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Chapter I



General introduction

The main part of plant biomass ends up in the pool of dead organic matter, as only a minor fraction is consumed by herbivores (McNaughton *et al.* 1989; Cebrian 1999; Coleman *et al.* 2004). Recycling of carbon and nutrients, bound into dead organic matter, is a life-sustaining process on earth. The recycling process is driven by the activity of decomposer organisms (Swift *et al.* 1979). More specifically decomposition is merely a byproduct of the decomposers' activity. Decomposers feed either directly or indirectly on litter thereby fulfilling their stoichiometric requirements of carbon, nutrients and other chemical elements. During decomposition carbon dioxide is released to the atmosphere and nutrients are fed back to the primary production by decomposers' feeding, releasing faeces and involvement in multi-trophic interactions. Thus, decomposition is a key ecosystem process that controls both carbon and nutrient fluxes.

Although research on plant litter decomposition dates back at least to the Rothamsted long-term experiments in the 19th century (Johnston 1994) and has strongly intensified during the last two decades (Prescott 2010), various aspects of plant litter decomposition remain still unclear or unknown (Hättenschwiler *et al.* 2005; Coleman 2008; Prescott 2010). For example, Coleman (2008) addressed the need to identify the soil organisms influencing the specific soil activities, Hättenschwiler *et al.* (2005) pointed at the uncertainties in the link between biodiversity and decomposition and Prescott (2010) emphasized the need to know what controls carbon sequestration during decomposition. Furthermore, given the crucial role of litter decomposition in the global cycles of carbon and nutrients, it is important to know how factors such as global climate change (Lemke *et al.* 2007) and global loss of biodiversity (Sala *et al.* 2000), important components of global change, affect this process. This is a pressing issue as alterations in climate and communities of plants and decomposers are expected and shown to affect plant litter decomposition (Meentemeyer 1978; Coueteaux *et al.* 1995; Hobbie 1996; Aerts 1997; Cadish & Giller 1997). These factors that control plant litter decomposition are further elaborated below.

Factors that control decomposition

Plant litter decomposition is controlled by three main factors: abiotic environment (climate, soil texture and conditions), the quality of the dead organic matter (chemical and physical litter properties) and decomposers (fungi, bacteria, faunal detritivores etc.) according to Swift (1979) and Cadish & Giller (1997) (Fig. 1). Importantly, these three main factors and their various aspects do not operate independently, but instead they interact with each other. For instance climate broadly determines the plant community that can thrive on a given area and plant community in turn affects the local climatic conditions. Similarly decomposers are affected by the litter the plant community sheds and the decomposers modify the plant community with the nutrients that are released by their feeding activities. Importantly, the role of decomposers on plant litter decomposition is central as all the factors affecting decomposition are mediated through them. Nevertheless, decomposers have largely been neglected in many decomposition studies (Hättenschwiler & Gasser 2005; Wall *et al.* 2008; Strickland *et al.* 2009) Instead, most litter decomposition studies have focused on assessing the effects of the abiotic environment and litter quality without the consideration of these factors affecting decomposition only via decomposers. This omission of the decomposers' role leaves the underlying mechanisms elusive or at least unverified. Thus, there is clearly a need for a better understanding of the decomposers' role in the decomposition process.

A mechanistic exploration and understanding of the community structures can be reached by functional trait assessment (McGill *et al.* 2006; Suding *et al.* 2008), where both changes in communities and how these changes affect ecosystem processes, can be assessed. Unlike a purely taxonomic assessment of species interactions, a trait assessment allows scaling from individuals to ecosystems and thus it directly links patterns in communities and ecosystem processes (Suding *et al.* 2008). During the last decade, trait-based research has been widely used in the analysis of: plant community assemblages (Ackerly & Cornwell 2007; Douma *et al.* in press), induced and predicted changes in plant communities in response to environmental change (Lavorel & Garnier 2002; Garnier *et al.* 2007; Suding *et al.* 2008), and litter decomposition (Melillo *et al.* 1982; Quested *et al.* 2007; Cornwell *et al.* 2008; De Deyn *et al.* 2008). Unfortunately the use of traits in fauna studies is lagging behind the plant studies mainly due to lack of data. Nevertheless, trait-based studies of fauna communities have recently gained momentum (Mason *et al.* 2007; Moretti *et al.* 2009; Mateos *et al.* 2011). Also soil ecology has contributed to this for the analysis of e.g. feeding strategies of nematodes (Viketoft *et al.* 2009) and ecophysiological microbial traits (Mulder *et al.* 2005). However, functional trait analysis of the soil fauna in relation to plant litter decomposition is still in its infancy. Next, I will introduce further the three factors controlling plant litter decomposition and indicate some specific processes that are in need for a better understanding. I will start with the decomposers because we can only understand the effects of the abiotic environment and plant litter quality on decomposition by their effects on decomposers, and thus the decomposers should be introduced first.

