THE ROLE OF ABOVE- AND BELOWGROUND LINKAGES IN ECOSYSTEM FUNCTIONING

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Summary

It is well established that apart from plants (being the primary producers), a range of other organisms play key roles in terrestrial ecosystems. The functional importance of their diversity, however, is poorly known. Roughly, terrestrial ecosystems can be divided into an aboveground and a belowground compartment, which are tightly linked by plants. In both compartments, heterotrophic organisms are involved in numerous interactions with plants. In this chapter, we first explore the effects of plant diversity on higher trophic levels. Subsequently, we review what is known about the roles of herbivores, pathogens, mutualists and predators in controlling plant productivity and diversity, decomposition and related ecosystem functions, both above- and belowground. Thereafter we explore what is known about the linkages between these

interactions and how they affect ecosystem processes. Based mainly on indirect evidence and only a handful of experimental studies, we argue that in future studies a combined aboveground-belowground food-web approach is needed to identify and comprehend these interactions. Only then will we be able to understand the consequences of biodiversity loss for ecosystem functioning.

1. Introduction

The relationship between biodiversity and ecosystem functioning in terrestrial ecosystems has mostly been addressed by investigating the effect of changes in plant species diversity on plant productivity. Primary productivity tends to decline with reduced number of plant species present, although neutral responses have also been observed [1]. An increase of productivity with increasing diversity is mainly attributed to enhanced resource use efficiency via complementing interactions among plant species. Plant diversity may also affect decomposition, an ecosystem process underlying maintenance of ecosystem productivity. Decomposition rate has been found to increase with plant diversity, but many studies reported neutral or idiosyncratic effects [2].

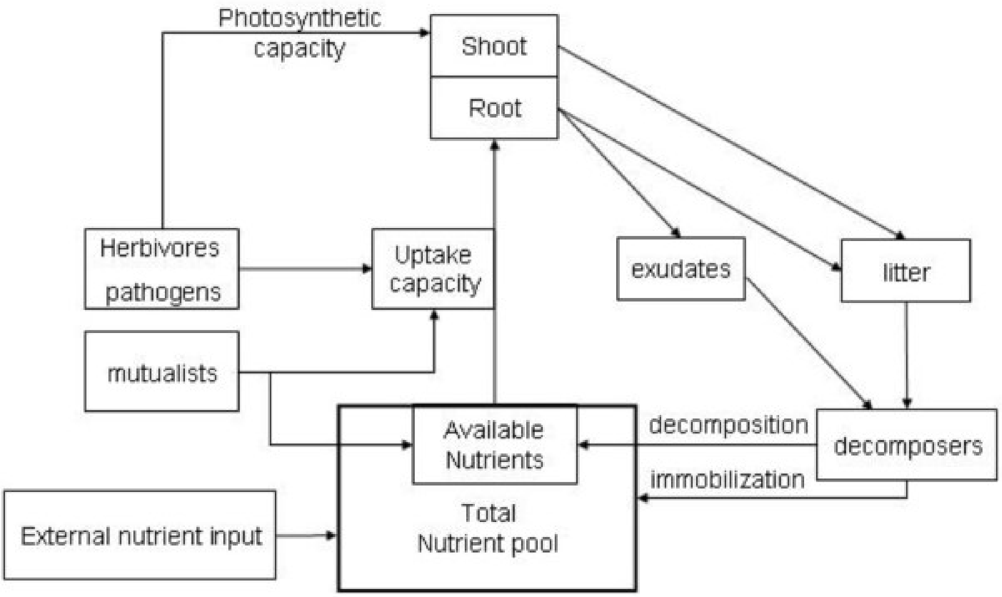

Figure 1. Plant and soil biota interaction in relation to nutrient cycling and productivity. Plants acquire water and nutrients from the soil, where soil biota influence the availability and acquisition of nutrients. Living roots directly interact with mutualistic (e.g. mycorrhizal fungi, N-fixing bacteria), pathogenic (e.g. disease causing bacteria and fungi) and herbivorous soil organisms (e.g. plant-feeding insects and nematodes). Mycorrhizal fungi enhance plants' nutrient and water uptake capacity by extending the root system. N-fixing bacteria increase nutrient availability by capturing atmospheric nitrogen, while root herbivores and root pathogens reduce the root system and plant growth. Indirectly, soil organisms (e.g. saprophytic bacteria, fungi, nematodes, micro-arthropods) are crucial for plant nutrient provision by decomposing plant-derived organic matter and releasing mineralized nutrients. Aboveground herbivores and pathogens may reduce plant photosynthetic capacity and biomass.

