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Soil organism influence on ecosystem-level processes – bypassing the ecological hierarchy?

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Abstract

We discuss the paradox of the apparent simplicity of ecosystem process control and the high diversity of (soil) organisms. Simple process models usually can predict, e.g., decomposition and nitrogen mineralization, without explicitly including organism biomass, species diversity or abundance dynamics.

Based on these and other observations, we discuss a way of describing ecosystems that is consistent with observations at only two organizational levels (the ecosystem and the organism level). The usefulness of intermediate organizational level is questioned and the ecosystem is compared with a gas container, acting as an 'averaging engine'. We also discuss under which conditions this simple approach may not be sufficient for a valid description of an ecosystem process. © 1999 Elsevier Science B.V.

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1. Introduction

Soil animals exist.
I like soil animals.
They respire too little.
Ergo, they must CONTROL something!

Most soil ecologists, or even most ecologists, sooner or later are faced with the paradox of the apparent simplicity of ecosystem process controls and the bewildering diversity of organisms contributing to these processes. This is clearly illustrated by the success of fairly simple mathematical models, without inclusion of organism interactions or biomass dynamics, in accurately describing, e.g. organic matter turnover at the ecosystem level (Smith et al., 1998; Paustian, 1994; Ågren and Bosatta, 1996).

During the last decades, we have been involved in large integrated projects, to a great extent dealing with the scaling from organism to ecosystem. These projects were: 'The IBP Tundra Biome' (Holding et al., 1974), 'The Swedish Coniferous Forest Project' (Persson, 1980), 'Ecology of Arable Land' (Andrén et al., 1990c) and 'the Dutch Programme on Soil Ecology of

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Arable Farming Systems' (Brussaard, 1994). From this background, we present a conceptual model of the relationships between ecosystem-level process such as organic matter decomposition and the organisms actually performing the various tasks involved. Finally, we discuss how acceptance of this conceptual model would affect our approach to studies of environmental problems such as global change, particularly in tundra ecosystems.

2. Ecosystem views

The organism/ecosystem paradox is related to the 'holist' vs. 'reductionist' perception of ecosystems. 'Holistic' is a very ambiguous term, but here is one interpretation:

> "*A further step in the direction of making pseudo-explanations has been to rationalise them in terms of 'holistic' philosophy. Higher levels of organisation, so goes the argument, have properties which tend to be qualitatively different from the sum of the constituent components. From which should follow that an understanding can and should be obtained in terms of the properties of the intact system...A holistic approach to an alarm clock, I suppose, is to observe that when wound, it will run. To arrive at a real understanding of the device one must take it apart in order to see how it works, or to remain in the jargon, to take a 'reductionist' approach. ...a true understanding of ecological systems can only be achieved in terms of the properties of lower organisational levels*" (Fenchel, 1987 p. 17).

More positive accounts of holistic view of ecosystems can be found: "*It is not necessary to cite the other genuine properties of ecosystems to be convinced that ecosystems are wholes, in the definitional sense proposed by philosophers. We note genuine properties are not exclusively biological. Rather, they involve a mixture of biological and physical-chemical processes in the system... For example, a family can be a whole. It is not merely the sum of its members; it has a historical, genetic, psychological and cultural reality as well*". (Golley, 1993 p. 194). See also Likens (1992) and more comprehensive overviews of the holist/reductionist (or process-functional vs. population-community) debate (Simberloff, 1980; O'Neill et al., 1986, pp. 8–19, McIntosh, 1985; pp. 252–256; Peters, 1991 p. 303–304).

We must admit that 'holism' remains a bit ambiguous to us, and perhaps we have to turn to fiction to find cases where a truly holistic view (defined as a general belief in the interconnectedness of all things) has been successful in getting tangible results (Adams, 1987). Consequently, we will abandon the term 'holistic' and instead use the term 'ecosystem-level approach' in the following.

