Chapter one
Introduction
Aboveground-belowground interactions

Terrestrial ecosystems consist of aboveground and belowground subsystems that differ vastly in physical structure. The aboveground world is open and contains mainly air, while the belowground one consists of a matrix of soil particles and pores filled with water or air. This has major consequences for the mobility of organisms living aboveground and belowground. Aboveground organisms may explore areas of several kilometers within a day, whereas most soil organisms are constrained to areas of millimeters to centimeters in their whole lifetime and mostly stay in the vicinity of an individual plant (Mortimer et al. 1999, van der Putten et al. 2009).

Despite these large differences in scale, medium and mobility, aboveground and belowground organisms interact because they are connected by plants that position their functionally linked organs in both aboveground and belowground worlds and mediate flows or carbon, nutrients and energy between them (Bardgett and Wardle 2003, Wardle et al. 2004). Plants provide organic carbon for decomposer organisms, as well as resources for root and shoot herbivores, pathogens and symbiotic mutualists. In turn, these aboveground and belowground organisms influence plant performance and plant community composition via direct removal of plant material, by enhancing access to limiting resources, and by altering soil nutrient cycling. As a result, both aboveground and belowground organisms can be important drivers of plant community composition, structure and diversity (e.g. Grime et al. 1987, Crawley 1989, Huntly 1991, Milchunas and Lauenroth 1993, Olff and Ritchie 1998, van der Putten and van der Stoel 1998, van der Heijden et al. 1998b, Klironomos 2002, Wardle 2002, De Deyn et al. 2003, Bardgett and Wardle 2010). Moreover, by affecting plants aboveground and belowground organisms influence each others performance as well (e.g. Gange and Brown 1989, Masters and Brown 1992, Masters et al. 1993, Masters et al. 2001, Bezemer et al. 2003, Soler et al. 2005, Soler et al. 2007). As a result, interactions between aboveground and belowground subsystems will have major consequences for community structure and ecosystem functioning in terrestrial systems (Wardle et al. 2004, van der Putten et al. 2009).

Only few studies have investigated how aboveground-belowground interactions affected mixed plant communities (Brown and Gange 1989, Brown and Gange 1992, van Ruijven et al. 2005, Ilmarinen and Mikola 2009). These studies mainly focused on effects of invertebrate aboveground and belowground organisms. How vertebrate aboveground grazers and soil organisms interact to drive plant community structure and ecosystem processes is still poorly understood. Therefore, in this thesis I focus on consequences of interactions between aboveground vertebrate herbivores and soil organisms for plant community structure and composition.
Aboveground vertebrate herbivores

Aboveground vertebrate grazers are identified as key determinants of community composition and functioning of grassland systems worldwide (Olff and Ritchie 1998, Knapp et al. 1999). Aboveground vertebrate herbivores affect plant community composition and ecosystem functioning via different pathways. Firstly they remove aboveground biomass, which alters competitive interactions between plant species (Olff et al. 1997, Knapp et al. 1999). Secondly they alter the quality and quantity of nutrient input into the soil by changing root exudation patterns, litter quantity and quality, and the return of excreta (Bardgett and Wardle 2003). Finally they affect the plant community and soil biotic and abiotic properties physically, for example, via trampling (Hobbs 1996, Knapp et al. 1999).

Depending on the scale of observation, herbivore size and ecosystem productivity, aboveground vertebrate herbivores have contrasting effects on plant community structure and diversity. In productive grasslands, vegetation patches created by vertebrate herbivores harbor a higher plant community diversity than ungrazed patches, because the removal of foliar biomass by herbivores will often relax the competition for light between plant species (Bengtsson et al. 1994, Olff et al. 1997). This promotes subdominants to become more abundant which generally results in an increase in local plant community diversity (Collins et al. 1998, Knapp et al. 1999, Bos et al. 2002, Bakker et al. 2003, Veen et al. 2008). Moreover, vertebrates increase colonization possibilities by transporting seeds and disturbing soil (Olff and Ritchie 1998, Bakker and Olff 2003, Ozinga et al. 2009). In contrast, in unproductive habitats, plants not always recover from grazing which leads to lower diversity (Proulx and Mazumder 1998). This can lead to a decrease in the local species pool and may reduce colonization possibilities for plants (Milchunas and Lauenroth 1993, Olff and Ritchie 1998).

