Regulation of Litter Decomposition in Forest Ecosystems of Sweden and New Zealand

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Cover: Understory of temperate rainforest, Island Hill,
       Westland, New Zealand (photo: B.Jackson)

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Abstract

Litter decomposition is a core ecosystem process critical for carbon and nutrient cycling, and the functioning of terrestrial ecosystems. This thesis explores two contrasting ways by which plants can influence litter decomposition in forested ecosystems. The first half of the thesis examined the role of feather mosses in mediating the environmental conditions on the soil surface in boreal forests and the impact this has on litter decomposition. The feather moss layer intercepts much of the litterfall in boreal forests as well as retaining significant quantities of rainfall. The results showed that the pattern of moisture inputs to the moss layer was a major driver of litter decomposition and moss-associated cyanobacterial N_2-fixation. Under conditions of limited moisture availability the mosses promoted the decomposition of leaf litter within the moss layer by preventing the desiccation of the litter, maintaining decomposer activity. In this way the effect of the moss layer was dependent on the prevailing moisture conditions. Further, the results showed that the moss layer promoted the decomposition of intercepted leaf litter to a similar extent across all stages of a 360-year successional gradient, despite a large increase in the depth of the moss layer and changing ecosystem properties. The second half of the thesis investigated two poorly explored aspects of the relationships between plant functional traits, litter quality and litter decomposition in temperate rain forests in New Zealand. The results showed that the decomposition of leaf, twig and wood litter of 27 co-occurring tree species was uncoordinated. This lack of coordination occurred because wood decomposition was driven by differences in the wood density of trees, which itself was unrelated to the chemical traits driving the decomposition of leaf and twig litter. The results also revealed a high degree of intraspecific variation in the leaf functional traits and leaf litter decomposition of 16 co-occurring plant species. Within species, leaf traits varied predictably in response to a soil nutrient gradient but were not related to the variations in decomposition. Overall, the results of this thesis illustrate the important and contrasting impacts that plants can have on litter decomposition, and contributes to the understanding of the complex interactions between multiple factors that regulate litter decomposition in forest ecosystems.

Keywords: boreal forest, temperate rain forest, litter decomposition, feather moss, succession, plant functional traits, coarse wood debris, intraspecific variation.

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Dedication

To Mum and Dad

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Jackson B.G., Martin P., Nilsson M-C. & Wardle, D.A. (2011). Response of feather moss associated N_2-fixation and litter decomposition to variations in simulated rainfall intensity and frequency. *Oikos* vol 120(4), 570-581.

II Jackson B.G., Nilsson M-C. & Wardle, D.A. The effects of the moss layer on the decomposition of intercepted vascular plant litter across a post-fire boreal forest chronosequence. *Submitted manuscript*.

III Jackson B.G., Peltzer D.A. & Wardle, D.A. (2012). Are functional traits and litter decomposability coordinated across leaf, twig and wood tissues? A test using temperate rainforest tree species. *Oikos* In press doi: 10.1111/j.1600-0706.2012.00056.x

IV Jackson B.G., Peltzer D.A. & Wardle, D.A. The within-species leaf economic spectrum does not predict intraspecific leaf litter decomposition, nor improves the power of community trait measures to predict decomposition. *Manuscript*.

1 Introduction

1.1 Decomposition: a fundamental ecosystem process

The decomposition of organic matter has long been studied as a fundamentally important ecosystem process (Cadisch & Giller, 1997; Swift *et al.*, 1979). In terrestrial ecosystems, the decomposer subsystem broadly performs two key functions, the degradation and mineralisation of dead organic matter, and soil formation and development (Swift *et al.*, 1979). Together these functions exert major controls over the carbon cycle, soil nutrient availability, and consequently, plant growth and community structure (Bardgett, 2005; Wardle, 2002). An understanding of the factors that influence decomposition is thus essential to the broader understanding of ecosystem functioning and our ability to forecast the effects on ecosystems of global change phenomena such as biodiversity loss, land use change, eutrophication, and climate change.

A long-standing challenge in ecological research is to understand how the great diversity of organisms in any given ecosystem contributes to the overall functioning and development of that ecosystem (Maestre *et al.*, 2012; Loreau *et al.*, 2001). Research efforts directed towards answering the underlying questions of how biodiversity and ecosystem process are related, are of particular importance given: (i) the unprecedented rates of biodiversity loss world wide (Cardinale *et al.*, 2012) and (ii) the extensive changes to ecosystems including the loss and gain of species caused by other global change drivers (Wardle *et al.*, 2011). In the last twenty years, much of the initial focus of biodiveristy-ecosystem function research was on above ground processes and in particular, primary productivity (Loreau *et al.*, 2001). However, more recently over the last decade, the role of biodiversity in below ground processes including decomposition has received much greater attention (Gessner *et al.*, 2010). The decomposer subsystem is the most complex component of terrestrial ecosystems, in particular because of the numbers and

diversity of organisms it involves. There are many pathways and mechanisms by which microbial, fungal, animal and plant diversity can influence decomposition and other below ground processes.

1.2   Regulation of litter decomposition

In general, three principle factors regulate the decomposition of plant organic matter in terrestrial ecosystems (Figure 1;Aerts, 1997; Couteaux *et al.*, 1995): (i) Across broad regional scales, plant litter decomposition rates are strongly related to mean annual temperate and precipitation. Actual evapotranspiration (AET) is commonly used as an effective predictor of litter decomposition in global biogeochemical models (Aerts, 1997; Couteaux *et al.*, 1995); (ii) At local scales where climatic conditions are relatively constant, litter quality dominates as the principle determinant of decomposition rates (Cornwell *et al.*, 2008). Litter quality is governed by the relative proportions of its chemical constituents. Plant litter of higher quality will tend to have greater concentrations of nutrients such as nitrogen (N) and phosphorus (P) and labile carbohydrates, while plant litter of lower quality will tend to have greater concentrations of complex, stable organic compounds, in particular lignin but also secondary compounds such as tannins and phenolics; and (iii) Specific groups and assemblages of decomposer soil fauna such as earthworms, nematodes, mites and collembola as well as the relative abundance of bacteria vs. fungi in the decomposer flora can have major impacts on how litter decomposition proceeds (Bardgett & Wardle, 2010; Wall *et al.*, 2008; Hattenschwiler *et al.*, 2005). In addition, all three of these major regulating factors can interact at varying spatial and temporal scales making the understanding of the drivers of decomposition significantly more difficult. Further, plants are known to directly or indirectly impact all three of these factors. This thesis focuses on two pathways by which plant functional groups and plant diversity can influence litter decomposition in forested ecosystems, namely: (A) through the modification of local environmental conditions; and (B) by determining the quality and quantity of litter entering the decomposer subsystem (Figure 1).