The reductionist approach, i.e. to take the system apart and rebuild it from the little pieces, is the common one in scientific research, but it is doubtful whether this approach is useful for building an ecosystem-level understanding. How do we construct an ecosystem out of a square meter harbouring 50 000 microorganism species, 50 mite species, 10 enchytraeid species, 1000 insect species, 100 plant species etc. – and a varying number of individuals of each species? And the adjacent square meter, where careful sampling revealed a slightly, but statistically significant, different species composition, is that another ecosystem?

In spite of the dangers in using analogues, conflicting views of ecosystems can be illustrated by comparing a television set with a gas container.

If we believe that the ecosystem is similar to a television set, i.e., that all parts (species or integrated circuits) are interconnected and necessary for the function, we are in the good company of Linnaeus (1760) and ancient Greek metaphysics (Simberloff, 1980), although perhaps a bit outdated. See Oksanen (1988) and Andrén et al. (1995) for further discussion. A reductionist with this view of ecosystems would need to know all species and their development stages, their abundance, size and activity as well as all their interactions to properly describe the system. Every species and perhaps individual has a role, just like a cogwheel in an alarm clock or a resistor in the television set. Experiments with exclusion of organism X will reveal its 'role within the ecosystem', or 'importance for the ecosystem'. If we fail to describe the dynamics of an ecosystem-level process, we attribute this to 'lack of knowledge about property X of organism Y' and quickly conclude that 'more research is needed'. A quick scan of the (soil) ecological literature will reveal that many authors are at least influenced by this view of ecosystems.

The other extreme is to believe that the species and individuals act as gas molecules in a flask – we only measure the *average* pressure and do not deal with the fate of the individual molecules. This analogy can be pushed a bit further – external climatic influence such as a rise in temperature will, regardless of which gas or set of organisms that are contained, increase the activity or pressure. However, different gases of organism combinations will react slightly differently to a temperature increase. Many process-oriented ecosystem ecologists tend to think along these lines when modelling (Smith et al., 1998).

Viewing the ecosystem as a hierarchy may be seen as a compromise between the two extremes. According to this view, there are filters different organisational levels (individuals, species, populations, communities, ecosystem) and only a fraction of the properties at lower levels are transmitted to higher organisational levels (O'Neill et al., 1986; Andrén et al., 1990a; Beare et al., 1995; Parmelee, 1995). Pooling of species into 'guilds', or 'functional groups' or the admission that there are 'keystone species' and redundant species' can also be seen as steps towards a hierarchical approach.

The gas container analogy can be described as a two-level hierarchy – an *organism level* and an *ecosystem level*, where everything, except the responses of the organisms to influences from outside the system, is filtered out. Alternatively, the system can be viewed as a one-level hierarchy – the ecosystem level or gas container are just marking the borders of the system. The ecosystem or the gas flask are just containers of a size decided by humans. However, possibly 'ecosystem' can be replaced by the more objectively defined 'ecotrophic modules', based on the food web of a social group of the top predator species in a location (Cousins, 1990).

The 'gas container' ecosystem analogue, even if we accept it in general, should not be too rigidly interpreted. It is just as wrong to deny that there are patterns where they exist, as it is to find patterns where there are none. There might be cases when species interactions, populations dynamics or even biodiversity have major effects at the ecosystem level.

In this paper, we explore to what extent we have to go down the hierarchy, if at all, in order to gain a predictive understanding of ecosystem functioning, using the gas container analogy as the baseline.

3. Linking the levels

There are two basically different approaches used for linking the levels, i.e. interconnecting the ecosystem level with organism, population, or community levels. First, there is the 'bottom-up' of perhaps reductionistic approach, here called '*Measure and add*' or '*Measure, add and model*'. '*Linking organism/population theory to ecosystem theory*' is also predominantly of the 'bottom-up' approach. Second, there is the 'top-down' approach, here discussed under the heading '*Start from the top, use Occam's razor*'.