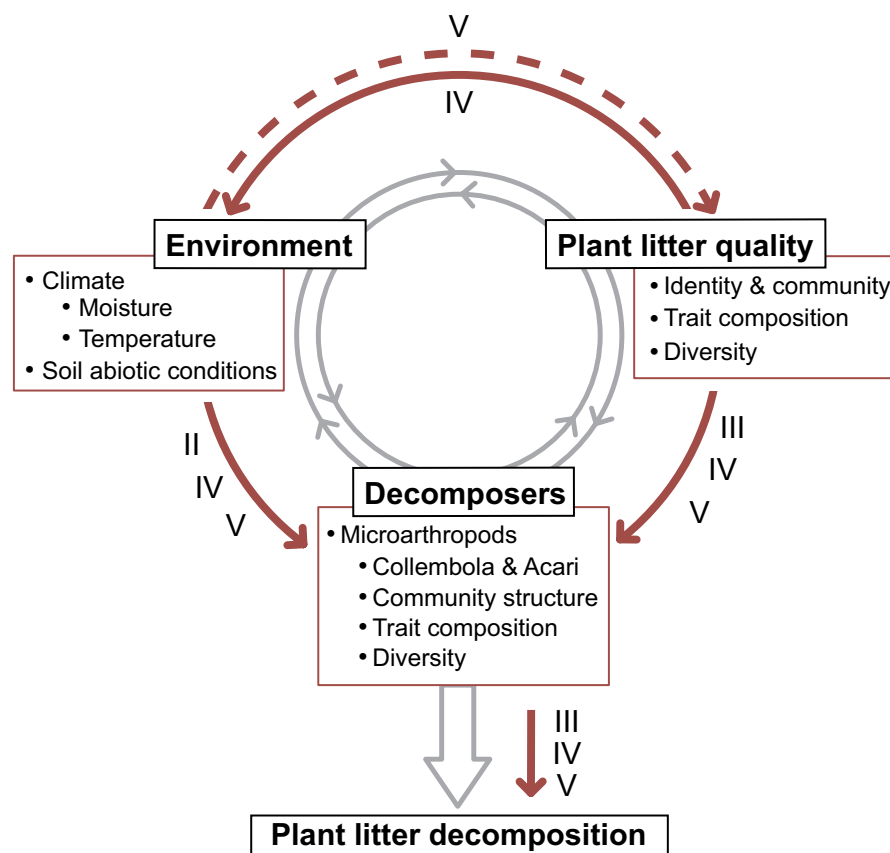


Figure 1. Conceptual diagram of the controlling factors over plant litter decomposition (grey arrows and black boxes) that additionally summarizes the aspects assessed in this study (red arrows and boxes with bulleted lists). Numbers along the outer arrows indicate the specific chapters of this study.

Decomposers

Decomposition is driven by a vast number of soil-dwelling organisms (Berg *et al.* 2001; Lavelle & Spain 2001; Berg & Laskowski 2006). The term ‘decomposers’ refers to organisms at various trophic levels in the soil food web. As these trophic groups are both bottom-up and top-down controlled, all soil food web groups affect the decomposition process. The most important levels and their interactions are briefly introduced below.

