Trophic interactions in a changing world: modelling aboveground–belowground interactions

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Abstract
The rate and scale of human-driven changes can exert profound impacts on ecosystems, the species that make them up and the services they provide that sustain humanity. Given the speed at which these changes are occurring, one of society's major challenges is to coexist within ecosystems and to manage ecosystem services in a sustainable way. The effect of possible scenarios of global change on ecosystem services can be explored using ecosystem models. Such models should adequately represent ecosystem processes above and below the soil surface (aboveground and belowground) and the interactions between them. We explore possibilities to include such interactions into ecosystem models at scales that range from global to local. At the regional to global scale we suggest to expand the plant functional type concept (aggregating plants into groups according to their physiological attributes) to include functional types of aboveground–belowground interactions. At the scale of discrete plant communities, process-based and organism-oriented models could be combined into "hybrid approaches" that include organism-oriented mechanistic representation of a limited number of trophic interactions in an

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otherwise process-oriented approach. Under global change the density and activity of organisms determining the processes may change non-linearly and therefore explicit knowledge of the organisms and their responses should ideally be included. At the individual plant scale a common organism-based conceptual model of above-ground–belowground interactions has emerged. This conceptual model facilitates the formulation of research questions to guide experiments aiming to identify patterns that are common within, but differ between, ecosystem types and biomes. Such experiments inform modelling approaches at larger scales. Future ecosystem models should better include this evolving knowledge of common patterns of aboveground–belowground interactions. Improved ecosystem models are necessary tools to reduce the uncertainty in the information that assists us in the sustainable management of our environment in a changing world.

Zusammenfassung

Rate und Ausmaß menschen-gemachter Veränderungen wirken sich auf Ökosysteme, die Arten die diese zusammensetzen und Ökosystemfunktionen von denen die Menschheit abhängt aus. Angesichts der Geschwindigkeit dieser Veränderungen ist es eine der großen Herausforderungen der Gesellschaft miteinander und in Ökosystemen zu leben und deren Ökosystemfunktionen nachhaltig zu nutzen. Die Auswirkungen plausibler Szenarien des Globalen Wandels auf Ökosystemfunktionen können mit Hilfe von Ökosystemmodellen untersucht werden. Solche Modelle sollten die Ökosystemprozesse oberhalb und unterhalb der Erdoberfläche („oberirdisch und unterirdisch") und die Interaktionen zwischen diesen Prozessen angemessen abbilden. Auf Skalenebenen, die von global bis lokal reichen, erkunden wir in diesem Artikel Möglichkeiten solche Interaktionen in Modelle einzubauen. Auf der regionalen bis globalen Ebene schlagen wir vor das Konzept der funktionellen Pflanzentypen (Pflanzenarten, die aufgrund von physiologischen Ähnlichkeiten in Gruppen zusammengefasst sind) auszudehnen, so dass Typen von oberirdisch-unterirdischen Interaktionen mitenthalten sind. Auf der Skalenebene eigenständiger Pflanzengesellschaften könnten prozessbasierte und organsimen-orientierte Modelle zu „Hybridmodellen" verschmolzen werden, die organismen-orientierte, mechanistische Abbildungen einiger trophischer Interaktionen enthalten, aber ansonsten prozessbasiert sind. Der Einfluss des Globalen Wandels auf die Häufigkeit und Aktivität von Organismen und die Ökosystemprozesse, die sie bestimmen, ist sehr wahrscheinlich häufig nicht-linear, so dass im Idealfall explizites Wissen über die Organismen und ihre Reaktionen in Modellen enthalten sein sollte. Auf der Skalenebene der einzelnen Pflanze hat sich ein gebräuchliches, organismen-basiertes Konzeptmodell der oberirdisch-unterirdisch Interaktionen herausgebildet. Dies erleichtert die Formulierung von Hypothesen und Fragestellungen in Experimenten, die nach gemeinsamen Mustern innerhalb von Ökosystemen und Unterschieden zwischen Ökosystemtypen und Biomen suchen. Dies ist die Basis für Modellierungsansätze auf größeren Skalenebenen. Zukünftige Ökosystemmodelle sollten die gemeinsamen Muster oberirdisch-unterirdischer Interaktionen besser berücksichtigen, die sich neuerdings abzuzeichnen beginnen. Verbesserte Ökosystemmodelle sind notwendige Werkzeuge um die Unsicherheit in der Information zu vermindern, auf der nachhaltiges Umweltmanagement in einer sich wandelnden Welt beruht.