The physical forms of plants and plant communities as well as the functions they perform can significantly modify local environmental conditions and create heterogeneous patches of microclimatic conditions (Maestre *et al.*, 2005), with consequences for ecosystem processes such as decomposition. Examples include: (i) the interception of light by tree canopies that prevent the passage of solar radiation to the forest floor and reduce soil temperatures; (ii) the modification of the passage of water through ecosystems by the

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interception of rainfall and fog by plant structures or by hydraulic uplift by deep rooted plants transferring water to surface soils (Eviner & Chapin III, 2003). However, as with other aspects of the structure and functioning of ecosystems, the effects of plants on environmental conditions can differ significantly between species. A longstanding approach to understand plant species in terms of their effects on ecosystems has been to classify species into functional groups, groups of species that have common characteristics and consequent effects on a particular ecosystem process. In forest ecosystems, trees have been long studied as a predominant functional group of plants having important effects on ecosystem processes including their modification of local environmental conditions. However, understory plants are now increasingly recognized as also having groups of species, with important effects on the functioning of some forest ecosystems (Hart & Chen, 2008; Nilsson & Wardle, 2005). Feather mosses are an important functional group of plants in the understory of boreal forests known to mediate environmental conditions that may have important potential consequences for litter decomposition.
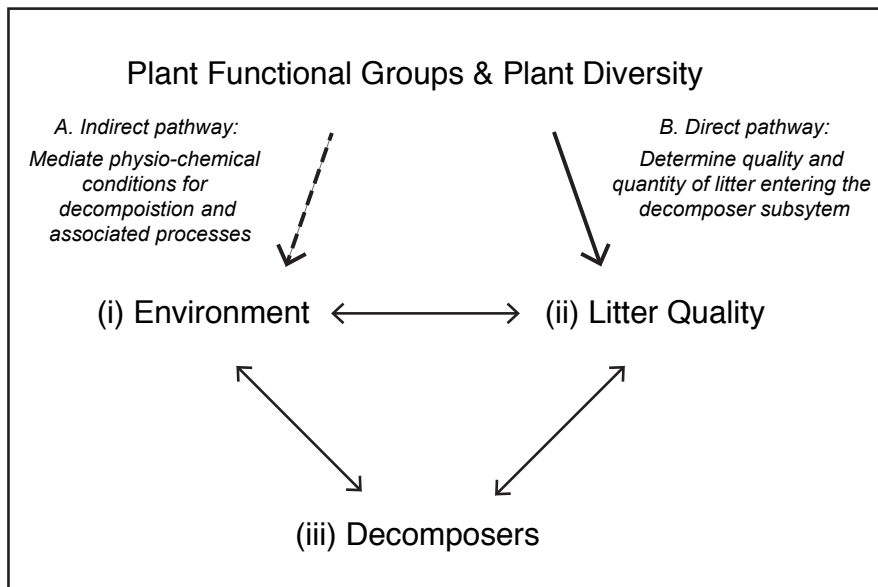

Figure 1. This thesis focuses on two pathways (A and B) by which plant functional groups and plant diversity can influence the principle factors regulating litter decomposition in terrestrial ecosystems (i, ii, and iii).

In addition to modifying environmental conditions in terrestrial ecosystems, plants are usually the main sources of dead organic matter entering the decomposer subsystem, with up to 90% of plant productivity channelled as detritus (McNaughton *et al.*, 1989). The quality of plant-derived litter varies greatly between plant species and between different plant organs. As such, consideration of the composition and relative abundance of species in plant communities are central to the understanding of the quality of plant litter entering the decomposer subsystem and hence litter decomposition rates. Characterizing and comparing the differences in litter quality between plant species can be achieved through the measurement of plant functional traits (PFTs). These PFTs are indicators of how plants respond to their biotic and abiotic environments and/or how they affect ecosystem processes and properties (Suding *et al.*, 2008; Violle *et al.*, 2007), in this case decomposition. Extensive research into PFTs has shown that many of the functional attributes of living plant tissues are well conserved after senescence (Cornelissen, 1996) and are effective predictors of litter decomposition rates (Cornwell *et al.*, 2008). However, there remain many aspects of the relationships between plant functional traits, litter quality and decomposition that have not been explored.

1.3   Mosses in the understory of boreal forests

The understory is an important component of boreal forests known to have strong effects on the decomposer subsystem and soil properties of these ecosystems (Nilsson & Wardle, 2005). Two distinct functional groups of plants dominate the boreal forest understory, ericaceous dwarf shrubs and feather mosses. Feather mosses are the most abundant moss species in boreal forests and typically dominate the ground layer forming a dense, continuous mat covering the soil surface. Both the mosses and the structure of the moss layer possess a number of characteristics with important consequences for carbon and nutrient cycling that remain poorly characterized. The dense and contiguous structure of the moss layer intercepts most of the litter fall from the trees and shrubs. Few estimates exist of the extent of the interception of litter by understory species but it has been shown to be as high as 60-70% in some forests (Hendricks *et al.*, 2002; Alvarez-Sanchez & Guevara, 1999). However, by preventing the litter from reaching the soil surface, the interception and retention of litter in the moss layer in boreal forests has potentially important but largely unexplored consequences for the subsequent decomposition of the litter. To date, a handful of studies have quantified the effects of mosses on litter decomposition, and these have provided conflicting results. While on one hand mosses can insulate the soil surface, buffering soil temperatures and thus

retarding decomposition (Vancleve *et al.*, 1991; Bonan & Shugart, 1989), they may also promote litter decomposition through moisture retention and maintaining the water content of decomposing litter (Hoorens *et al.*, 2009; Wardle, 2003).