3.1. Measure and add

The fully reductionistic or 'bottom-up' approach is seldom used to reach the ecosystem level. One of the reasons is the great amount of work needed; only well-funded integrated projects have been able to approach the goal of measuring 'all the components' and adding them together in the end. There are, however, a few attempts. Some research groups have counted and sometimes weighed organisms, calculated their activity (often using the same energetic quotients, estimated by Heal and McLean (1975)), pooled them into 'functional groups' and, finally, come up with ecosystem-level annual C and/or N budgets or even simple, quantified, food webs (Persson and Lohm, 1977; Persson, 1980; Hendrix et al., 1986; Hunt et al., 1987; Andrén et al., 1990b; Paustian et al., 1990; Lebbink et al., 1994). See Fig. 1 for one example generated by this approach.

3.2. Measure, add and model

Food-web, or organism-oriented, models have been developed, based on the results cited above (Hunt et al., 1984; Rutherford and Juma, 1992a; Rutherford and Juma, 1992b, b; De Ruiter et al., 1994; Moore et al., 1996). See also review by Smith et al. (1998). One can put forward a number of reservations to this approach (Brussaard, 1998):

> First, there is very little known concerning the quality of the organic matter and biomass consumed by the various organisms, and current food web models are sensitive to, e.g. C : N ratio of consumed food. Thus the models are difficult to validate.

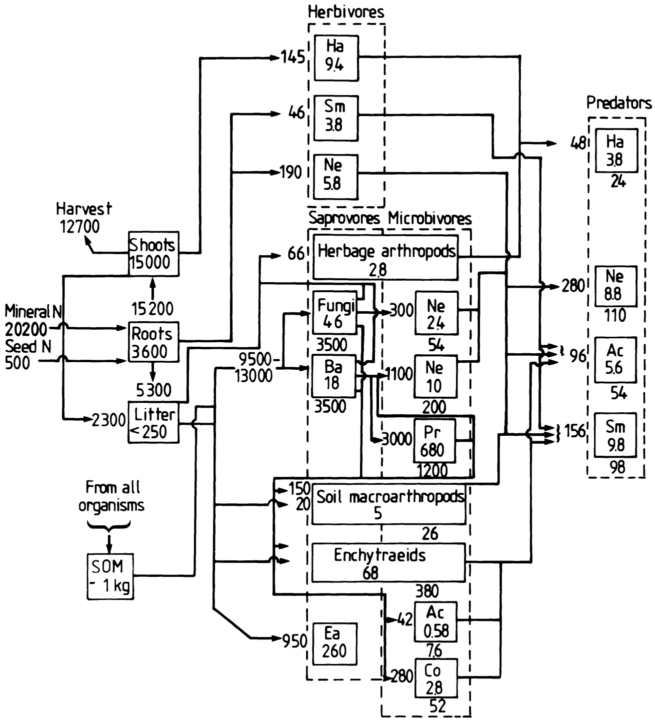

Fig. 1. Nitrogen food web of the Kjettslinge field in central Sweden, exemplified with data from nitrogen-fertilised barley (B120). Values in the boxes indicate biomass nitrogen (mg N m^{-2}); for the plant at harvest, as well as for other organisms, mean values for September 1982–1983 are given. On the left side of each box consumption (mg N m^{-2} yr^{-}) is indicated, calculated using energetic quotients. All biomass values are given for the top soil, 0–27 cm depth. Nitrogen mineralisation is indicated by values under each box. (Bacteria, Ba; Protozoa, Pr; Nematodes, Ne; Herbage arthropods, Ha; Soil macroarthropods, Sm; Acari, Ac; Collembola, Co; Earthworms, Ea). Data partly from Paustian et al. (1990). Nitrogen mineralisation was divided between bacteria and fungi for practical reasons; only the sum (7000) is relevant. (From Andrén et al., 1990b).

Second, why do the food web models perform well when a number of functional groups are neglected (root-feeding insects, plant pathogens, macroinvertebrate decomposers and predators)?

Third, how can the models function without accounting for the different home ranges and spatial restrictions, related to soil structure, for different organisms?

Fourth, many biological interactions in the soil are of a non-trophic nature. For example, an earthworm makes burrows, which affect the living conditions of other organisms. How does a food web model account for this?