Introduction

This paper deals with a traditional bias in ecosystem models: the long history of regarding above- and belowground systems as separate entities that have little to do with each other. This view is surprising, given that plants cross the "border" between above- and belowground by living in both spheres simultaneously. Some heterotrophic organisms inhabit these spheres in different life-stages (e.g. many Coleoptera and Diptera species) or dwell in both as adults (e.g. most ant (Hymenoptera) and termite (Isoptera) species). A growing number of observational and experimental studies reveal the importance of interactions between above- and belowground organisms (Wardle, 2002; Moore, McCann, Setälä, & De Ruiter, 2003; Wardle et al., 2004). For example, nutrient and energy

transfers are influenced through effects of aboveground herbivory on belowground processes (Gange, Bower, & Brown, 2002), root herbivores may increase aboveground flower visitation (Poveda, Steffan-Deventer, Scheu, & Tscharntke, 2003) or change aboveground secondary defense metabolites (Bezemer, Wagenaar, Van Dam, & Wäckers, 2003; Hol, Machel, Van Veen, & Van der Meijden, 2004), symbionts such as mycorrhiza act as essential mediators of nutrients and consumers of energy (Lindahl, Taylor, & Finlay, 2002), and soil fauna can affect the composition of aboveground vegetation (Wall & Moore, 1999; De Deyn et al., 2003).

Anthropogenic global changes influence both subsystems and their interactions in several ways (Swift et al., 1998; Wolters et al., 2000). Recent reviews summarise observations of global change effects in a wide range of ecosystems and at various scales. Some reviews concentrate on climatic changes (Parmesan & Yohe, 2003; Root et al., 2003) while others include a variety of global change drivers, such as land use, climate, nitrogen deposition, biotic exchange and atmospheric carbon dioxide concentration (Smith, Tilman, & Nekola, 1999; Sala et al., 2000; Wall, Adams, & Parsons, 2001). There is evidence that global changes are affecting the phenology of plants and animals (e.g. bud break of trees, flowering period of plants, spring arrival of birds), their species ranges and distribution, and the composition and dynamics of communities (Stenseth et al., 2002; Walther et al., 2002).

One of society's challenges is to manage ecosystem services in a sustainable way. Therefore, one of the central questions about the magnitude of global changes is: Do they threaten the provision of ecosystem services that sustain and fulfil our lives? Taking this ecosystem service perspective on ecosystems is an approach that is directly relevant to our human perspective (Alcamo et al., 2003). It stresses that humans depend on ecosystem services, such as clean water and food production, and leaves room to express our need for services that appear less essential in the short term, e.g., biodiversity values or recreational opportunities in a landscape.

Models are both organisational and predictive tools that can be used to better understand the current and future effects of global change on ecosystem services. However, most models used to assess global change focus on aboveground interactions giving marginal consideration to belowground interactions, let alone the synergies that arise from the coupling of the two. Aboveground–belowground interactions should be included in ecosystem models that serve as tools to study

global change impacts whenever such interactions significantly influence the ecosystem service of interest. For example, limited representation of soil–plant interactions in dynamic global vegetation models (DGVMs) leads to considerable uncertainty in estimates of the terrestrial carbon balance at the regional to global scale (Dufresne et al., 2002). We use the term *ecosystem model* for a formalised attempt to describe an ecosystem — a model is any kind of stringent, internally consistent concept. Models can be viewed as complex hypotheses about the structure and operation of a system (Kowal, 1971 in Hunt & Parton, 1986). In some cases, models are developed into a numerical representation which allows for computational processing based on time series data. In global change impact assessments such as the global Millennium Ecosystem, Assessment[1] and the European project ATEAM[2] the role of numerical ecosystem modelling is the projection of future states of the system.

In this paper we explore possibilities to include above- and belowground interactions into terrestrial ecosystem models at three partly overlapping scales, i.e. the scale of regions, biomes or the biosphere (scale 1), the scale of discrete plant communities and landscapes (scale 2), and the scale of the individual plant (scale 3). All three scales have been shown to be relevant for understanding aboveground–belowground linkages (Ettema & Wardle, 2002). Plants are central to these scale definitions for three reasons. First, plants are the source of energy for all other organisms and processes through net primary production (NPP) (with the exception of a few chemo-autotrophic microorganisms). Second, plants connect the aboveground and belowground. Third, landscapes and biomes are usually defined by macroscopic vegetation cover. We will concentrate on trophic interactions, although some reference to indirect interactions (i.e. interactions which affect organisms, ecosystem properties or processes through other organisms, ecosystem properties or processes) is made. We hypothesise that there are common patterns of aboveground–belowground interactions that involve the same functional groups of organisms. However, the weights and strengths of the interactions will differ according to ecosystem type. We describe common features,

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[1]Millennium Ecosystem Assessment (see Alcamo et al., 2003), www.millenniumassessment.org.

[2]ATEAM — Advanced Terrestrial Ecosystem Analysis and Modelling. ATEAM applies a framework of large-scale ecosystem models to project processes across Europe at one of the smallest scales so far tackled in global change studies (grid resolution $10' \times 10'$). The project is funded under FP5 of the EU, No. EVK2-2000-00075, www.pik-potsdam.de/ateam.