Like all bryophytes, feather mosses are also poikilohydric organisms, lacking roots and a cuticle to prevent desiccation and are thus dependent on rainfall inputs to maintain their water status (Busby *et al.*, 1978). However, the moss layer is well adapted to intercept and retain moisture and nutrient inputs and under favorable conditions can be highly productive (Rydgren *et al.*, 2001; Okland & Okland, 1996). Further, boreal feather mosses host cyanobacteria capable of fixing atmospheric N that can be the principle source of biologically fixed N in these forests (DeLuca *et al.*, 2002a). In northern Sweden, during forest succession the rates of N_2-fixation in the moss layer increase with stand age and can exceed 2 kg N ha^{-1} yr^{-1}. This represents ~50% of total N inputs in mid- and late-successional forests (Lagerstrom *et al.*, 2007; Zackrisson *et al.*, 2004). Although the growth of feather mosses has been shown to be limited by water availability (Frolking, 1997; Busby *et al.*, 1978) and the nitrogenase enzyme in some cyanobacterial species is susceptible to droughting (Scherer *et al.*, 1984; Coxson & Kershaw, 1983), it is not known if N_2-fixation occurring within the moss layer in boreal forests are also affected by water availability. Similarly, it is unclear if the decomposition of intercepted leaf litter in the moss layer may also be affected by moisture availability. These questions are important for two reasons. First, past records indicate that the boreal zone in northern Sweden has strong inter-annual variation in rainfall both in terms of the amounts and frequency of events (SMHI, 2000). Such variations may strongly affect moss-associated processes. Second, precipitation patterns are expected to change as a consequence of global climate change. The predictions based on the IPCC models for the boreal region in northern Europe, indicate increases in both mean summer precipitation and the frequency of rainfall events during summer over the next 80 to 100 years (Meehl & Stocker, 2007). It is also increasingly recognized that changes in the frequency and intensity of rainfall events will have stronger effects on ecosystem functioning than will shifts in mean values of global change drivers such as temperature and CO_2 (Jentsch & Beierkuhnlein, 2008). Despite this, the potential consequences of changing precipitation regimes for the functioning of boreal ecosystems have attracted little attention.

In the prolonged absence of wildfire, succession in the plant communities of boreal forests results in important changes in both the overstory and understory (Turetsky *et al.*, 2010; Nilsson & Wardle, 2005). Together with changes in the plant community, several important ecosystem properties shift, including a

reduction in productivity, and declines in the rates of litter decomposition and nutrient cycling (Wardle & Zackrisson, 2005). In the understory, the ericaceous dwarf shrubs are known to play an important role in driving the changing ecosystem properties. Early successional shrub species provide higher quality resources and enhance microbial growth (Wardle & Zackrisson, 2005), while later successional species produce recalcitrant litter which are rich in secondary compounds and that have inhibitory effects on the decomposer subsystem (Joanisse *et al.*, 2007; Bloom & Mallik, 2006; Nilsson, 1994; Nilsson *et al.*, 1993). However, changes also occur to the moss layer during succession. While feather mosses remain the dominant moss species throughout succession, in the absence of fire the biomass and density of mosses increases as forest stands age. Further, in comparison to the vascular species in boreal forests, feather mosses produce recalcitrant litter that decomposes relatively slowly (Lang *et al.*, 2009), resulting in an increase in the depth of the moss layer (including both live and dead moss segments) over time. These changes to the characteristics of the moss layer during ecosystem succession may also have important effects on litter decomposition and nutrient dynamics but have not previously been explored.

1.4   Afterlife effects of plant functional traits

Over the last 20 years, the vast bulk of research on plant functional traits has been focused on the traits of leaves as key plant organs that perform essential functions, and that reflect aspects of the plant's ecological strategy. Leaf functional traits are readily measured and this has resulted in the generation of many large trait data sets. Global syntheses of these trait data have lead to significant insights including the identification of the leaf economic spectrum (LES) (Diaz *et al.*, 2004; Wright *et al.*, 2004; Grime *et al.*, 1997). The LES describes an axis of specialization along which all vascular plants trade off the rapid acquisition of resources and rapid leaf growth and turnover, with the conservation of resources and leaf protection and longevity (Wright *et al.*, 2004). Further, many of the same leaf economic traits have also been shown to be the principle determinants of the quality of the leaf litter produced by plant species and are thus a major factor regulating litter decomposition rates world-wide (Cornwell *et al.*, 2008; Santiago, 2007).

Despite these and other significant advances in plant functional trait research, there are important gaps in our understanding. Two such gaps have been attracting attention recently. First, the functional traits of plant organs other than leaves, such as stems, branches and roots are typically more difficult to quantify, and in comparison with leaf traits have rarely been measured.

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However, it is now recognized that in order to more accurately understand the ecological strategies of whole plants and their contributions to ecosystem processes, it is necessary to corroborate the insights made from leaf traits analyses with comparative analyses of the traits of other plant organs. Second, it has been generally believed that functional traits are relatively invariant within a species and that mean values of traits are sufficient to capture the strategy and function of a species. Nonetheless, a number of new data sets with highly replicated trait measures of individual plant species across communities, have brought into question this poorly tested assumption.

In addition to leaves, other plant organs are integral to the growth and survival of plants, and the traits of these organs should also reflect plant ecological strategies and determine important effects of plants on ecosystem processes (Freschet *et al.*, 2010; Suding *et al.*, 2008; De Deyn *et al.*, 2004). Wood plays a critical structural function in trees and other woody plant species. In forest ecosystems, standing stocks of live and dead wood can represent significant carbon and nutrient pools, but understanding of how differences between species in the characteristics of their wood impacts on decomposition and other ecosystem processes remains poor. Some of the most extensive measurements of wood traits across tree species has come from the Amazon, and these have identified a spectrum of wood trait variation across species analogous to the LES (Chave *et al.*, 2009). This wood economic spectrum (WES) describes physiological, structural and defensive tradeoffs across species in the characteristics of their wood. In support of the ecological significance of the WES, several other studies have since shown that key traits underpinning the WES are linked to demographic processes including growth, mortality and the life history strategies of wood species (Poorter *et al.*, 2010; Russo *et al.*, 2010). The integration and potential coordination of functional traits across plant organs has also been examined in three studies that have compared variation across species in their leaf traits with that of their stems and/or roots (Baraloto *et al.*, 2010; Freschet *et al.*, 2010; Ishida *et al.*, 2008). These include a recent study from the Swedish subarctic, which found the variation across species in the traits determining the rates of decomposition of their leaves, stems and roots to be highly coordinated (Freschet *et al.*, 2010). This resulted in consistent interspecific patterns of decomposition across the different plant organs. However, to date no study has established if processes driven by leaf and wood traits such as their decomposability are closely coordinated among organs for tree species.

Just as most studies of plant functional traits have focused on leaf traits, most have also focused on the differences between species to explain ecological patterns. An unintended consequence of this has been the neglect of

the potential importance of within species trait variability. However, a handful of data sets now show that the magnitude of within species trait variation (WSV) relative to between species variation (BSV) is much larger than previously thought. Further, through novel analyses these studies have demonstrated that the extent of the WSV is sufficient to impact measures of functional diversity (Albert *et al.*, 2011; Albert *et al.*, 2010a), community assembly (Jung *et al.*, 2010), and how communities respond to environmental gradients (Albert *et al.*, 2010a; Jung *et al.*, 2010). Accordingly, several authors have highlighted the need for further exploration of the circumstances and species for which WSV should be considered (Violle *et al.*, 2012; Albert *et al.*, 2011; Hulshof & Swenson, 2010). It has also been suggested that WSV may impact ecosystem processes like decomposition but as yet this remains untested. Significant WSV in leaf and litter traits have been observed to influence the decomposition of leaf litter for individual species (eg. Lecerf & Chauvet, 2008; Schweitzer *et al.*, 2004). However, as of yet, no multi-species studies have investigated the potential impact of WSV to drive differences in litter decomposition within species nor how this in turn may impact how decomposition varies between whole plant communities.