The body size of herbivores is also an important determinant of herbivore effects on the plant community. Digestive capabilities of herbivores increase with body size. Therefore, small herbivores need to select for high quality food while large vertebrate herbivores are dependent on high amounts of food, but can process relatively low quality food (Demment and Van Soest 1985, Hopcraft et al. 2010). Consequently, larger vertebrate herbivores make foraging decisions on a coarser grain (Ritchie and Olff 1999, Cromsigt and Olff 2006, Laca et al. 2010) and therefore tend to create more coarse-grained spatiotemporal patterns in the vegetation as well (Bakker 2003, Cromsigt and Olff 2008). Still, large herbivores are able to create small-scale plant community patches (Veen et al. 2008), for example through the selective removal of plant species, revisitation of grazed patches with enhanced food quality (Bakker et al. 1983), and patchy distribution of dung and urine (Steinauer and Collins 1995).
Plant-soil feedback

Effects of soil organisms on plants and plant communities can be understood by the concept of plant-soil feedback. This is a two-step process where plant species modify their soil biotic and abiotic environment (Bever et al. 1997, Yeates 1999), which in turn influences subsequent plant growth and the competitive ability of plant species (van der Putten and Peters 1997, Bever 2003, Wardle et al. 2004, Ehrenfeld et al. 2005, Manning et al. 2008). The biotic component of plant-soil feedback operates through direct, as well as indirect effects of soil organisms on plant growth (Wardle et al. 2004). Root herbivores, pathogens and symbiotic mutualists use and provide resources from plant tissues thereby directly affecting plants. Decomposer organisms drive soil nutrient cycling by converting organic material into inorganic nutrients, thereby regulating soil nutrient supply and, indirectly, growth of plants.

Plant-soil feedback effects can be highly species specific, particularly as a result of specific associations between plant species and soil organisms (van der Putten et al. 1993). It may range from positive to negative, depending on the balance between beneficial and parasitic interactions. On the one hand, symbiotic mutualists, such as some mycorrhizal fungi and rhizosphere bacteria, enhance the access of plants to limiting resources (van der Heijden et al. 2006). On the other hand, root herbivores and pathogens, such as plant-feeding nematodes, directly remove nutrients from plant tissues and reduce the capability of plants to take up soil nutrients, thereby reducing plant growth and competitive ability (van der Putten and Peters 1997).

Plant-soil feedback may enhance or reduce plant community diversity. Positive interactions between plants and symbiotic mutualists can promote seedling establishment (van der Heijden 2004). In general however, plant species that experience strong positive plant-soil feedback have been shown to outcompete other plant species (Klironomos 2002, Callaway et al. 2004), which reduces plant community diversity (Hartnett and Wilson 1999, Bever 2003) and enhances stability (Revilla 2009). In contrast, negative interactions reduce competitive exclusion (van der Putten and Peters 1997). A reduction in the competitive abilities of plants can stimulate replacement of plant species in space and time, which may result in increased coexistence, diversity and dynamics in the plant community (Olff et al. 2000, van der Putten 2003, Bever 2003, Kulmatiski et al. 2008, Revilla 2009).

Aboveground and belowground scale of operation

Effects of the various aboveground vertebrate herbivores and soil organisms take place at different spatial and temporal scales due to limited mobility belowground and less restrictions aboveground. This will have an important effect on the conse-
quences of interactions between vertebrate herbivores and soil organisms for plant community structure and composition (van der Putten et al. 2009). Previous work showed that aboveground and belowground herbivores that use the same individual plant can influence each others performance (e.g. Gange and Brown 1989, Masters and Brown 1992, Masters et al. 1993, Masters et al. 2001, Bezemer et al. 2003, Soler et al. 2005, Soler et al. 2007). However, aboveground vertebrate herbivores that operate across much larger scales than many soil organisms may not be able to respond to changes at the level of an individual plant, for example resulting from interactions with soil organisms. In that situation aboveground vertebrate herbivores may be expected to overrule or modify belowground effects on the plant community.