Furthermore, the complex food web models have not been tested on a wide range of independent data sets, since such do not exist. One might even argue that they cannot exist, since every complex food web such as Fig. 1 is dependent on subjective large-scale pooling of species and life stages, and a lot of guesswork, especially concerning feeding habits is involved in its construction. Also, food webs will change with changing conditions (Paine, 1988), i.e. the average food web will be different in wet and dry months. For example, the effects of mesofauna on microbial activity can be quite different if the conditions are moist or dry (Persson, 1989; Sulkava et al., 1996). There is also a clear risk that the food webs reflect the competence of the research group more than the actual organism composition, e.g., where nematologists are present, nematodes are included, otherwise not (Andrén et al., 1990b, pp. 118–126). (See also Paine (1988) for a critical discussion on subjectivity in food web theory.)

One may conclude that the food web approach is useful for picturing 'this is what we think about who eats who and how much they eat at a given point in space and time' – but this is quite far below the ecosystem level – typically expressed as amounts processed m^{-2} $year^{-1}$.

3.3. Linking organism/population theory to ecosystem theory

There have been attempts to link the levels using a more theoretical approach, not so much burdened with the need for lots of data of questionable quality (DeAngelis, 1992; O'Neill et al., 1986; Jones and Lawton, 1995; Zheng et al., 1997).

This approach can be described as working out the mathematical consequences of a set of initial assumptions, and would usually fall under the heading 'theoretical ecology'. Theoretical ecology has been very successful in generating scientific papers, but not as successful in explaining phenomena commonly seen in the field. To avoid impossibly complex algebra, the assumptions have to be extremely simple. For example, it is possible to mathematically describe the interactions between one predator population and one prey population. However, most ecosystems are not only composed of, e.g. snowshoe hares and lynx. This creates a major problem of testing the hypotheses on data from real ecosystems – they have too many components and possible interactions to fit into the theory. And there is no reason to expect that there is a sensible way to scale up interaction data from two species in a glass jar in the laboratory to an outdoor ecosystem. Therefore, the linking from bottom (organism) to top (ecosystem) using a mathematical approach seems problematic.

Scaling up from the level above single species, i.e. the functional group level, to the ecosystem level may be more promising. For example, De Ruiter et al. (1995) were able to show that food webs, modelled with interaction strengths among groups based on field data, were more stable than those modelled with random interaction strengths.

There are also a few attempts to discuss the links using both 'top-down' and 'bottom-up' approaches, mainly based on actual observations, e.g., (Andrén et al., 1990a; Anderson, 1995; Bengtsson et al., 1995). The main advantage of starting from observations instead of theory is that the observations do not have to be filtered to fit into a simple, mathematically expressed theory. For example, we do not have to assume that omnivory is rare (Pimm, 1982), or that all species are equal in any respect, to make our algebra palatable. The disadvantages are a high potential for subjective selection of observations as well as for unclear logic.

3.4. Start from the top, use Occam's razor

Occam's razor, invented in the 13th century, is still one of the sharpest tools used in science. It can be described as: "Use the simplest description (or model) that works for your purpose."

Simple models using this approach have been successfully used for predictions of, e.g. decomposition processes. We have a fairly good idea of the process theory, commonly based on *first-order kinetics*, i.e. a constant fraction is lost per time unit:

$$\frac{\mathrm{d}M}{\mathrm{d}t} = -kM \tag{1a}$$

In the integral form, the same equation becomes:

$$\frac{M_t}{M_0} = \mathrm{e}^{-kt} \tag{1b}$$

M_t denotes the remaining mass after time t, k the decomposition constant (the fraction disappearing per time unit), and M_0 the initial mass. This is the familiar 'exponential decay function', which results in a constant proportion of the substrate lost per time unit – but in a diminishing mass lost per time unit, since M, the remaining mass, is decreasing with time. Additional factors are often used, such as rate modifiers based on measured temperature and moisture. Models often include a number of pools (e.g. 'litter' and 'humus'), interconnected in various ways, each with a specific k. Only the simplest models can be analytically solved (as Eq. (1b)) and, therefore, numerical simulation methods are often used (Andrén and Paustian, 1987; Andrén et al., 1990b; Paustian, 1994; Smith et al., 1998).