Table 1. Scales, ecosystem services and processes typically modelled at specific scales

Scale	Ecosystem service	Modelled ecosystem state or process
Regions, biomes, the biosphere	Climate protection	Carbon storage in vegetation and soil, net fluxes
	Landscape diversity maintenance	Vegetation structure
		Biome distribution
Discrete plant communities, landscapes	Crop and timber yield	Primary production
	Soil fertility maintenance	Litter production
	Species diversity maintenance	Net nutrient fluxes
	Water storage and purification	Net carbon fluxes
		Number of species
		Water runoff
Individual plants	Stress resistance	Nutrient uptake
	Pollination	Nutrient content of the plants
		Plant production
		Water stress resistance
		Pest resistance

demands and research aims of current conceptual as well as numerical ecosystem models that (1) include or could include aboveground–belowground interactions, and (2) could be used to increase our understanding of global change effects on ecosystems and the services that they provide. We will begin with the largest scale and then work our way down to the smaller scales, exploring which added (biological) detail may improve the performance of a model. We then consider the relevance of anticipated effects of global change on aboveground–belowground interactions for future investigations. Finally, we discuss difficulties in modelling ecosystems and characterise potential research and communication needs to solve them.

Ecosystem models at the regional, biome and global scale (biosphere)

Ecosystem models at the landscape, regional and global scale are process-orientated and naturally require substantial simplification. The current generation of ecosystem models at this scale are the DGVMs, designed to simulate transient changes in vegetation structure and ecosystem processes (Cramer, 2002). DGVMs are based on equilibrium models of biome distribution (e.g. Prentice et al., 1992), equilibrium models of biogeochemical fluxes (e.g. Raich et al., 1991) and combinations of both (e.g. Woodward, Smith, & Emanuel, 1995; Haxeltine & Prentice, 1996). DGVMs run globally or at smaller scales at the resolution of the input data (e.g. climate and soil texture data), typically at the

$0.5° \times 0.5°$ longitude/latitude grid scale (TEM: Raich et al., 1991; LPJ: Sitch et al., 2003)[3]. At this scale detailed representations of ecosystem processes in DGVMs are superfluous and models often work well without even considering heterotrophic organisms (Cramer et al., 2001). Plants are represented in the models by plant functional types, defined by physiological attributes (e.g. BIOME: Prentice et al., 1992; FORSKA: Prentice, Sykes, & Cramer, 1993; LPJ: Sitch et al., 2003). At large spatial and long time scales DGVMs successfully quantify and project terrestrial vegetation structure (in terms of plant functional type distribution) and processes (Cramer et al., 2001), such as net biome exchange, the resulting carbon flux from NPP and carbon losses due to soil heterotrophic respiration, fire, harvesting, and land use change. The ecosystem services linked to vegetation structure and net biome exchange include, for example, landscape diversity maintenance and climate protection (Table 1).

The representation of above- and belowground interactions in DGVMs is limited to a function describing the amount of primary production that is transferred to the belowground system as biomass to the root system or as litter input to the soil, and fluxes of nutrients and water from the belowground to the plant. Belowground processes are described as decomposition of different soil

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[3]The Raich et al. (1991) terrestrial ecosystem model (TEM) is sometimes not considered to be a DGVM, since it does not directly simulate vegetation dynamics. However, the model represents dynamic soil processes such as nutrient fluxes, and is therefore included in this discussion.

organic carbon (SOC) pools (usually partitioned by recalcitrance). Carbon fluxes due to decomposition are captured by a decay function following first-order kinetics using fixed parameters that depend on soil moisture and temperature (e.g. LPJ: Sitch et al., 2003). A few DGVMs contain a representation of the nutrient cycle (e.g. TEM: Raich et al., 1991; HYBRID: Friend, Stevens, Knox, & Cannell, 1997; SDGV: Woodward, Lomas, & Betts, 1998) and therefore capture feedbacks to primary production via the nutrients that are released during decomposition.

The uncertainty in current estimates of global carbon and nitrogen fluxes to a large extent results from our limited understanding of the soil and the decomposition processes mediated by the soil organisms (Dufresne et al., 2002). Improving DGVMs by better representing above- and belowground interactions needs to start with a better description of decomposition and its feedbacks to aboveground dynamics. Currently, decomposition of litter produced by different plant functional types is described using an equation with one fixed set of parameters, independent of the environmental context. However, the description of decomposition and nutrient cycling should acknowledge the importance of biological, physical, and chemical traits of the soil and the interactions with the aboveground subsystem. A first step might link plant functional types (PFTs) to specific functional groups of belowground organisms involved in major aboveground–belowground interactions, such as for example symbiotic fungi. A new set of functional types could emerge: aboveground and belowground functional types (ABFTs). For example, plant species with traits associated with fertile, intermediate and infertile habitats have already been shown to support mainly arbuscular, ecto- and ericoid mycorrhizal fungi, respectively (Cornelissen, Aerts, Cerabolini, Werger, & Van Der Heijden, 2002). If this were widespread, then the associations between plant functional types and belowground symbionts could be merged into a limited number of ABFTs. These ABFTs could be linked to biogeophysical conditions, such as specific combinations of soil fertility, soil texture, climate and plant functional type. Model representation of decomposition and nutrient fluxes linked to these ABFTs could then be refined by ABFT-specific parameters, thereby implicitly including belowground organisms. This approach parallels the approach adopted for the modelling of aboveground processes in global vegetation models. NPP was initially described by a simple regression model linking NPP to temperature and precipitation. This single monotonous equation developed

by Lieth (1975) was the first global equilibrium biogeochemical flux model (Cramer, 2002). Since then this flux model has been refined by explicit numerical descriptions of aboveground processes using the concept of plant functional types and plant compartments (e.g. canopy, stem, roots, etc.). Process description of aboveground–belowground dynamics within DGVMs (i.e. through ABFTs and more belowground carbon pools) could substantially reduce the uncertainty in current global carbon and nitrogen fluxes.