1.5 Objectives

The overall aim of this thesis is to further our understanding of how functional groups of plants and plant functional traits influence the decomposition of plant organic matter in forested ecosystems (Figure 1). Papers I and II examine the role of mosses in Swedish boreal forests in decomposer processes through the interception of litterfall. Specifically, Paper I examines how the moss layer buffers moisture availability within the moss layer and the consequences of this for litter decomposition and N_2-fixation rates occurring within the moss layer Meanwhile, Paper II explores the effect of the moss layer during the successional development of boreal forests. Papers III and IV focus on the role of plant functional traits in determining the litter quality and decomposition of plant litter in temperate rainforests of New Zealand. As such, Paper III explores the links between the traits of the leaves, twigs and wood of tree species and their relationships to the decomposition of litter from these plant organs. Meanwhile Paper IV compares within and between-species variation in leaf and litter traits of co-occurring forest species and their importance in driving the litter decomposition for individual species and whole plant communities.

The central questions of each of the papers in this thesis are:

I   How do variations in the amount and frequency of rainfall affect litter decomposition and N_2-fixation occurring within the moss layer in boreal forests?

II   During succession in the boreal forests, how does the presence and development of the moss layer influence the decomposition of intercepted vascular leaf litter?

III Are the functional traits of leaves and litter of trees coordinated such that species with high quality leaf litter also have high quality twig and wood litter, resulting in coordinated interspecific patterns in the decomposition of different litter types?

IV   Does within-species variation in leaf traits drive within species variation in litter decomposition and what impact does this have for community level measures of traits and litter decomposition?

2 Materials and Methods

2.1 Experimental designs

In Paper I a greenhouse pot experiment was constructed to assess the combined influence of simulated rainfall intensity and frequency as well as the presence vs. absence of mosses on litter decomposition and N_2-fixation within the moss layer. A total of 432 plastic pots were each filled to 15 mm with soil and then a moss layer of *Pleurozium schreberi* was reconstructed over the soil surface in half of the pots. In addition, one ionic resin capsule was placed on the soil surface in each pot to estimate the cumulative N and P availability during the course of the experiment. Then six *Pinus sylvestris* needles of known weight were placed into each pot. The needles were inserted vertically into the moss layer in pots with mosses or placed on the soil surface in pots without mosses. Once constructed, pairs of pots, one with and one without mosses, were divided between treatment groups in a fully factorial design with n=8 replicates per treatment combination. Three different frequencies of water application (infrequent, moderate and frequent) were combined with three volumes of water (low medium and high) in a "frequency × volume" design for a total of 9 treatments groups. Water treatments were chosen to represent the range of conditions observed in the region as well as probable changes to rainfall regimes that are expected to occur with climate change by 2080-2100. Water treatments were applied for a seven-month duration and three separate destructive harvests, each representing one third of the total number of pots, were performed after 51, 130, and 214 days. At each harvest, the influence of the watering regimes on N_2-fixation in the moss layer and the decomposition of the needle litter together with the accumulation of N and P in the resin capsules were assessed. In addition, at the final harvest the relative activity of the soil microbial biomass was assessed by measuring substrate-induced respiration (SIR).

In Paper II a "removal experiment" approach was used to examine the effects of specific functional groups of plants within the understory of boreal forests, mosses and shrubs, on the decomposer subsystem. Ten forest stands varying in age from 43 to 362 years since the last wildfire were used and in each stand four 1×1 m plots were established. Moss and shrub removal treatments were applied in June 2007 to these four plots i.e. mosses removed, dwarf shrubs removed, mosses and shrubs removed and a control with both functional groups present. Given the focus of this study on the effects of the moss layer on decomposition that occur at particularly fine scales, the use of litter bags was deemed unsuitable for the purposes of this experiment. Instead, unconfined, tethered needle and leaf litter from three litter species *Pinus sylvestris*, *Betula pubescens* and *Vaccinium vitis-idaea* were introduced into each of the plots in June 2008.

Figure 2. Tethered birch leaves strung up in boxes before their installation into the experimental plots. Leaves and needles were tethered to facilitate retrieval of the unconfined litter after the decomposition period.

Ten individual air-dried leaves or needle pairs of known weight were carefully tied sequentially onto tethers made of dental floss (Figure 2). A total of 80 tethers for each litter species were constructed each containing 10 leaves or needle pairs for a total of 2400 leaves and needles. At each stand the two plots with mosses removed received one tether of each litter species with the litter placed on the soil surface within the plot. The two plots with mosses present received three tethers from each species. One tether per species was

installed on the surface of the moss layer, one carefully inserted within the moss layer and one underneath the moss layer at the interface with the soil. After a full year of decomposition in the field, all litter was recovered with over 96% of individual leaves and needles successfully retrieved.