For example, over 99% of the variance in the rate of decomposition of barley straw in the field during two years could be explained using extremely simple models with daily time steps, including only effects of climate and substrate properties on the rate (Andrén and Paustian, 1987). This was possible in spite of observed fluctuations in faunal species composition and activity (Lagerlöf and Andrén, 1985) as well as microorganism abundance (Andrén et al., 1995).

In general, modelling of soil carbon and nitrogen pools and fluxes using simple models excluding organism dynamics seems to be highly successful. This applies to both models with one year time steps (Smith et al., 1998; Paustian, 1994) describing processes ranging from ca. five to 100 years, and models with one-day time steps, describing a growing season or a few years (De Willigen, 1991).

These simple models are devised according to Occam's razor, and perhaps they can be described as 'holistic' or 'top-down'. All have a few compartments, e.g., litter, humus, etc. and some have a 'soil organism' pool, but this pool is mainly used as a short-term store, particularly for N, and measured organism dynamics are seldom used. There is even one compartmentless approach assuming continuously changing average decomposability (Hyvönen et al., 1996; Ågren and Bosatta, 1996 and papers cited therein).

Several of these models have been successfully applied to a wide range of systems, such as forests, grasslands, arable soils with, and without, organic amendments, fertiliser applications, irrigation, etc. as well as to soils of various types and to very different climates – from hot and dry to cold and wet. It seems that the soil organisms more or less always are there in sufficient numbers and, therefore, have 'a constant attack rate' (Andrén et al., 1988), or, in other words, their activity can be described by simple first-order kinetics (Eqs. (1a) and (1b)).

When we refer to 'simple models', this is only in relative terms. For example, the two-component, five-parameter carbon balance model (ICBM) by Andrén and Kätterer (1997) is one of the simplest models. However, the state equation for the mass of older soil carbon (O) looks like this in integral form:

$$O = h\frac{i}{k_2 r} + \left(O_0 - h\frac{i}{k_2 r} - h\frac{k_1 r Y_0 - i}{r(k_2 - k_1)}\right)\mathrm{e}^{-k_2 r t} + \left(h\frac{k_1 r Y_0 - i}{r(k_2 - k_1)}\right)\mathrm{e}^{-k_1 r t}$$

where h is the humification coefficient, i the annual C input, k_1 and k_2 the decomposition constants, t the time and r a factor summarising external influence.

This level of complexity seems to be enough to deter, frighten, or alternatively impress most ecologists. It may also be questioned if ecosystem processes really can be governed by so complex functions – and, in this case, the starting point was a serious attempt to minimise complexity.

A large part of the theoretical and basic experimental background, e.g. for decomposition modelling is not of a recent origin (Tenney and Waksman, 1929 Jenny et al., 1949; Holding et al., 1974; Flanagan and Bunnell, 1975), and recent advances may be more due to the rapid development of computers and hard work in the laboratory and in the field, producing data, than to new theoretical insights.

4. A conceptual model of organism–ecosystem process relations

In the following, we will present the process modeller's view of the ecosystem and explore under which circumstances and to what extent explicit knowledge about organisms is useful for understanding ecosystem processes. In developing our argument, we will use the following, admittedly subjectively chosen, observations and conclusions as building blocks:

4.1. A. Homo sapiens' properties

We humans are unfortunately pre-programmed to recognise patterns such as species, and it comes very naturally to us to consider them as building blocks, e.g. for ecosystems O'Neill et al., 1986, p. 9; Weiss, 1971). In fact, it is possible that every organisational level above the organism level is mostly a consequence of human pre-programming. The view of an ecosystem as an intricate machine has also been supported by the niche theory; 'filling holes in the niche space'. The fact that the niche theory hardly survives a comparison with the real world (Siepel, 1994, pp. 117–120) has, however, reduced its popularity.

Randomness also seems to be counter-intuitive to us – we have to *learn* that after ten tosses of a coin, yielding only 'tails', there is still exactly 50% chance of a 'tail' coming up the next time.