The group of the primary decomposers is formed by fungi and bacteria (Swift *et al.* 1979; Berg & Laskowski 2006). They have the biochemical and enzymatic capabilities needed to degrade litter chemically, i.e., they break down complex chemical compounds, such as polyphenols, lignins, tannins, cellulose and hemicelluloses into water, carbon dioxide, nutrients and simpler organic compounds. This unimaginably vast but poorly understood group (Finlay & Clarke 1999; Groombridge & Jenkins 2002; De Deyn & Van der Putten 2005) is in charge of organic compound degradation not only by their own activity but also by influencing the activity of other soil organisms. Micro-organisms influence their subsequent trophic groups, for instance by increasing the palatability of litter for faunal detritivores by degrading waxes on the leaf surface and breaking down secondary metabolites. The detritivores consist of faunal groups such as, Enchytraeidae, Oribatida, Collembola, isopods, millipedes, and fly larvae that primarily fragment and ingest dead organic matter. The interactions between detritivores and micro-organisms are rather complicated. As the microbes enhance the palatability of litter, detritivores provide new growth surface for microbes on both plant litter and the digestive tracts of the detritivores. Detritivores, similarly to other soil fauna that feed on microbial residues and micro-organisms (i.e., microbivores) are classified as secondary decomposers because their effect on litter degradation depends on primary decomposers, the microbes. Both fauna groups provide faeces that micro-organisms use as a source of nutrients. Microbivores also increase the turnover rate of microbes by their grazing activities, as grazing on microbes regulates the microbial community structure and spreads microbial populations.

The higher trophic level i.e. predators regulate soil detritivore and microbivore communities and indirectly affect plant litter decomposition by limiting the grazing of detriti- and microbivores. The net effect of predators on plant litter decomposition can be either positive or negative depending on environmental conditions and the trophic community composition (Lawrence & Wise 2004). Grazing on microbes and microbivores releases nutrient-rich faeces (and thus increases the amount of available nutrients) for microbes to re-utilize and thus improves decomposition as microbes consume more carbon in the form of plant litter when they are not limited by nutrients. On the other hand, overgrazing on microbes retards decomposition rates.

Micro-arthropods

The most important and the most abundant groups of both secondary decomposers and soil micro-arthropods are Collembola and Oribatida (Petersen & Luxton 1982). These soil micro-arthropod groups are generally considered to be fungivores (Seastedt 1984). In forest soils of high organic matter content the population densities of Collembola and Oribatida can reach values up to 100,000 and 400,000 per m², respectively (Petersen & Luxton 1982). As these groups are evolutionally ancient (Lindquist 1984; Hopkin 1997) and truly omnipresent (Coleman *et al.* 2004), their taxonomy has attracted great interest. As a result, the taxonomic resolution is high in both groups although the vast number of Oribatida taxa (Schatz 2002) offer still plenty

of work. As the taxonomic development is a key requirement for trait level assessment, micro-arthropods offer good ground for trait-based community assessments. Chapters II and III assess micro-arthropod communities in soil and litter, respectively. Specifically a trait assessment on the micro-arthropod community is conducted in Chapter II, where traits are used to help us understand the responses of soil Collembola community to altered soil climatic conditions. Chapter III instead looks at both, Collembola and Oribatida, communities associated with plant litter decomposition.

Abiotic environment

The abiotic environmental factors controlling the composition and activity of the decomposer community structures are captured by climate and soil conditions (Swift *et al.* 1979; Cadish & Giller 1997). Soil conditions are mainly determined by geology (soil texture and structure) and environmental conditions (e.g. pH, temperature), and they regulate the flow of water and gases and the ability of soils to retain nutrients (Bardgett 2005). Thus, together the indirect and direct effects of climate play a major role in controlling the decomposer communities and thus plant litter decomposition.

As the most crucial characteristics of climate for decomposers are temperature and moisture, and their interactions, good proxies for their combined effect on plant litter decomposition are the actual evapotranspiration (AET: Aerts 2006; Berg & Laskowski 2006) and the climatic decomposition index (CDI: Parton *et al.* 2007). Both temperature and moisture are positively correlated with litter decomposition rates, when the extremes are not considered (Lensing & Wise 2007). For example, the activity of micro-arthropods is directly linked to temperature, but to colonize the plant litter and thrive in the given temperature regime, the moisture conditions have to meet their moisture preferences (Whitford 1989; Hodkinson *et al.* 1999; Lindberg 2003). Microbes are similarly controlled strongly not only by temperature (Hobbie 1996), but also by moisture as is shown by soil respiration (Reichstein *et al.* 2002; Cisneros-Dozal *et al.* 2007) and soil enzyme activity assessments (Sardans & Penuelas 2005). Moreover, fecundity, development rate, sex ratio and dispersal of soil fauna species are affected by temperature and thereby they mediate temperature effect on decomposition. Soil fauna species and groups differ and interact in their responses to changes in moisture and temperature. Thus trait-based assessments are good in studying and predicting the responses of soil fauna communities to environmental change and the subsequent effects on plant litter decomposition.