Numerical models at the scale of discrete plant communities and landscapes

Just as at larger scales, most models at the scale of discrete plant communities are process-oriented and include little or no detail on specific organisms (Smith et al., 1998). In fact, the distinction between the two scales in process-oriented modelling is smooth and depends on the goals of the application and the availability of the input datasets. Models that tend to be applied at community scale are plugged into DGVMs to be used at regional to global scale, representing a certain compartment. For example, the CENTURY model (Parton, Stewart, & Cole, 1988) is used to describe soil processes in the DGVMs HYBRID (Friend et al., 1997) and SDGVM (Woodward et al., 1998).

Process-oriented models such as CENTURY (Parton et al., 1988), SOMM (Chertov & Komarov, 1997) or SUNDIAL (Smith, Bradbury, & Addiscott, 1996) account for organisms implicitly, treating them as an ''average engine''. This usually works sufficiently because the main determinants of processes are often abiotic factors (Andrén, Brussaard, & Clarholm, 1999). However, only organism-oriented models can be used to study the importance of functional groups and community structure (Brussaard, 1998). At the plant community scale organism-oriented models operating on comparatively great detail do exist: the food web models, based on a study in a short grass prairie (Hunt et al., 1987). In this type of model, trophic relationships are modelled mechanistically by numerical representations of the feeding relationships of all functional groups of organisms within the food web. However, these models focus on the belowground food web, and aboveground processes are represented at less detail via carbon and nitrogen inputs through plant roots and litter fall.

Food web models have been used to study carbon and nitrogen fluxes in agricultural systems and

grasslands (Hunt et al., 1987; Moore & De Ruiter, 1991; De Ruiter et al., 1993; De Ruiter, Neutel, & Moore, 1994, 1998) and forest ecosystems on various scales (Berg et al., 2001; Schröter, Wolters, & De Ruiter, 2003). Recently, a food web model has been used to study the effect of soil biodiversity loss on ecosystem processes (Hunt & Wall, 2002). These model applications are useful to study ecosystem services of interest at the plant community scale such as crop yields and species diversity maintenance (Table 1). However, as opposed to the process-oriented models, organism-oriented models so far do not run in dynamic mode. Nevertheless, organism-oriented approaches have been used in a wide range of environments. Generic temperature and moisture response functions derived from laboratory measurements of the resulting net carbon turnover have been used in an organism-orientated approach to adapt trophic interactions to the environmental context (Schröter et al., 2003). This required the simplification that all functional groups involved in mediating the process responded equally and constantly to changes in environmental factors. This simplification is also inherent in the process-orientated models mentioned here but nevertheless unlikely to reflect reality.

For predictive purposes in the global change context, process-orientated models of trophic interactions are used instead of organism-orientated models for five main reasons: (1) process-orientated models require less information to be parameterised; (2) they are of simpler structure than organism-orientated models and allow less time consuming computation (Brussaard, 1998; Smith et al., 1998); (3) organism-orientated models have so far not been successful in dynamic mode and provide comprehensive static budgets only (Andrén, Brussaard, & Clarholm, 1999); (4) existing organism-oriented models focus on carbon and nutrient fluxes and do not explicitly model water fluxes; and (5) there is a greater wealth of observed data to validate process-orientated models than to validate organism-orientated models. Modelling organism-orientated in a changing environment requires knowledge of the effect of changing abiotic factors on the activity rates of all organisms or functional groups involved.

Both types of models could include above- and belowground trophic interactions more explicitly. Including this detail will not change the fundamental ways in which these models are constructed or how they operate. Both approaches should inform each other and could be merged in a mainly process-oriented "hybrid model" that includes organism-oriented mechanistic representation of a limited number of trophic interactions. In this "hybrid model" main energy and nutrient pathways like the trophic interactions between plants and root symbionts as well as root herbivores, or microbial grazers and microbes could be represented in detail, while other trophic interactions would remain implicit within process-oriented functions. Already, the main groups of organisms have at least inspired the development of linear differential equations, e.g., in the so-called SOMM model (Chertov & Komarov, 1997) that was built on the basis of a detailed understanding of interacting organisms. At the community scale it is possible but labour-intensive to obtain data on the actual organisms involved in above- and belowground interactions. The starting point for a hybrid modelling approach could be the rich datasets already available, which were used to develop the food web models (e.g. Moore, Walter, & Hunt, 1988; De Ruiter et al., 1993; Andrén et al., 1999; Berg et al., 2001; Schröter et al., 2003). Hybrid models of different levels of detail can then be compared to see how much simplification is feasible and necessary.