4.2. B. Where do we find too low biodiversity?

It is very uncommon when walking through a landscape to see a spot where the biodiversity is so low that the ecosystem processes do not function properly, without there being an abiotic reason for it. For example, if we see a big boulder in a pine forest, the reason for lack of pine growth on it is not to be found in population dynamics, the food web theory or niche theory – it is simply so that pines do not grow well on bare rocks.

Abiotic factors, such as climate or soil parent material are the major determinants of ecosystem composition and function. Even in agroecosystems with fairly large differences between treatments (e.g. long-term grassland vs. annually ploughed barley) climate and soil type can overshadow the treatment effects (Andrén and Lagerlöf, 1983).

The biological factors, such as species present and their interactions may be overrated by ecologists - who usually have their main interest and training in biology (see also Section 4.1). However, there are critical biological feedbacks to the abiotic world – and they may shape the ecosystem as we see it (Lavelle et al., 1993; Brussaard, 1998). The challenge is to identify these feedbacks and to assess whether and how we need to address those in ecosystem models.

4.3. C. Simple ecosystem-level models work well, but need some knowledge about the organism

It is generally possible to model ecosystem-level processes, such as carbon and nitrogen mineralisation, without explicitly including the organisms that perform them (Paustian, 1994; Smith et al., 1998). However, the structure of the models as well as the parameter values are based on information from the organism level. The functions used in ecosystem process models for predicting responses to, e.g. changes in temperature and moisture are almost exclusively derived from biological response data, such as measurements of microorganism and faunal respiration under a given set of conditions.

4.4. D. Complex bottom-up models are unsuccessful

Studying the population dynamics of a great number of species and trying to add up their activities to ecosystem levels has resulted in comprehensive static budgets, but little or no dynamic models comprising details at organism or community level (Persson, 1980; Paustian et al., 1990; Andrén et al., 1990c; Brussaard, 1994).

4.5. E. Evolution cannot produce ecosystem 'superorganisms'

Is there any way evolution could have produced 'television set ecosystems', where thousands of species all are dependent on one another? Every species has been created by recombination, some part mutation, isolation, selection – and then the constancy of the genetic setup maintains the species for some time. Species are fairly easily developed; we have many millions at present. There are usually a high number of species competing for more or less the same resources and most of them seem to be redundant (Walker, 1992; Lawton and Brown, 1993; Andrén et al., 1995). Species come and go and, in general, the ecosystem processes maintain their rates. Evolutionary ecologists have shown that ideas among ecosystem ecologists that 'the ecosystem is an organism' just do not hold (Dawkins, 1976; Oksanen, 1988). However, this does not mean that ecosystems are entirely random assemblages of species. For example, soil fauna in temperate forests can show a high degree of constancy over 20-year periods (Bengtsson, 1994), which indicates that a fairly stable soil faunal community can exist under stable conditions.

The ecosystem seen in this way becomes fairly simple, typical for the ecosystem view expressed in, e.g. models of soil organic matter (SOM) turnover. The modeller's ecosystem proposed in Fig. 2 indicates that, as a general rule, the influence of external, abiotic factors is the major determinant. More precisely, the biological responses to these factors are crucial for the ecosystem processes, e.g. the temperature response in organisms active in litter decomposition. The temperature and moisture control of an ecosystem process is almost exclusively indirect, affecting the organism activity which, in turn, affects the ecosystem process, e.g. SOM decomposition. The abiotic controls also directly affect the chemical reactions catalysed by the endo- and exoenzymes produced by the organisms. Thus, even simple ecosystem models have to be based in biological knowledge, and if our knowledge about the biology changes, the model parameter values or even the model structure may have to be changed (Smith et al., 1998).