In both Papers III and IV all litter was decomposed in standardized laboratory bioassays (Wardle *et al.*, 2002) in order to assess the relationships between the PFTs of the leaves and litter and the decomposability of the litters. Accordingly, for the leaf litter from each individual from each species and from each species × plot combination in Papers III and IV respectively, three 9 cm Petri dishes were two thirds filled with a standardized humus substrate amended to 300% moisture content and covered with nylon mesh with 1 mm holes; to each Petri dish 1g subsamples of air dried leaf litter were cut into $2cm^2$ fragments and placed on the surface of the mesh; the Petri dish was then sealed to prevent water loss and incubated for 4 months at 22 °C. Similarly, for the twig and wood litter in Paper III from each individual from each species, three glass jars were one-third filled with a standardized humus substrate amended to 300% moisture content. For the twig litter, a nylon mesh (as above) was place on the soil surface in the jars and 1g air-dried twig litter cut to 30mm lengths added to each jar. For the jars with wood litter, one cylindrical plug of wood (10 mm in diameter and 30 mm in length) was placed directly on the soil surface (Figure 3). Twig and wood litter was incubated for 20 months at ~20 °C and after five, ten and 15 months the moisture content of the humus in a subset of the jars was checked and the moisture content of all jars adjusted to 300%.
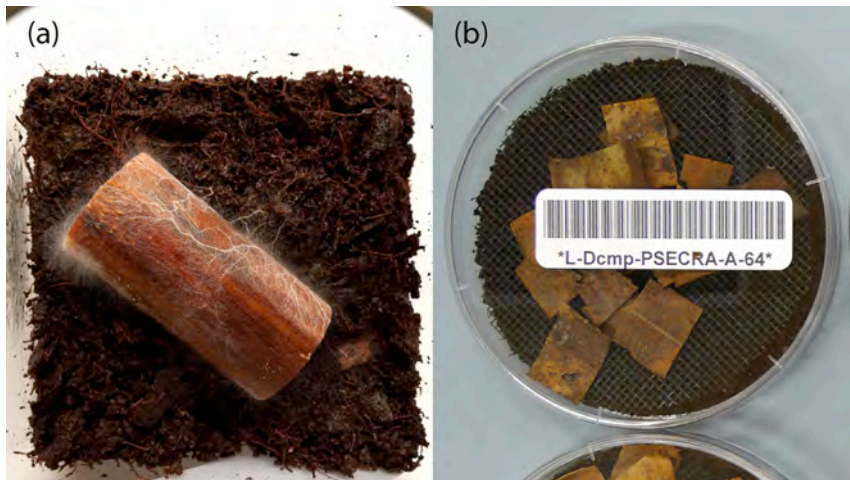

Figure 3. Examples of (a) wood litter and (b) leaf litter decomposing under controlled conditions. Photos: B.Jackson

2.2 Study Systems

2.2.1 Boreal forests

Papers I and II focus on boreal forests situated around the town of Arvidsjaur in northern Sweden (65°35'–66°07'N, 17°15'–19°26'E) (Figure 4a). The area has a cold temperate humid climate with a mean annual temperature of -2 °C (July temperature 12 °C, January temperature -14 °C) and a mean annual precipitation of 600 mm. The studied forests have developed on soils consisting of granitic glacial till, classed as either Typic or Entic Haplocryods (Zackrisson *et al.*, 1996). Forests in this region are dominated by the tree species *Pinus sylvestris*, *Betula pubescens* and *Picea abies* (Figure 5). The forest understory or field layer is principally comprised of three ericaceous dwarf shrubs, *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum hermaphroditum*. The ground layer consists of mosses and lichens and is typically dominated by the feather moss *Pleurozium schreberi*. Together these species typically account for over 95% of the standing plant biomass in these forests.

2.2.2 Temperate rain forests

Papers III and IV center on temperate rainforest in the Westland region of New Zealand (Figure 4b). These forests are characterized by two main types, broadleaf-conifer forests made up of a mixed canopy of evergreen angiosperms and emergent podocarps (gymnosperms; Figure 6), and southern beech forests dominated by evergreen *Nothofagus* tree species (Wardle, 1991). The region has a wet temperate climate. The annual average temperature is 11° C (Hessel, 1982), while the average annual rainfall varies across locations from 2.5 to more than 6 m. The Westland region has a considerable spatial variability of basal substrate. The most abundant substrate is schist that has derived from glacial outwashes and is heavily leached (Leathwick *et al.*, 2003). However, as a result of the complex geomorphology of the region, several other basal substrates also commonly occur including greywacke, granite and limestone.

2.3 Field work and sampling

2.3.1 Stand and plot characterization, and plot establishment

In Paper II stand and vegetation characteristics were characterized in September 2009. The basal area of the three tree species present (*P. sylvestris*, *P. abies* and *B. pubescens*) on the plots was determined using a 15-point relascope survey in each stand (Bitterlich, 1984). In each stand the biomass of the three dominant understory shrub species (*E. hermaphroditum*, *V. myrtillus*
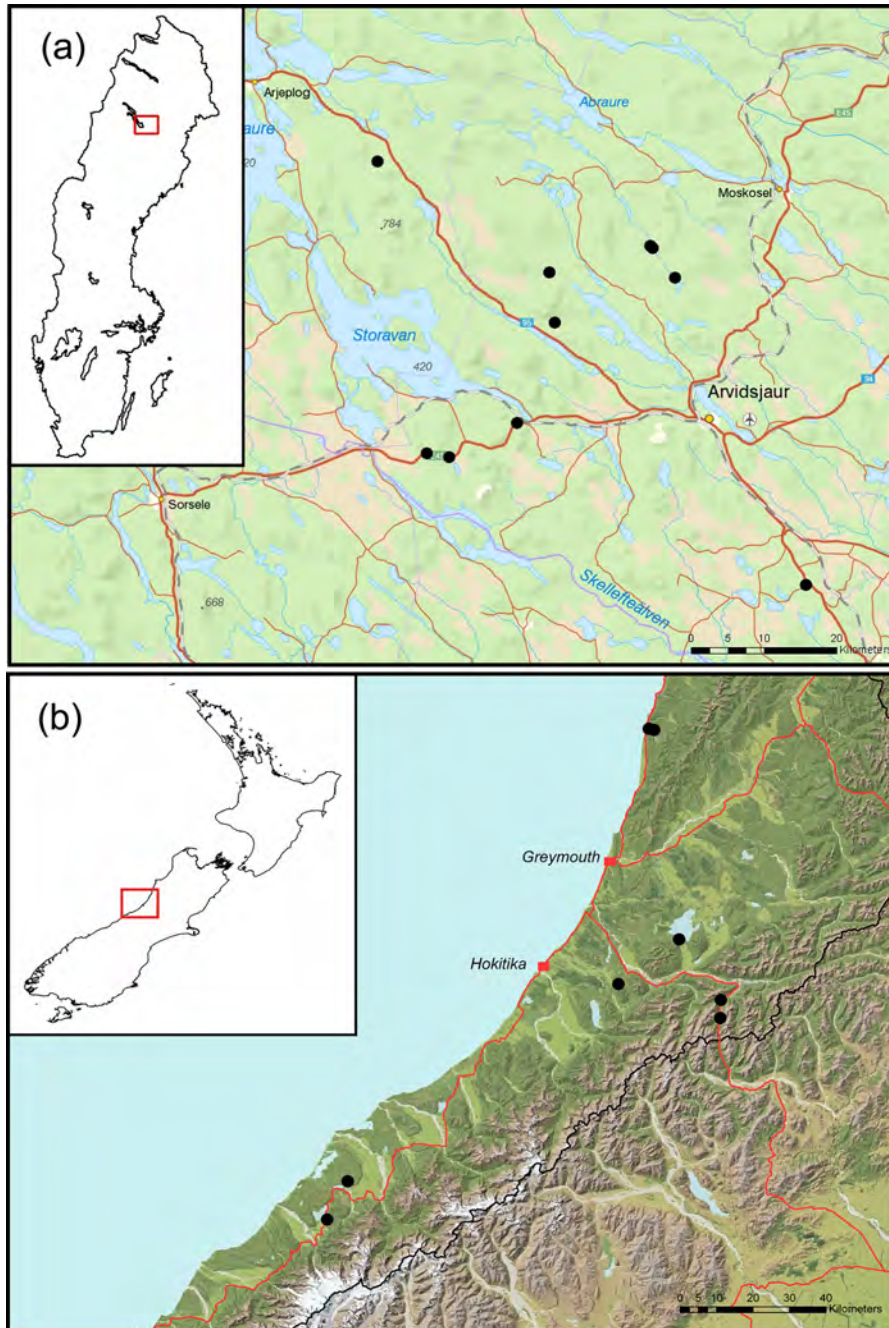
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Figure 4. Locations of (a) the ten stands forming a 362 year post-fire chronosequence in northern Swedish boreal forests used in Paper II and (b) the 8 topographic sequences situated in pairs on each of the four major basal rock types found in the West Coast region of New Zealand used in Paper IV.