Conceptual models at the individual plant scale

At the individual plant scale, recent experimental field and laboratory studies have revealed examples of feedbacks between the aboveground and belowground components that have encouraged further effort in this new field of investigation (reviewed by Wardle, 2002, and more recently e.g., Bardgett & Wardle, 2003; De Deyn et al., 2003; Moore et al., 2003; Porazinska et al., 2003; Poveda, Steffan-Dewenter, Scheu, & Tscharntke, 2003; Wardle et al., 2004). In the following we will describe an emerging conceptual model of above- and belowground interactions between main functional groups in the ecosystem as illustrated in Fig. 1. We summarise the current understanding of the nature and control of the interactions and then draw conclusions how this model can inform numerical modelling at larger scales.

Some aboveground–belowground interactions are based on the consumption of parts of the living plant (Fig. 1, Table 2). Aboveground herbivores have idiosyncratic effects on the belowground processes through positive or negative effects on soil biota (Bardgett & Wardle, 2003; Porazinska et al., 2003). Plant traits are important in these linkages, as indicated by plant species specific effects of herbivory by large mammals
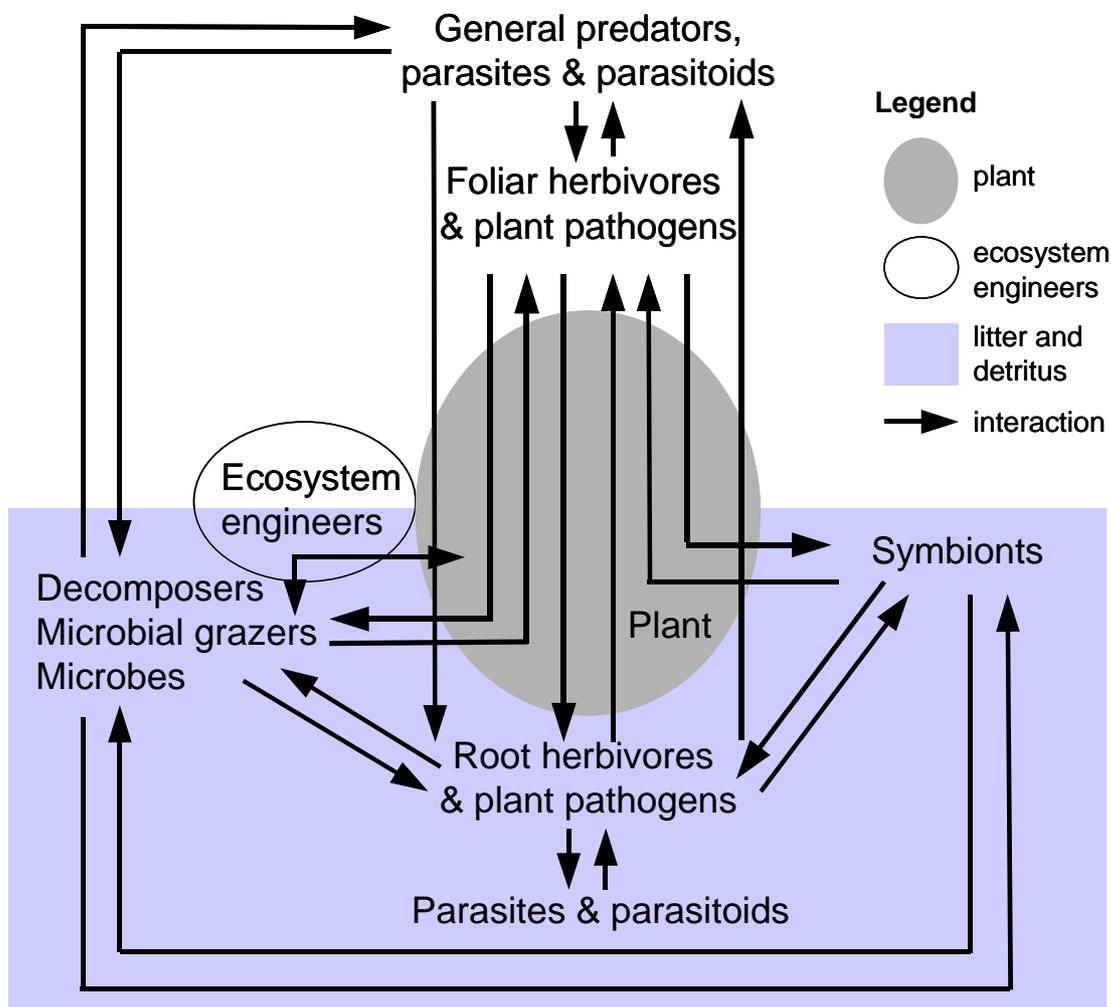
Figure 1. A possible common structure for the nature of below–aboveground interactions between main functional groups. Examples of organisms in functional groups are given in Table 2. Arrows depict indirect and direct interactions, operating on a wide range of time scales.

