (2) with a functional response of the HV type agrees well with the data, except that the estimate of the parameter of mutual interference, m , is surprisingly much higher than 1. Additional observations over a wider range of litterfall L would provide a more precise assessment of the relationship between L , D^* and P^* . This might give a lower estimate of m or not. If the high value of m is confirmed, this may suggest that a further addition to the model has to be taken into account. Among the alternative additions that have been considered here, only the hypothesis of a decreasing detritivore vulnerability to predation with increasing annual litterfall yielded a possible estimate of $m < 1$. This hypothesis deserves some further investigation, in particular behavioral studies. Our work does not settle entirely the question of which model of trophic interactions is the

best, but it contributes to setting the question of top-down vs bottom-up control in the soil fauna in terms of simple food chain models.

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Appendix A. Equilibrium responses to productivity

The system is in equilibrium when $dD/dt = 0$ and $dP/dt = 0$. Solving Eq. (2b) for g and plugging the solution into Eq. (2a) yields the relation (8). Thus, any model of structure (2), irrespective of the type of functional response, predicts the top level of a trophic chain to be food limited, and predicts its equilibrium abundance to be directly proportional to the input at the bottom of the chain. For the relation between detritivores (D^*) and both other variables L and P^* , however, the equilibrium predictions of the Prey-d and Pred-d models become different. The equations are given in Fig. 1, and the definitions of the constants k_1 to k_5 in terms of the parameters of the models are the following:

$$\text{Prey-D: } k_1 > 0, \quad \text{such that } g_{\text{Prey-d}}(k_1) = \frac{\mu}{e}$$

$$\text{BDA: } k_2 = \frac{1}{c} \quad \text{and} \quad k_3 = \frac{\mu}{(e - \mu \cdot h) \cdot a}$$

$$\text{HV: } k_4 > 0, \quad \text{such that } g_{\text{HV}}(k_4) = \frac{\mu}{e}, \quad m > 0$$

$$\text{RD: } k_5 > 0, \quad \text{such that } g_{\text{RD}}(k_5) = \frac{\mu}{e}$$

Appendix B. Errors in variables

The functional relationships between the state variables L , D and P that are studied in this paper are of the same type for all four models: two coupled equations that describe two variables as a function of the third (see Appendix A and Fig. 1). McCarthy et al. (1995) drew attention to the fact that the standard least-squares linear regression method, which is widely used to analyze statistical relationships among abundances, is not appropriate because the measurement of both regression variables is subject to error. They recommend the use of “model II” linear regression (Sokal and Rohlf 1995), but this is not appropriate in our case since (1) the relations are not all linear and (2) the measured standard deviations for D^* and P^* were usually correlated with the means (a typical feature of population abundance estimates). Standard log-transformation would not solve the first problem: it linearizes the equilibrium equations for the HV model (Fig. 1), but it cannot be applied to those of the BDA model because of the axis intercepts.

The Errors-in-Variables technique (Reilly and Patino-Leal 1981, Schnute 1994) is similar to a model II regression for general (non-linear) relations. It estimates the likelihood of a model while taking uncertainties in all involved variables into account. In this approach, the values of the regressor variable are considered as unknown parameters that have to be estimated together with all the other parameters. Errors-in-variables was pioneered in ecology by Ludwig and Walters (1981), but the technique has only rarely been used by ecologists since then (e.g., Schnute 1994). We present the technique with the example of the BDA functional response. The relations are

$$P_i = k_2 \left(\frac{D_i}{k_3} - 1 \right) \stackrel{\text{def}}{=} f_1(D_i, k_0, k_2, k_3) = f_1(\theta) \quad (\text{A2.1})$$

$$L_i = \frac{k_2}{k_0} \left(\frac{D_i}{k_3} - 1 \right) \stackrel{\text{def}}{=} f_2(D_i, k_0, k_2, k_3) = f_2(\theta), \quad i \leq i \leq n \quad (\text{A2.2})$$