Figure 5. A late successional boreal forest stand in the Vaksliden nature reserve in northern Sweden. Photo: B.Jackson

Figure 6. Mixed broadleaf and coniferous temperate rainforest lining the banks of Kawhaka creek in the Westland region of New Zeland. Photo: B.Jackson

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and *V. vitis-idaea*) was determined by the point intercept method (100 points × ten 1m^2 plots in each stand) converting point counts to biomass based on calibrated relationships (Wardle *et al.*, 2003a). Depth of *P. schreberi* was measured at 10 random points and humus depth was measured at 6 random points in each stand. In Paper IV the vegetation in each of the 32 plots was surveyed in 10 × 20 m subplots and the diameter at breast height (135cm) of all trees greater than 2 cm was recorded.

2.3.2 Sampling of plant and soil materials

For both Papers I and II litter material was collected from the Reivo Nature reserve (65°46'N 19°06'E) in September 2007. Fresh senescent litter was collected from *P. sylvestris* and *B. pubescens* by shaking branches and intercepting the falling litter with a tarpaulin. Litter from *V. vitis-idaea* was collected by hand by picking blackened leaves still attached to the plants. In Paper II, soil samples were taken from each of the four removal plots from each stand to assess the effect of the removal treatments on the availability of mineral N and P in the soils across the chronosequence. Three 5 cm diameter cores were taken from each plot to a depth of 15 cm and the organic layer retained and bulked.

In Paper III fresh leaf material and leaf, twig and wood litter were collected from paired live and dead trees. In Paper IV fresh leaf material and leaf litter were collected from the target species occurring in each of the plots. For both Papers III and IV, fresh leaf material was collected using an orchard pruner or a shotgun. Fully emerged green leaves were collected from mature individuals; sunlit leaves for canopy tree species and leaves of subcanopy and ground ferns were collected from the highest light environments in which they occurred. All fresh leaf material was then immediately sealed in plastic bags. Fresh senescent leaf litter was collected by hand from the forest floor beneath the individuals from which the green foliage was taken. In Paper III, fresh senescent twig litter was collected from the live tree from which the fresh leaf material was taken. Wood litter was collected from the dead tree by cutting a disc or partial disc 10 cm in thickness 130 cm from the base of the bole. In Paper IV, soil samples were taken from within the 10 x 20 m subplots used for the vegetation surveys. A minimum of three cores, 10 cm in diameter were taken from each plot, the top 10 cm of the organic layer retained and bulked to form a single sample per stand.

2.4 Methodology

2.4.1 N_2-fixation

In Paper I the rates of N_2-fixation occurring within the potted *P. schreberi* moss communities were measured using a calibrated acetylene reduction assay (Schöllhorn & Burris, 1967) following the procedure of Zackrisson *et al.* (2004). Briefly, the method is based on the observation that acetylene competes with N_2 as substrate for the nitrogenase enzyme, and is reduced to ethylene. Ethylene production correlates with the rate of N_2-fixation in the *Pleurozium–Nostoc* association at a ratio of 3 mol ethylene to 1 mol N_2 fixed (DeLuca *et al.*, 2002b). Thus the rates of ethylene production were measured by placing ten randomly selected individual moss shoots from each pot into a 22 ml glass vial. The moss shoots were moistened with 3 ml dH_2O and the vial fitted with a septum. Then 10% of the total headspace in each vial was evacuated and replaced with acetylene and the vials incubated under greenhouse conditions for 24 h. Total ethylene production was measured by gas chromatography using a flame ionisation detector. Rates of N_2-fixation were expressed by dry weight of moss or by unit area with ten *P. schreberi* moss shoots corresponding to 2 cm^2 (DeLuca *et al.*, 2002b).

2.4.2 Decomposition

In Papers I-IV the mass loss and loss of N and P from the litter was measured following standard procedures. After the period of decomposition under greenhouse, field or laboratory conditions all remaining undecomposed litter was recovered, picked, brushed or washed clean of fungal hyphae and soil particles and then oven dried to constant mass. Litter mass loss was determined as the percentage of the initial mass (corrected for water content) lost during incubation. Net loss of N and P from the litter was calculated as the difference between the total mass x nutrient concentration prior to incubation and that after incubation. The N and P lost from the litter as proportions of the total initial quantities were calculated from these values.

2.4.3 Trait measurements

In Papers III and IV the plant functional traits (PFTs) of leaves and litter were measured following standard protocols (Cornelissen *et al.*, 2003). All sampled leaves and litter (leaf, twig and wood) were measured for C and N by dry combustion in an element analyser and for P by the Kjeldhal acid digestion method. Total phenolics (Paper III) were quantified as tannic acid equivalents following Price and Butler (1977). To determine the specific leaf area (SLA)

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and leaf dry matter content (LDMC) of the green leaves, the fresh and oven dry weights of the leaves were measured together with the projected area of the fresh leaves. In Paper III the density of the wood litter samples was measured as the air-dry volume per unit oven dry weight (g cm^{-3}) using the displacement method. The lumen fraction and potential hydraulic conductivity were measured by microscopy and digital analysis of the micrographs using the ImageJ software (Ferreira T. and Rasband W, Montreal, Canada). Lumen fraction was calculated as the proportion of the total area consisting of vessel and tracheid lumens. Potential hydraulic conductivity was calculated according to the Hagen-Poiseuille equation (Poorter *et al.*, 2010; Russo *et al.*, 2010; Sterck *et al.*, 2008), which is a function of the conduit density and the hydraulically weighted diameter.