Plants grow in ecosystems and interact with many heterotrophic organisms at several trophic levels (see Figure 1). These interactions, occurring both above and below ground, may reduce or enhance plant growth and consequently community diversity and ecosystem properties. However, these interactions have only recently been incorporated into biodiversity-ecosystem functioning studies. Knowledge of the interactions between plants and higher trophic level organisms is crucial to understanding and predicting the consequences of changes in biodiversity. In this chapter, we will first discuss the effects of changes in plant diversity on above- and belowground organisms and *vice versa*. In the second part, we present how these separate links may interact in communities and review what is known about these interactions. We conclude that a combined above-belowground dynamic food-web approach is essential to fully understand the consequences of changes in biodiversity for ecosystem processes. To keep this chapter a reasonable size, we have chosen to focus the review on decomposers, herbivores and their predators, and pathogens. This does not mean, however, that the organisms left out of this review (e.g. pollinators) are not important.

2 Effects of plant diversity on higher trophic levels

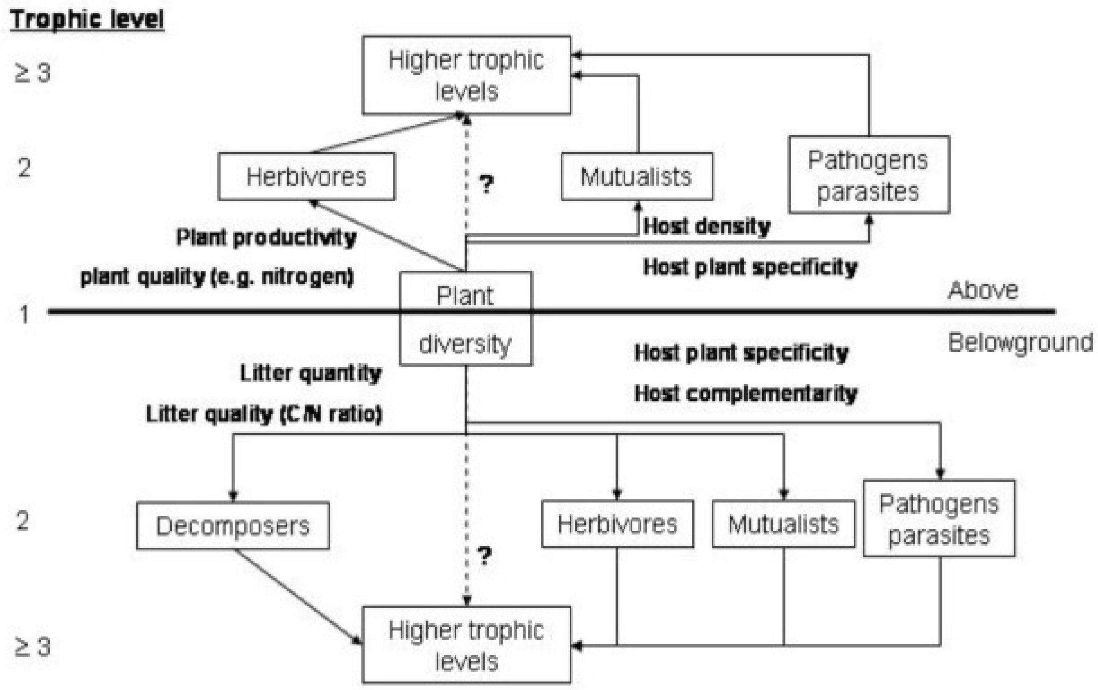

Figure 2. Plant diversity effects on above and belowground organisms.
Plant diversity affects the diversity and abundance of heterotrophic organisms. Effects on primary consumers and decomposers are best studied and reveal so far mainly plant or litter composition (quality) effects. Few studies have addressed effects of plant diversity on higher trophic levels.

Decomposition of dead organic matter is essential for primary productivity. Litter of multiple plant species may decompose quicker than that of single species, but the results are often idiosyncratic [see 2 and references therein]. To explain these different results we need to investigate the underlying mechanisms, i.e. the interactions between plant species and the organisms which perform the ecosystem processes. As a first step in exploring ecosystem level implications of plant interactions with other trophic groups, we investigate the mechanisms via which plant species diversity affects separate (functional) groups of organisms above- and belowground (see Figure 2 for an overview).

2.1. How plant diversity affects the soil food-web

Several studies indicate that there is no straightforward relationship between plant diversity and the abundance or diversity of soil organisms. In a European-wide field study on former agricultural land, species diversity of introduced plants resulted in idiosyncratic effects on the diversity of decomposer microbes, mites, nematodes and earthworms [3].