The standard errors of the measured variables P , D and L are estimated from the replicate measurements and denoted by s_{P_i} , s_{D_i} and s_{L_i} , respectively. For a given value of the parameter vector θ , $\hat{\theta} = (\{\hat{D}_i\}_{1 \leq i \leq n}, \hat{k}_4, \hat{k}_5, \hat{k}_6)$, the likelihood is equal to the product of the probabilities of obtaining the observed state variables given $\hat{\theta}$,

$$\Lambda(\hat{\theta}) = \prod_{i=1}^n \Pr(P_i|\hat{\theta}) \cdot \prod_{i=1}^n \Pr(L_i|\hat{\theta}) \cdot \prod_{i=1}^n \Pr(D_i|\hat{\theta}) \quad (\text{A2.3})$$

Assuming that the error is of Gaussian type, this gives the negative log likelihood (Pavé 1994)

$$\begin{aligned}
\ell(\hat{\theta}) = & -\log \Lambda(\hat{\theta}) = \frac{3}{2} n \log(2\pi) \\
& + \sum_{i=1}^n (\log s_{P_i} + \log s_{L_i} + \log s_{D_i}) \\
& + \frac{1}{2} \sum_{i=1}^n \frac{(P_i - f_1(\hat{\theta}))^2}{s_{P_i}^2} \\
& + \frac{1}{2} \sum_{i=1}^n \frac{(L_i - f_2(\hat{\theta}))^2}{s_{L_i}^2} \\
& + \frac{1}{2} \sum_{i=1}^n \frac{(D_i - \hat{D}_i)^2}{s_{D_i}^2} \quad (\text{A2.4})
\end{aligned}$$

To find the parameters $\hat{\theta}$ that minimize the negative log likelihood, we implemented the function $\ell(\hat{\theta})$ in Mathematica and estimated the parameters and the likelihood with the built-in function "FindMinimum". Initial values of the parameters were estimated by standard linear regression of the individual equations and by a Monte Carlo random search in parameter space in order to detect the global maximum of the likelihood.

Appendix C. Alternative hypotheses in the HV model

Detritivore vulnerability decreasing with productivity
Instead of being a constant, as it has been assumed so far, the vulnerability of detritivores to predation could decrease with increasing annual litterfall. A simple way of representing this in the case of a linear HV functional response is to change constant a , the attack rate, into $a(L) = a \cdot L^{-n}$, with n being a positive constant. In such a case, system (2) becomes:

$$\frac{dD}{dt} = \gamma \cdot L - a \cdot L^{-n} \cdot \frac{D}{P^m} \quad (\text{A3.1a})$$

$$\frac{dP}{dt} = e \cdot a \cdot L^{-n} \cdot \frac{D}{P^m} - \mu \cdot P \quad (\text{A3.1b})$$

The relationships between P^* , D^* and L are of the form (13) with α_1 , α_2 and α_3 as indicated in Table 2 and:

$$A_1 = \left(\frac{e}{\mu}\right)^{m-1} \cdot \frac{\gamma^{m+n}}{a} \quad (\text{A3.1c})$$

$$A_2 = \left[a \cdot \left(\frac{\mu}{e}\right)^{n-1} \right]^{1/(m+n)} \quad (\text{A3.1d})$$

with $A_3 = A_2 \cdot A_1^{\alpha_2}$

Three trophic levels instead of two
Consider a three-level trophic chain:

$$\frac{dD}{dt} = \gamma \cdot L - a_1 \cdot \frac{D}{P^{m_1}} \cdot P \quad (\text{A3.2a})$$

$$\frac{dP}{dt} = e_1 \cdot a_1 \cdot \frac{D}{P^{m_1}} \cdot P - a_2 \cdot \frac{P}{Q^{m_2}} \cdot Q \quad (\text{A3.2b})$$

$$\frac{dQ}{dt} = e_2 \cdot a_2 \cdot \frac{P}{Q^{m_2}} \cdot Q - \mu \cdot Q \quad (\text{A3.2c})$$