Climate change

According to the IPCC 2007 report, global climatic change includes world-wide changes in both temperature and moisture conditions (Meehl *et al.* 2007). Thus, climate change will most likely affect litter decomposition rates and soil organic matter content. Moreover, global climatic warming will continue and precipitation patterns will change as well (Meehl *et al.* 2007). The magnitude and directions of these changes will vary quite extensively between regions (Christensen *et al.* 2007). Climate warming will be most manifested at higher latitudes, as the annual mean temperature increase in the arctic will be two-fold compared to the global mean. Ecosystems at higher latitudes are especially vulnerable to changes in the climatic parameters (ACIA 2005), as the organisms living there are already most northern in their distribution. Chapter II assesses the effect of mimicked climate change on micro-arthropod community in high latitudinal subarctic area.

Plant litter quality

Plant litter provides the basic substrate for decomposers and thus regulates plant litter decomposition bottom up. The quality of litter encompasses both their physical and chemical characteristics (Swift *et al.* 1979) and varies greatly among species (Pérez-Harguindeguy *et al.* 2000; Cornwell *et al.* 2008). Especially, the ratios between nitrogen (N), lignins and other secondary organic compounds (i.e. humic substances) are strongly related to litter decomposition rates (Couteaux *et al.* 1995; Aerts 1997; Hättenschwiler & Vitousek 2000; Trofymow *et al.* 2002; Cornwell *et al.* 2008; Zhang *et al.* 2008; Currie *et al.* 2009; Prescott 2010). Nitrogen is often limiting the growth and turnover of microbial and detritivores' biomass. Thus, a lower litter C:N ratio usually implies faster microbial and faunal growth, followed by enhanced degradation rates. Unlike nitrogen, lignin has a negative correlation with plant decomposition rates. The large molecular size and aromatic structure of lignin demand energy consuming degradation processes by micro-organisms (Ander & Eriksson 1978). Other important chemical characteristics of litter for decomposition are pH, other nutrients and (heavy) metals (Berg & Laskowski 2006).

The control of physical plant traits on litter decomposition has received less attention than that of the chemical controls. It has been shown that leaf toughness (Gallardo & Merino 1993; Cornelissen & Thompson 1997) and Specific Leaf Area (SLA) (Cornelissen *et al.* 1999; Vaieretti *et al.* 2005; Santiago 2007) are important physical characteristics of litter quality that affect plant litter decomposition rates. Similarly, other physical characteristics, such as surface properties, particle size, moisture holding capacity are hypothesized to be important (Swift *et al.* 1979) but are only seldomly included in decomposition studies. The lack of plant litter physical traits' use in decomposition studies is a clear omission as these are important determinants of the community structure and activity of decomposers. In contrast with the vast majority of plant litter decomposition studies, Hansen (2000) considered the effect of litter architecture on decomposer community and De Oliveira *et al.* (2010) the tri-dimensionality and foliar resistance on litter consumption by macro detritivores. Both studies suggested a strong causal link between these effects and the fate of plant litter, although they did not explicitly test them.

A link between plant litter and soil fauna diversity

In many studies litter decomposition is assessed at the level of individual plant species. However, in nature litter usually decomposes in multi-species mixtures. Unfortunately, decomposition rates in mixtures cannot be predicted from the decomposition rates in monocultures (Wardle *et al.* 1997; Gartner & Cardon 2004). This so-called non-additivity in litter mixtures does not only occur because litter quality varies strongly among species and during the decomposition process, but also because co-occurring litter species affect each other both chemically and physically (Hättenschwiler *et al.* 2005).