and invertebrates on the belowground (Wardle, Barker, Yeates, Bonner, & Ghani, 2001; Schädler, Jung, Auge, & Brandl, 2003). Furthermore, aboveground foliar herbivores indirectly affect belowground root herbivores and vice versa (Brown & Gange, 1989). A recent review by Van Dam, Harvey, Bezemer, Van der Putten, and Vet (2003) emphasises above- and belowground induced responses against herbivory in relation to known plant-physiological defence mechanisms (Van Dam et al., 2003). Results from chemical ecology, e.g., on cross talk between signals, such as salicylic and jasmonic acid, may improve our understanding of how plants mediate effects between different groups of organisms (Van der Putten, Vet, Harvey, & Wäckers, 2001; Bezemer et al., 2003).

Like herbivores, belowground symbionts interact with the living plant (Fig. 1, Table 2). The effect of this symbiosis on the plant ranges from positive (mutualism) to negative (parasitism), depending on

multiple factors, such as nutrient availability (Johnson, Graham, & Smith, 1997), plant species, and the presence of pathogens (Gange et al., 2002; Klironomos, 2002). Furthermore, the symbiosis between mycorrhizal fungi and plant roots is influenced by aboveground herbivores as well as by belowground decomposers (Wall & Moore, 1999; Gange, 2000). Living plant consumption, whether above- or belowground, influences the decomposer system and vice versa.

Within the decomposer subsystem, interactions are based on consumption of detritus and dead plant material, therefore affecting plants indirectly and vice versa through changes in soil structure (Edwards & Bohlen, 1996), as well as energy and nutrient fluxes (Swift, Heal, & Anderson, 1979). Belowground decomposers and microbial grazers, such as protozoa, nematodes and microarthropods, can influence aboveground plant–herbivore interactions (Moore et al., 2003;

Table 2. Examples of organisms in the functional groups depicted in Fig. 1

Functional group	Examples of organisms
Primary producers	Plants: individuals, species, plant functional types
Symbionts	Mycorrhiza (arbuscular, ecto- and ericoid mycorrhizal fungi) Nitrogen-fixing rhizobacteria Protozoa in the rhizosphere
Herbivores	Phytophagous insects, e.g. Aphidae, insect larvae Nematoda Browsing mammals
Microbes	Bacteria, fungi, protozoa (e.g. Flagellata)
Microbial grazers	Bacterial grazers (e.g. Testate Amoebae, Tardigrada, Nematoda) Fungal grazers (e.g. Collembola, Acari)
Decomposers	Detritivores (liquid feeders, e.g. Rotifera) Comminutors (fragmentors, e.g. Microarthropoda, Enchytraeidae, earthworms)
Parasites & parasitoids	Plant parasitic nematodes Arbuscular mycorrhizal fungi Gall flies Ichneumon wasps
Pathogens	Fungi
Ecosystem engineers	Ants, termites, earthworms
Predators	Predatory mites, spiders, staphylinid and carabid beetles

Fig. 1, Table 2). For example, Bonkowski, Geoghe-gan, Birch, & Griffiths (2001) found an increase in number and biomass of aphids in the presence of Protozoa. In the rhizosphere, protozoa can function as bacteria-mediated mutualists which can pro-mote plant growth, both by hormonal feed-back mechanisms and by nutrient release from grazed bacterial biomass (Bonkowski & Brandt, 2002).

Generalist predators, parasites and parasitoids influence aboveground- and belowground interac-tions directly and indirectly (Fig. 1, Table 2). Generalist predators such as spiders, staphylinid and carabid beetles act directly since they are predators on animals in both the aboveground- and belowground compartments, i.e., they feed on belowground decomposers and microbial grazers, and on aboveground herbivores (Polis, 1991). In this

way, generalist predators, supported by the below-ground community, can reduce plant damage due to aboveground herbivory (Scheu, 2001). Below-ground parasites, such as entomopathogenic nema-todes, can influence aboveground vegetation dynamics indirectly through parasitic interaction with root-dwelling herbivores (Strong, 1999; De Goede & Brussaard, 2002). Those interactions affecting plant diversity will, in turn, affect pollinators and higher trophic levels, e.g. birds.

Ecosystem engineers can have a fundamental influence on trophic interactions between other groups, through mostly non-trophic activities (Fig. 1, Table 2). They can influence the physical properties of soil and the diversity and activity of the decomposer subsystem, with subsequent im-pacts on nutrient fluxes (Lawton & Jones, 1995). In terms of their numerical and biomass densities, geographical distribution and functional roles, earthworms and termites are regarded globally the most important terrestrial ecosystem engineers (Lavelle et al., 1997). Other macro-arthropod ecosystem engineers such as ants, diplopods, isopods and diptera larvae form a substantial part of the total biomass in temperate deciduous and coniferous forests (Petersen, 1982). Among these, ants, for example, influence above- and below-ground interactions between soil biota and plants by altering their chemical and physical environment (Folgarait, 1998; Dauber, Schröter, & Wolters, 2001).