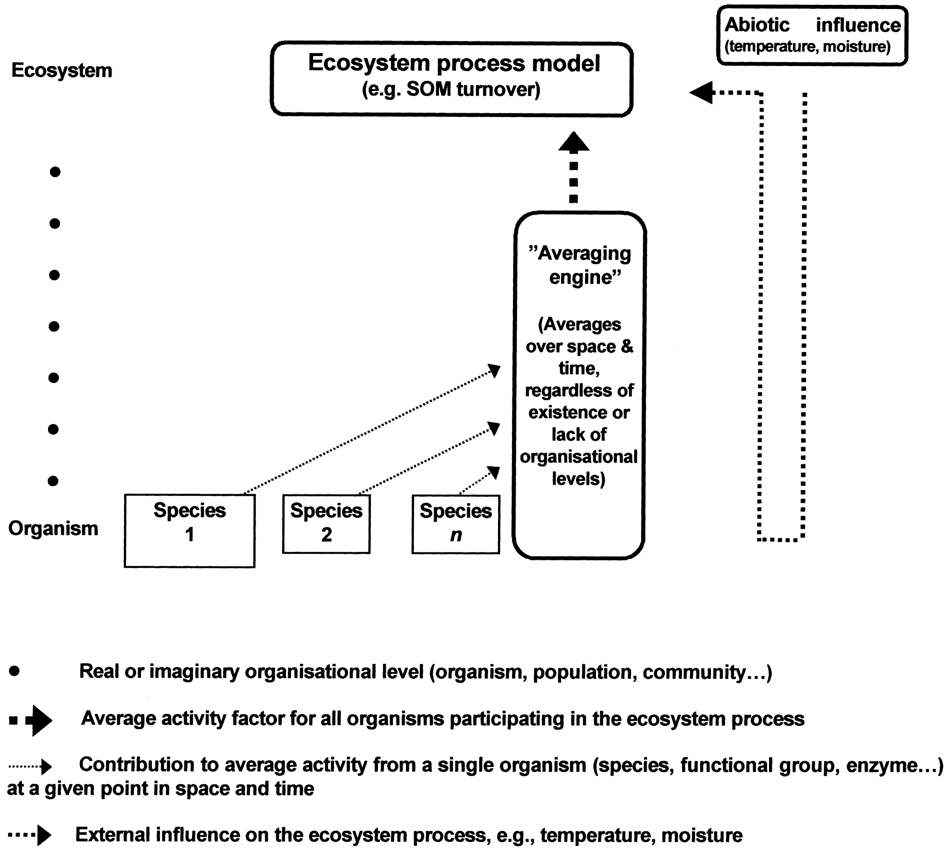

Fig. 2. A process modeller's view of the ecosystem. Only the components and information/control flows necessary for explaining (or at least modelling) an ecosystem process are indicated. Two organisational levels are indicated: ecosystem and organism levels. The organism level is normally not included in the model – only through the 'average engine' which averages organism activity, e.g. serves the ecosystem process with the total activity of litter decomposers. Abiotic influences control the process rates of the model, but the actual responses to these influences are dependent on the organisms actually present.

The intermediate levels (population, community, 'guilds', 'functional groups') can, if they really exist at all, affect the process details, but the process modeller's approach is that there are more than enough organisms present, and the sum (or average) of their activities is what matters.

The 'averaging engine', handling all the random events and serving the ecosystem process an overall average of organism activities works both for spatial and temporal reasons (O'Neill et al., 1986; Patten et al., 1990) and this is why the simple models work so well. This device is, partly for reasons given under Section 4.1, only little investigated and understood. There may even be cases when the averaging does not work, if all patches comprising a number of organisms in a square metre or hectare were to become synchronised in both space and time (Anderson, 1995). We strongly suggest more research in this area.

At this point the question comes up: What would be reasonable modifications to the model, i.e. what other biological information do we need to incorporate to allow for the fact that the system may enter into a different state under conditions of change? The different state may be due either to the extinction or colonisation of organisms. We propose (but see Section 4.1) that the following questions are crucial:

1. Which species are keystone species, i.e. they affect process rates disproportionately to their numbers and/or biomass, e.g. ecosystem engineers

sensu Jones et al. (1994) such as earthworms?