Similarly, no clear relation between plant species diversity and the soil community was found in a field survey of established grassland. However, species-specific effects of different grass species on bacteria and nematode groups were apparent [4]. In a plant-removal study in grassland, plant community composition was found to affect the community structure of soil microbes, nematodes and arthropods, but earthworms and collembolans did not respond. Apparently, plant species identity rather than plant species diversity affects the soil community.

It has been argued that it is the trophic groups closely associated with plant roots (e.g. herbivores, mycorrhizal fungi, rhizosphere bacteria and bacterivores) that mainly respond to plant species diversity [5]. However, one study showed stronger effects of plant species composition on higher (voles and earthworms) than on lower (microbes) trophic levels [6].

In general, decomposer abundance and biomass are primarily controlled by litter quantity and quality. Litter with low C/N ratio tends to support higher microbial biomass than litter with high C/N ratio, due to nitrogen limitation of microbes. Plant diversity effects on decomposer fauna appear to be more variable. Mixed litter of different plant species can support more saprophagous mites than litter of monocultures, suggesting facilitative effects.

Recent publications suggest that microbivorous as well as root-feeding soil invertebrates are controlled by food quality (i.e. concentration of primary and secondary plant metabolites) rather than quantity of organic matter. As regards diversity of decomposers, the presence of certain plant species and functional groups rather than the number of plant species and functional groups present seem to matter most [see 2 and references therein].

2.2. Links between plant diversity and aboveground organisms

In experimental studies, a decrease of plant diversity generally leads to an increase in the invasion success of other plant species. Changes in plant diversity can generate invasions of new plant species and herbivores associated with them, thus changing

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community structure at multiple trophic levels, as has been shown for invading *Solidago canadensis* and associated spittle-bugs [7]. Disease outbreaks are often host density-dependant and it has been proposed that high plant diversity may buffer against plant productivity loss due to outbreaks of specialist herbivores and pathogens by keeping their densities low. Apart from numerous mixed-cropping studies in agricultural systems, a reduction of the incidence of fungal leaf pathogen infestations with increasing plant species richness has been found in experimental plant communities [8].

Most studies investigating the effects of changes in plant diversity on aboveground organisms focused on arthropod communities. Higher plant species diversity in grasslands may result in an increase of arthropod herbivore, predator and parasite diversity when they are bottom-up controlled [8].

However, in similar systems a reduction of arthropod diversity with increased plant species diversity, due to a decline of the diversity of parasites and predators, has also been reported [9]. These idiosyncratic results may be attributed to invertebrate species-specific responses to plant species or plant functional group traits like nutritional quality (e.g. pollen as alternative food source) or to plant community structure complexity, governed by the component plant species [10].

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Biographical Sketches

Dr. ir. Gerlinde B. De Deyn was born in October 1975, in Aalst (Belgium). She graduated from Ghent University (Belgium) in 1998 at the Faculty of Agricultural and Applied Biological Sciences. Thereafter she worked on the biological control of plant parasitic nematodes in glasshouse crops at the Center for Agricultural Research in Merelbeke. From February 2000 to 2004 she did her PhD study on soil fauna and plant community interactions in relation to secondary succession and diversity, directed by Prof. Peter

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de Ruiter (University of Utrecht, Netherlands) and Prof. Wim van der Putten (Centre for Terrestrial Ecology, Heteren, Netherlands). The study was part of a large biodiversity project involving close collaboration with colleagues at Wageningen University (Dr. Jasper van Ruijven and Prof. Frank Berendse) and the Free University, Amsterdam (Prof. Herman Verhoef). Since completing her PhD dissertation in 2004, a postdoctoral grant has allowed her to continue investigating plant-soil biota interactions. Since February 2005 she works at Guelph University (Canada) with Prof. John Klironomos on a fellowship of the Netherlands Organization for Scientific Research (NWO), investigating interactions between plant defenses, plant pathogens and mycorrhizal fungi. In 2004 she was Joint Winner of the 2004 John L Harper Young Investigator's Prize awarded by *Journal of Ecology*.

Dr. Jasper van Ruijven was born in October 1974 in Enschede, the Netherlands. He studied Biology at Utrecht University from 1993 to 1998, specializing in Botanical Ecology and Evolution Biology. From 2000 to 2004, he carried out his PhD research at the Nature Conservation and Plant Ecology group of Wageningen University (the Netherlands). The dissertation is entitled “Biodiversity loss in grasslands: consequences for ecosystem functioning and interactions with above- and below-ground organisms”.

In October 2004, he started as a postdoc at the Ecology and Evolution section of Imperial College London (UK).

His main research interest is plant coexistence. What allows so many plant species to persist in a single community? What is the role of above- and belowground organisms (herbivores, pathogens, mycorrhizal fungi)? What are the major causes of changes in plant diversity and how do these changes affect ecosystem processes?

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