2.4.4 Soil analyses

In Paper I the total mineral N and P sorbed by the ionic resin capsules and in Paper II the extractable mineral N and P in subsamples of the soil from each of the soil from each of the plots from the chronosequence stands were quantified by colorimetry. Nitrate, ammonium and phosphate were desorbed from the resin capsules and extracted from the soils using 1M KCL. The eluates and extracts were stored frozen prior to analysis on a segmented flow colorimeter.

In Papers I and II substrate-induced respiration (SIR) was measured on a subsample of the soil from each of the pots and plots, respectively. This method provides a relative measure of the active microbial biomass in soils, and the method used followed Anderson and Domsch (1978) as modified by West and Sparling (1986) and Wardle (1993). Each soil subsample was placed into a glass vial and adjusted to 120% gravimetric water content before being amended with glucose; the glass vials were then sealed and incubated at 22°C and the rate of CO_2 released between 1 and 4h estimated by measuring the concentrations of CO_2 in 1ml subsamples of the headspace of the vials by infra-red gas analysis.

In Paper IV the bulked organic soils from each plot were analyzed for a suite of chemical properties (Table 1). These analyses were performed by the Environmental Chemistry Laboratory of Manaki Whenua Landcare Research in Palmerston North, New Zealand.

Table 1. *List of chemical properties measured for the soils sampled in Paper IV and the respective analytical methods used.*

Soil property	Analytical method
pH	Overnight suspension in H_2O
C (%)	Dry combustion, IRGA
N (%)	Dry combustion, FID
NO_3^- (mg/kg)	Extraction in 2 M KCl; Cd reduction and NEDD
NH_4^+ (mg/kg)	Extraction in 2 M KCl; indophenol reaction
P -Kjeldhal (mg/kg)	Acid digestion H_2SO_4; molybdenum blue
P - Ohlson (mg/kg)	Extraction in 0.5M $NaHCO_3$; molybdenum blue
Ca ($cmol^+$/kg)	Leach with 1M ammonium acetate; flame atomic absorption spectroscopy
Mg ($cmol^+$/kg)	Leach with 1M ammonium acetate; flame atomic absorption spectroscopy
K ($cmol^+$/kg)	Leach with 1M ammonium acetate; flame atomic absorption spectroscopy
Na ($cmol^+$/kg)	Leach with 1M ammonium acetate; flame atomic absorption spectroscopy
Cation exchange capacity ($cmol^+$/kg)	Ammonium ion displacement, indophenol reaction
Base saturation (%)	Calculation

2.5 Statistics

In Paper I analysis of variance (ANOVA) was used to test for the effects of the treatments and their interactions, with individual pots as the units of replication. The response of N_2-fixation to rainfall intensity and frequency was analysed by two-way ANOVA while the response of all other variables to rainfall intensity and frequency and the presence vs. absence of mosses were analysed by three-way ANOVA. In Paper II, individual forest stands were used as the principle units of replication and several permutations of ANOVA were used to test for treatment effects. As such, data on stand characteristics were analysed by one-way ANOVA testing for the effect of successional stage on each variable. Then, data on litter decomposition was analysed in two steps using split plot ANOVA. First to test for the effects of the presence of mosses and shrubs, successional stage and their interactions on decomposition, a subset of the data set was used, i.e., data for the litter placed on the upper-most soil surface from all four plots in each stand. The ANVOA was structured such that successional stage, moss removal and shrub removal were fixed factors, with moss removal and shrub removal nested within forest stand, with forest

stand as a random factor. Second, to test for the effects of the position of litter placement in the moss layer, shrub removal and successional stage and their interactions on decomposition, a second subset of data was used, i.e., data for the litter placed at different depths in the two plots with mosses present in each stand. The ANOVA was structured so that successional stage, shrub removal, position in the moss layer were fixed factors with depth nested within shrub removal, and shrub removal nested within forest stand, with forest stand as a random factor. Finally, data for soil moisture content, soil mineral nutrients and SIR were analysed by split plot ANOVA testing for the effects of moss and shrub removal and successional stage as described above for the litter decomposition variables. In both Papers I and II following ANVOA, post-hoc comparisons between treatments were performed using Fisher's least significant difference (LSD) test, adjusted for Type 1 error following the method of Benjmaini and Hochberg (1995).

In Paper III, a multivariate approach was used to test for coordinated patterns of interspecific trait variation across the different plant materials (leaves, and leaf, twig and wood litter). Trait data for each material was analysed by principle component analysis (PCA) in order to summarise the measured trait variation and covariation into fewer variables i.e. the axes derived from the PCAs. Correlation analyses were then used to test for relationships between the scores of each of the pairwise combinations of the PCA axes across the four plant materials. Then, to test for coordination in the decomposability among the leaf, twig and wood litters, correlation analysis was used to test the relationships of mass, N and P loss for each of these three litter types with each of the other litter types. Finally, to identify which traits were the best predictors of decomposition of each litter type, we used multiple regression analyses to assess the extent to which decomposability could be predicted by interspecific variation in individual traits, trait combinations and the axes of trait covariation from the PCAs. All analyses in Paper III were initially performed across all 27 species and then separately across the 18 angiosperm and the nine gymnosperm species.

In Paper IV, the variability of individual traits and litter decomposability both within and between species were quantified by coefficients of variation (CV; ie. SD/mean). Variability in N and P loss from the leaf litter were compared directly by comparing SDs because negative values prevented the calculation of CVs. Patterns of trait covariation within and between species were then examined by PCA. Further, for both individual species and for the tree species community as a whole, regression analyses were performed to examine the extent to which variation in the leaf traits was related to the soil C/N and C/P ratios (as measures of soil fertility) among plots, as well as to

variation in mass loss and N and P release during decomposition. For community level analyses a weighted traits approach (Fortunel *et al.*, 2009; Garnier *et al.*, 2007) was used, where the contributions of individual species to community level trait and decomposition measures were weighted by the relative basal area of each of the species in a plot:

$$\text{trait}_{agg} = \sum_{i=1}^{n} p_i \times \text{trait}_i$$

where trait_{agg} is the aggregated (or weighted average) value of that trait for all tree species collected in that plot, p_i is the basal area of a tree species i as a proportion of the total basal area for all tree species collected in that plot, and trait_i is the value of the trait or decomposition variable for tree species i. Plots for which the 16 species we measured collectively accounted for less than 70% of the total basal area were excluded from community level analyses (Garnier *et al.*, 2004). In addition, the relative contributions of the turnover of species among plots, intraspecific variation of species, and their covariation to the relationships between community level trait values and soil nutrient status across the plots, were estimated following the Sum of Squares decomposition method described by Lepš *et al* (2011). All statistical analyses were performed using R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria).