2. Are there groups of species with similar functions ('functional groups') that are species-poor, i.e. constituting a high risk of ecosystem-level change following extinction?
3. Are there entire functional groups with low dispersal abilities, i.e. with low capacity for recolonisation after extinction, or immigration after creation of new, favourable conditions?
4. Are there 'narrow-physiology' microorganisms that exert crucial steps in biological processes, which may affect ecosystem functioning after extinction or colonisation following change? Examples may be basidiomycete fungi that decompose lignin; nitrifying bacteria that convert ammonium into nitrate, which is prone to leaching and/or favours denitrifying bacteria that produce the greenhouse gas N_2O, or methanogenic bacteria that produce the greenhouse gas CH_4.
5. Are there interactions, such as predation, root herbivory or mutualisms like mycorrhizae/trees and rhizobia/legumes, that exert controls on ecosystem functioning that may vanish or appear under conditions of change?

These questions can be discussed in reference to Fig. 2. The box marked 'Species 1' can be assumed to be the keystone species (Question 1), and perhaps the other species can be ignored. However, if presence or absence of keystone species, functional groups 'narrow-physiology' microorganisms is critical for ecosystem function, then the model may need major modifications. Smith et al. (1998) pointed out that there may even be feedbacks between climate change and organism activity. For example, if climate cooling changed the decomposer community to a higher degree of cryotolerance, this would mean that the changed response to temperature would have to be included for successful modelling. This would need a model far more complex than that shown in Fig. 2. However, instead of including the factors that induce a higher level of cryotolerance into the ecosystem-level, it would most likely be sufficient to simply switch parameter settings of the simple model when conditions change.

If the answer is yes to Question 5 above, concerning interactions between species that are crucial for ecosystem-level processes and may change when external conditions change, the simple model will probably have to be abandoned. The question is: how often is this necessary?

There is not much room for 'the importance of high biodiversity' per se in this ecosystem model (Fig. 2). This is contrary to some of the current ideas and, particularly, funding opportunities. Fairly recent experiments have produced results that may be interpreted as effects of biodiversity per se (e.g., Naeem et al., 1994; Tilman, 1996), although other interpretations are possible (Huston, 1997). The hypothesis that biodiversity per se affects ecosystem functioning has not yet been rigorously and fully tested (Naeem et al., 1994), but there is a growing mass of evidence indicating that this hypothesis may not stand up to the test (Andrén et al., 1995; Grime, 1997 and references cited therein).

The approach here, using Occam's razor for describing an ecosystem-level process such as SOM turnover, is intentionally kept very narrow. Other approaches should be used depending on the questions asked – in other words, we do not claim that soil zoology/microbiology or population dynamics studies should be abandoned. We only question how tightly these subjects can be linked to ecosystem-level processes.

Now, what would the consequences be of this view of the ecosystem for our studies effects of global change on tundra soil biology? The problem with tundra is not that it lacks highly productive species – the problem is the present climate, and perhaps also a low ability to change to another state of functioning associated with climate change. Clearly, a major effort should be put into studies of ecosystem process (e.g. primary production and SOM turnover) responses to global change, e.g. changes in temperature and moisture. However, there is also a need for studies of the response of individual species, since the organisms actually do the work. Particularly in tundra, with its comparatively low number of species, often living at the extreme end of their tolerance range, autecological studies of individual species response to climate change become crucial. In other words, the 'averaging engine' may not work so well in tundra. Therefore, we should not only include measurements of the organism activity responses to, for instance, temperature change, but also studies of their general biology. The emphasis should be on species (groups) selected according to questions 1–5 above.

Finally, regardless of ecosystem view, there are a number of questions that are central to studies of global change or, more generally, the effects of human activities on ecosystems. Perhaps the most central one is: What do we fear? The answer to this question should be as honest as possible – and often the fear is more related to ourselves than to Nature. If we like the tundra the way it is and want to keep it that way, we should say so – it is not necessary to prove that the entire planet is in danger (which is not impossible) if we have induced detectable changes in the tundra. For further discussion and a list of relevant questions, see Reynolds and Tenhunen (1996), p. 15. They propose a general strategy for studying anthropogenic influences on tundra landscapes, based on descriptions of disturbance, response, recovery and uncertainty.

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