**Aim of this thesis**

The main objective of this thesis is to explore how aboveground vertebrate herbivores and soil organisms interact to drive plant community composition, structure and diversity. I aim to understand the potential of soil organisms to drive plant community dynamics and ecosystem processes in grazed grasslands. In particular I address (1) via which pathways aboveground vertebrate herbivores modify soil community composition, (2) how soil organisms in turn can drive plant community composition and dynamics, (3) how soil organisms drive plant community structure and dynamics in the presence and absence of vertebrate herbivores, (4) how differences in scale of operation of aboveground herbivores affect the outcome of aboveground-belowground interactions and (5) how large vertebrate herbivores affect soil nutrient cycling.

**Thesis outline**

I start with examining the effects of cattle (*Bos taurus*) on soil community composition (chapter 2). I use a long-term exclosure experiment to investigate if cattle grazing changes species composition, functional group composition and diversity in the nematode community of a river floodplain grassland. In a structural equation model I combine data on nematode community composition, plant community composition and soil abiotic properties to explore via which pathway cattle modify the soil community.

In turn, changes in soil community composition and structure may feed back to change plant community composition and dynamics (chapter 3). I use a modeling approach to study how plant-soil interactions drive plant community dynamics and structure. I use an existing model describing plant-soil feedback effects (Bever
2003) and perform a detailed analysis on all possible interactions between plants and soil organisms. Results from the analysis are used to interpret how soil organisms drive plant community dynamics and to discuss their possibility to enhance or reduce plant community diversity.

In chapters 4, 5 and 6 I study how the interactions between vertebrate herbivores and soil organisms influence plant community patterns in time and space. I explore the potential of soil organisms to drive spatiotemporal plant community dynamics in the absence and presence of cattle (chapter 4). Cattle operate on a landscape scale, whereas soil organisms act on the scale of an individual plant. Consequently, cattle may determine large-scale plant community patterns, thereby altering the possibilities for soil organisms to affect plant community dynamics. I use a combination of a greenhouse and a field enclosure experiment to determine the potential of soil organisms to affect plant community dynamics and to investigate plant community dynamics in different grazing regimes respectively. In chapter 5 I study the interaction between aboveground grazers and soil organisms in more detail. In a full factorial greenhouse experiment I investigate how simulated grazing, presence of mounds of yellow meadow ants (*Lasius flavus*), and the actual presence of yellow meadow ants themselves affect plant community structure and composition. In this greenhouse experiment aboveground clipping was non-selective to imitate cattle grazing. However, in the field different-sized aboveground vertebrate herbivores that are more or less selective co-occur. The degree of selectivity, i.e. the scale of operation, of aboveground herbivores is expected to affect the outcome of aboveground-belowground interactions. Therefore, to follow up on the greenhouse experiment I study interactions between yellow meadow ants and different-sized aboveground vertebrate herbivores in the field (chapter 6). In a field experiment on the salt marsh of Schiermonnikoog I investigate plant community patches on mounds of subterranean yellow meadow ants (*Lasius flavus*) in the presence of European brown hares (*Lepus europaeus*; small aboveground herbivores) and cattle (large aboveground herbivores).

Aboveground and belowground organisms interact via direct interactions with plant species (e.g. through consumption of living biomass) and via indirect pathways (e.g. by affecting the soil decomposer food web and hence soil nutrient cycling). Soil nutrient cycling has been indicated as an important pathway via which large vertebrate herbivores and soil organisms interact (Bardgett and Wardle 2003). Large herbivores have been shown to enhance or slow down nutrient cycling by affecting the quality and quantity of resources (e.g. litter, herbivore excreta) entering the soil food web. However, contrasting effects of vertebrate herbivores on soil nutrient cycling are not always satisfactorily explained by changes in resource input into the soil. In chapter 7 I use a literature review combined with empirical examples which shows that incorporating effects of vertebrate herbivores on soil physical conditions into existing theories on nutrient cycling in grasslands will help
us to better understand when herbivores speed up or slow down soil nutrient cycling.

In chapter 8 I synthesize the findings of this thesis. I first discuss direct and indirect pathways via which aboveground and belowground organisms interact. Then, I look at the consequences of aboveground-belowground interactions for plant community structure and composition, thereby particularly regarding effects of differences in the scale of operation between aboveground and belowground organisms. Finally, I indicate future challenges in aboveground-belowground research.