Such examples of experimental evidence illus-trate the complexity of aboveground–belowground interactions at the scale of the individual plant. Summarising the interactions in a conceptual diagram gives a possible common structure in the nature of above–belowground interactions (Fig. 1, Table 2). Basically, all functional categories of organism may be connected to all others, either directly or indirectly. However, different systems differ in the relative strength of the interactions, while in some cases such knowledge is lacking. The field observations suggest that interactions can be either negative or positive often depending on non-linear responses to a multitude of factors. The underlying mechanisms and possible causal chains are not yet fully understood. Nevertheless, by identifying functional groups and the main interac-tions between the above- and belowground system, Fig. 1 provides a basis for hypotheses and ques-tions. In the context of attempting to numerically model such interactions in a changing world five main questions arise:

1. *Quality of the interaction* — What is the impact of interacting functional groups on each other in

terms of ecosystem structure or processes of interest (e.g. abundance, biomass, nutrient content, reproductive success and/or diversity)?

2. *Quantification of the interaction: interaction strength* — What are the (relative) strengths of the interactions, and how do we measure and express them?

3. *Environmental factors* — Which environmental factors influence the interactions? Which of these factors are anthropogenic?

4. *Quantification of the environmental influence* — How and at what rate do these factors influence the interactions in the context of multiple actors and factors?

5. *Commonalities (in points 1–4) that allow generalisation* — Can we identify patterns of interactions, interaction strengths and environmental influences that are common within, but differ between, ecosystem types and biomes?

If there is adequate information about points 1–4 for a given system, we can project the impact of global changes on aboveground–belowground interactions using numerical models. If we have further information on point 5 — commonalities between systems that allow generalisation — we may scale up from the system at hand to other ecosystems, regions or even biomes.

Global change drivers and future projections

Global change impacts ecosystems via changes in process rates and system structure. There are a number of important first and second order global change drivers that influence aboveground–belowground interactions and the ecosystem services that depend on them. Second-order drivers are themselves effects, i.e., brought about by other global change drivers. Among the most important first-order drivers are atmospheric carbon dioxide concentration, temperature, precipitation, radiation, nitrogen deposition, and land use change. Important second-order drivers include species invasions, extinctions and alterations in species abundances and community structure. Here, we summarise our immediate concerns regarding the effect of these global change drivers on ecosystems.

The most important effects of enhanced atmospheric carbon dioxide concentration are likely to be carbon fertilisation and more efficient water use of plants, as well as indirect effects on the belowground system such as enhanced carbon allocation to the soil with subsequent changes in decomposition rate (Swift et al., 1998). Large-scale manipulative experiments to date have failed to find consistent effects of increased atmospheric carbon dioxide concentrations on terrestrial ecosystem carbon sequestration (Körner, 2000). A rise in atmospheric carbon dioxide concentration may cause shifts in the types of dominant vegetation, e.g., conversion of savannah to woodland through enhanced tree invasion (Bond & Midgley, 2000). Temperature changes will have immediate direct effects on process rates in both the above- and belowground systems. Temperature effects on the carbon balance will depend on which process is more limited by temperature. On a global scale, decomposition seems more temperature constrained than NPP resulting in little SOC storage in tropical, and high SOC storage in boreal systems.

Temperature changes may be tightly coupled with precipitation changes which can lead to enhanced drought stress, adding to a change in balance between primary production and decomposition. Radiation changes are likely to affect plant leaf structure and chemistry and consequently litter quality. The burrowing activity of aboveground organisms and top soil dwellers may increase as a behavioural strategy to avoid damage due to UV-B radiation. Global air pollution appears to be an important influence on the global carbon cycle (Holland et al., 1997). Nitrogen deposition from the atmosphere and additional inputs leached from agricultural soils will have fertilisation effects, additional to those induced by increased atmospheric carbon dioxide concentration. Thus aboveground- and belowground processes will be influenced by a multitude of interacting factors, such as intentional and unintentional fertilisation, acidification, and their effects on community structure and litter quality.

Land use change can be a powerful driver of global change in many regions, occurring either gradually (e.g. in management practice) or suddenly (e.g. clear felling a forest). Abrupt changes have different impacts to gradual habitat conversion or succession. Conversion of ecosystems, especially in intensively managed areas like Europe, will continue along with habitat fragmentation and its consequences for biodiversity. As a second-order driver, invasion of species can change the entire system both above and below ground. Extinction of species can have cascading effects on other species in the ecosystem (for examples see Bruno, Stachowicz, & Bertness, 2003). Organism-orientated models have been used to study the interaction strength between functional groups and

the effect of biodiversity loss, but stabilising mechanisms within ecosystems are not yet fully understood (de Ruiter et al., 1998, Hunt & Wall, 2002). Shifts in the belowground community structure, e.g., from fungal to bacterial based systems especially in high latitudes, may change the balance between primary production and decomposition with consequences for the global C and N cycle (Schröter et al., 2003). Organisms of the bacterial pathway are generally found resilient to change due to their ability to disperse rapidly in time and (passively) in space (Hedlund et al., 2004). It remains a future research challenge to determine how biodiversity dynamics, community structure and abiotic factors interact to drive ecosystem processes (Loreau et al., 2001). Research efforts in this respect need to take into account the fact that global change drivers will not act independent of each other but in concert.