where D , P and Q are, respectively, the abundances of the first, second and third trophic level, e_1 and e_2 are the conversion efficiencies of the second and third trophic level, m_1 and m_2 are their parameters of interference, and a_1 and a_2 are positive constants. Solving (A3.1) for zero, the equilibria of D and P are found to be of the form (13) with α_1 , α_2 and α_3 as indicated in Table 2 and:

$$A_1 = \left[\frac{\gamma}{a_1} \cdot k_6^{1/(1-m_1)} \right]^{1-m_2 \cdot (1-m_1)} \quad (\text{A3.2d})$$

$$A_2 = k_6^{1/[1/m_2 - 1 + m_1]} \quad (\text{A3.2e})$$

with

$$k_6 = \frac{e_1 \cdot a_1}{a_2} \cdot \left(\frac{\mu}{e_2 \cdot a_2}\right)^{1/m_2 - 1} \quad \text{and} \quad A_3 = A_2 \cdot A_1^{\alpha_2}.$$

Density-dependent mortality of the predator

We examined how a density-dependent mortality of the predators would affect the predicted equilibria in our system by changing Eq. (2b) to:

$$\frac{dP}{dt} = e \cdot g(D, P) \cdot P - \mu_0 \cdot P^\beta \cdot P \quad (\text{A3.3a})$$

where μ_0 and β are positive constants, while Eq. (2a) remained unchanged. For a functional response of the HV type $g(D, P) = (a \cdot D)/P^m$, the relationships between P^* , D^* and L then become of form (13) with α_1 , α_2 and α_3 as indicated in Table 2 and:

$$A_1 = \left[\left(\frac{\gamma}{a}\right)^{\beta+m} \cdot \left(\frac{e \cdot a}{\mu_0}\right)^{m-1} \right]^{1/(1+\beta)} \quad (\text{A3.3b})$$

$$A_2 = \left[\frac{e \cdot a}{\mu_0} \right]^{1/(\beta+m)} \quad (\text{A3.3c})$$

with $A_3 = A_2 \cdot A_1^{\alpha_2}$.

Non-proportional production of D with L

All the rest being equal, an increased amount of nitrogen available for the trees is likely to cause both the

weight of annual litterfall L and its relative nitrogen content p_N to increase. Therefore, p_N and L could be positively correlated, as for instance, $p_N = k_N \cdot L^v$, where k_N and v are positive constants. In this case, the annual amount of nitrogen falling onto the ground, $L_N = p_N \cdot L = k_N \cdot L^{v+1}$, would increase faster than L and Eq. (2a) should be changed to:

$$\begin{aligned} \frac{dD}{dt} &= \gamma \cdot L_N - g \left(\frac{D}{P^m} \right) \cdot P \\ &= \gamma \cdot k_N \cdot L^{v+1} - g \left(\frac{D}{P^m} \right) \cdot P \end{aligned} \quad (\text{A3.4a})$$

The relationships between P^* , D^* and L are then again of type (13) with α_1 , α_2 and α_3 as in Table 2 and:

$$A_1 = (k_0 \cdot k_N)^m \cdot k_4 \quad (\text{A3.4b})$$

$$A_2 = \left[\frac{1}{k_4} \right]^{1/m} \quad (\text{A3.4c})$$

with $A_3 = A_2 \cdot A_1^{\alpha_2}$.

Addition of a constant detritivore death rate

Replacing Eq. (2a) by Eq. (9) yields the following relations between P^* , D^* and L :

$$L = \frac{d}{\gamma} \cdot D^* + \frac{1}{k_0} \cdot \left(\frac{D^*}{k_5} \right)^{1/m} \quad (\text{A3.5a})$$

$$P^* = \left(\frac{D^*}{k_5} \right)^{1/m} \quad (\text{A3.5b})$$

$$L = \frac{1}{k_0} \cdot P^* + \frac{d}{\gamma} \cdot k_4 \cdot P^{*m} \quad (\text{A3.5c})$$