A further complication in mixed litters is that we do not know how the component litter species diversity affects the decomposer communities. As we are living in an era of major biodiversity loss (Secretariat of the Convention on Biological Diversity 2010), an important question in litter decomposition research is whether the diversity in plant litter species translates to decomposition rates and moreover whether it is regulated via changes in the diversity of decomposers. Chapters III and IV study the effects of litter diversity. In particular, Chapter III assesses the responses of micro-arthropod community to litter diversity and Chapter IV looks into the mechanisms of

litter traits modifying the decomposers' microenvironment in litter mixtures. Importantly both of these chapters use both chemical and physical litter traits.

Aims and outline of this thesis

The general aim of this thesis is to improve the mechanistic understanding of the biological and environmental controls on plant litter decomposition and decomposer communities in forest ecosystems. The mechanistic assessments are carried out by trait-based approaches. The work presented in this thesis is broad as I used two different climate manipulation methods (open-top chambers (OTC) and experimentally increased precipitation), assessed the effects of identity, community and diversity of leaf litters on decomposition rates and studied the responses of Collembola and Acari communities to both climate manipulation and variation in litter diversity. Altogether four separate field experiments were conducted, of which the three first ones were done exclusively in subarctic Sweden. Subarctic Sweden was the main study area because climate change is most manifest in high-latitude ecosystems. In that area, I focused on dry mountain birch forests and studied the effects of changes in temperature and moisture on soil fauna and leaf litter decomposition of forest plant species. In this study, I focused on specific research questions which are introduced below and the chapters assessing these are indicated in Figure 1.

Can we use fauna traits in understanding the responses of soil fauna communities to climate change?

Unlike the responses of plant communities (Arft *et al.* 1999; Walker *et al.* 2006), the responses of soil biota to climate change are still poorly understood. Although several studies have assessed the effect of mimicked climate change on soil fauna groups such as microbes (Rinnan *et al.* 2007), nematodes (Ruess *et al.* 1999), Collembola (Sjursen *et al.* 2005) and Acari (Webb *et al.* 1998), the information for each specific group is still scarce and we are still far away from understanding the general principles of how climate change will affect soil fauna and, in turn, how these relate to soil processes such as plant litter decomposition. Chapter II studies the effect of altered soil moisture and temperature conditions (an OTC treatment) on the soil Collembola community in a subarctic mountain birch forest. Moreover the aim was to unravel the mechanistic responses in Collembola communities to the OTC-induced changes in soil conditions by using various Collembola morphological and ecological traits.

Is there a link between diversities in plant litter and micro-arthropods and do physical traits of plant litter explain the litter mixing effects?

In order to improve the estimates of decomposition rates and its contribution to the global carbon cycle we should find the mechanisms controlling litter mixing effects. From the decomposer perspective I chose two topics for this study. First of all I wanted to assess how decomposer communities are affected by litter diversity. This was the main topic of Chapter III, where a link between diversities in plant litter and soil micro-arthropod communities was assessed. Chapter IV, on the other hand, focused on the mechanisms underlying the litter mixing effects that may rise from litter physical trait heterogeneity and investigates whether these mechanisms are modified by water availability.

Are there global patterns in the control of litter quality and decomposers on decomposition?

Experiments on small spatial scales can provide thorough mechanistic assessments of ecosystem processes. Nevertheless, the generality of these mechanisms cannot be assessed by these independent experiments as the factors that determine ecosystem structures and govern processes differ depending on spatial scales (Schneider 2001; Urban 2005). On a global scale a hierarchical order in the three main factors controlling plant litter decomposition has been assumed (Lavelle *et al.* 1993). The most important controlling factor is assumed to be the climate, after which comes litter quality and the decomposers with the weakest control. Nevertheless, this hierarchy has been questioned by recent meta-analysis (see Chapter V, Cornwell *et al.* 2008; Zhang *et al.* 2008) who found that plant litter quality was a stronger controlling factor for decomposition than climate. Furthermore the effect of decomposers has not been included in most of the assessments. In order to aid modeling purposes, the common biotic controls over plant litter decomposition were analyzed across a large latitudinal gradient in Chapter V. The large latitudinal gradient included four distinct biomes ranging from subarctic birch forest to tropical rain forest. In this chapter the fundamental mechanisms of global litter quality controls on plant litter decomposition were assessed in the presence of different decomposer communities grouped based on their size-classes.

Finally, in Chapter VI I synthesize the different elements of this study and formulate answers to the specific research questions introduced above.

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Chapter I

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