To study the possible effects of global change, we rely on future scenarios of the driving forces. The extent to which scenarios of global change drivers need to project into the future depends on the ecosystem services studied. Even though we are certain that global change is happening, there are large uncertainties associated with specific projections, some of which are unknowable. Therefore, it is important to analyse multiple plausible scenarios in a systematic way so as to cover the full range of possible futures envisioned by experts, for example those provided by the Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (IPCC-SRES, Nakicenovic & Swart, 2000).

Discussion

Scaling up from the scale of the individual plant to that of landscapes, regions and the globe is not simply a matter of asking the same questions at larger scales. Often the questions will change with scale and will rely on appropriate representation of knowledge derived at other scales. At the individual plant scale, questions often are: Does species X in the belowground system have an effect on species Y in the aboveground system, and if so how and why? At the scale of a discrete plant community, we ask: What is the rate of an ecosystem process? On which factors does it depend? What is the contribution of a species or functional group to ecosystem processes? Does community structure play a role? At a landscape to global scale, we ask: What is the contribution of an ecosystem type to the global carbon cycle? How will alterations in

environmental factors impact the carbon flux rates? Will the distribution of ecosystem types change? At all scales, we ask whether global change impacts structures or processes that are essential for ecosystem services, such as biodiversity maintenance, agricultural crop yield, or climate protection (Table 1).

At the individual plant scale quantification and projection to the future are often hindered by lack of information on the exact quality of the interaction, its relative strengths and amplitude, the environmental factors influencing it and the rate at which these factors influence the interactions in the context of multiple actors and factors. At larger scales processes are quantified, but the level of ecosystem detail included in the quantitative models decreases as larger spatial scales are reached (Smith et al., 1998; Andrén et al., 1999; Sitch et al., 2003). How much detail is needed to successfully model fluxes on large scales? Is it sufficient to assume organisms mediating the flux will be present, and will operate at a specific generic rate? In many cases, a model based on this assumption performs well and detailed representations of ecosystem processes are superfluous. However, in the case that global change alters the system fundamentally in the way the process is mediated, conclusions from this model will be false. For example, due to continuously increased nutrient input via nitrogen deposition, mycorrhizal fungi could shift from being mutualists to being parasites of their host plant species, thereby causing a non-linear shift in plant productivity. The same deposition impact could lead to a shift from a fungal to a bacterial dominated detritus based decomposer subsystem, causing non-linear changes in decomposition with indirect impacts on plant productivity in the long term. Significant functional shifts in soil due to global change are anticipated (Swift et al., 1998; Wolters et al., 2000). Studies on forests, arid lands, lakes, coral reefs and oceans have shown that gradual change can be interrupted by sudden drastic switches to a contrasting state (Scheffer, Carpenter, Foley, Folke, & Walker, 2001). No current models take into account such shifts, which will also change the way the system responds to global change in the future (Smith et al., 1998).

Long time series of observed data are needed to understand ecosystem processes and for validation and improvement of models by a more realistic representation of organisms and ecosystem processes. This can include improving the parameterisation of the model or refining the model to a more detailed representation of the studied system— even if more complexity may at first lead to even

poorer results, because additional uncertainty may be incorporated and multiplied. Modelling is a highly integrative exercise that requires both, research and communication between experts from field and laboratory experiments, theoretical ecology, and from different scales.

Models that more explicitly represent aboveground–belowground interactions will be based on existing approaches. At the landscape to global scale we have suggested to expand the plant functional type concept to include functional types in above- and belowground interactions. At this scale, the uncertainty in current carbon flux estimates provided by DGVMs is to a large extent due to limited representation of decomposition processes (Dufresne et al., 2002). Further communication[4] as well as research should improve the representation of the detritus based decomposer subsystems, with their indirect long-term effects on aboveground vegetation. Similarly important is the inclusion of the living plant-root based subsystem (including mycorrhiza and root herbivores), which impacts aboveground processes even more directly and on shorter time scales. At the scale of discrete plant communities, process-based and organism-oriented models could be combined into "hybrid approaches" that include organism-oriented mechanistic representation of a limited number of trophic interactions in an otherwise process-oriented approach. At the individual plant scale we summarised an emerging common conceptual model of aboveground–belowground interactions, which allows us to formulate research questions that can inform modelling approaches at larger scales. Future ecosystem models can better include our evolving knowledge of common patterns of aboveground–belowground interactions. Such improved models are necessary tools to reduce the uncertainty in the information we rely on in sustainable management of our environment in a changing world.

Acknowledgements

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[4]Further communication could, for example, be facilitated by joint workshops and research projects including field and laboratory researchers, as well as theoretical ecologists. Senior researchers should function as moderators and coordinators of this communication process.

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