3   Results and Discussion

This thesis investigates how plants can influence litter decomposition and nutrient cycling in forested ecosystems via two contrasting pathways (Figure 1). Papers I and II explore the role of boreal feather mosses in mediating the impacts of environmental conditions on the decomposition of intercepted leaf litter and related processes occurring in association with the moss layer. Papers III and IV examine the role of plant functional traits in determining litter quality and decomposition rates for a range of temperate rainforest species. The main findings of each of these studies and their implications are discussed below.

3.1   Moss effects on decomposition in boreal forests

3.1.1   Rainfall patterns drive moss effects on litter decomposition and moss-associated N_2-fixation

Paper I explored the effects of contrasting simulated rainfall regimes on litter decomposition and cyanobacterial N_2-fixation, two important ecosystem processes occurring within the moss layer of boreal forests. In the greenhouse experiment, pairs of experimental pots with and without communities of the feather moss *P. schreberi* received one of three different volumes of water applied (low, medium, high) at one of three frequencies (infrequent, moderate, frequent) for a total of nine different rainfall regimes. The results revealed that the decomposition of *P. sylvestris* litter in the pots was significantly affected by moss presence as well as by the volume and frequency of water applications. Furthermore, all three factors were interdependent with two and three-way interactions occurring. As such, higher water volume and greater frequency of watering both had positive effects on the mass loss of the litter, but they also augmented the effect of one another. Notably, frequency had particularly strong effects causing up to three-fold differences in the mass loss of litter for a

given volume of water. In turn, mass loss of the needle litter in pots containing mosses decomposed up to twice as fast as that in pots without mosses. However, this positive effect of moss presence only occurred in low volume and/or infrequent moisture treatments, when moisture availability was limiting. The N and P dynamics in the decomposing litter were similarly affected by interactive effects of the watering regimes and the presence of the mosses. Two further indicators of the activity of the decomposer subsystem were also influenced by the presence of mosses and the watering regimes. First, microbial biomass in the soil in each of the pots was buffered by the presence of mosses against the effects of watering frequency. Second, the availability of mineral N in the soil, measured by sorption by resins in resin capsules, was reduced by the presence of mosses with the most pronounced effects occurring when moisture availability was limiting. Cyanobacterial N_2-fixation rates also strongly responded to the volumes of water and frequency of water applications. Overall, both greater volumes of water and higher frequencies of application had positive effects on N_2-fixation. At medium and high water volumes, the frequency of watering caused up to five fold differences in the rates of N_2-fixation in the mosses. However, in contrast, at low volumes the rates of N_2-fixation were not influenced by watering frequency. This suggests that below a threshold of water availability, N_2-fixation is no longer responsive to the distribution of water addition over time.

Together these results have two major implications for ecosystem processes relevant for carbon and nutrient cycling in boreal forests. First, they show that above a minimum threshold, the distribution of rainfall over time is a significantly more important driver of litter decomposition and N_2-fixation in boreal forests than is the total volume of rainfall. This finding corroborates a number of studies in other ecosystems that have highlighted the importance of rainfall distribution time and stochastic rainfall events as major drivers of ecosystem processes (Chou *et al.*, 2008; Maestre & Reynolds, 2007; Austin *et al.*, 2004). Second, they identify a previously unknown role of feather mosses in mediating how rainfall affects the activity of decomposer organisms in breaking down litter intercepted by the moss layer. Past research has highlighted three important characteristics of feather mosses: (i) they are highly abundant plants in boreal forests (Turetsky, 2003) (ii) they produce recalcitrant litter contributing to humus accumulation (Lang *et al.*, 2009; Legare *et al.*, 2005); (iii) they host associated N fixing cyanobacteria that can contribute a significant proportion of the total N input to these forests (DeLuca *et al.*, 2002b). A few studies have also indicated that mosses may promote the decomposition of litter when in contact with the mosses (Hoorens *et al.*, 2009; Wardle *et al.*, 2003b). The results from this paper broaden these findings, by

showing that mosses moderate how the patterns of rainfall input affect the decomposer subsystem. The moss layer in boreal forests is known to have a significant water retentive capacity (Price *et al.*, 1997), and by acting as a reservoir of water, it prevents the limitation of decomposer activity in the absence of new rainfall inputs.

The findings of Paper I also have implications for the understanding of how past variations and future shifts in rainfall patterns may affect ecosystem processes relevant to carbon and nutrient cycling in boreal forests. Rainfall records for the study region in northern Sweden show that over the last 120 years, large inter-annual variations occur in the total volumes of rainfall received during the growing season. One in every two years received either less that 75% or more than 120% of the long-term mean inter-annual growing season rainfall. At the extremes, the driest years received less than 50% while the wettest years received up to 190% of the mean. Our results suggest that the moss layer in boreal forests may significantly reduce the sensitivity of decomposer processes to periods of limited water availability. Further, in the study region, annual rainfall is projected to increase together with a greater number of rainfall events as a result of global climate change (Meehl & Stocker, 2007). Guided by the results in this study, increasing rainfall should reduce the dependence of decomposer organisms on moss cover, and the rates of moss-associated cyanobacterial N_2-fixation and litter decomposition can be anticipated to increase significantly. Overall, this should in turn promote nutrient supply and cycling with consequences for plant productivity. Despite ample evidence that global change drivers will variously affect plant communities and the functions they perform, little is known about how the interactions between plants and other organisms like decomposers may be affected by drivers such as climate change (Tylianakis *et al.*, 2008). In this light, our results on the role of mosses in mediating the impacts of rainfall on decomposition in boreal forests are a significant step forward through providing a clear example of the sensitivity of such interactions to global change.

3.1.2 Moss layer promotes litter decomposition across a boreal forest chronosequence

Paper II examined the effect of the moss layer on the decomposition of intercepted leaf litter across a post-fire boreal chronosequence of ten forest stands, which varied in age from 43 to 362 years. A series of removal plots were established at each stand in which the moss layer and/or the ericaceous dwarf shrubs were removed from the plots in a factorial experimental design. Unconfined leaf and needle litter from three plants species were then installed

into the removal plots at each stand and left to decompose for a period of one year. After recovery of the litter, the analysis indicated that the decomposition of leaf and needle litter was significantly affected by the presence *vs.* absence of the moss layer across all ten stands of the chronosequence. On average, 12% more mass of litter was lost from litter decomposing within the moss layer than in plots from which the moss layer had been removed. Several other indications of the impact of the moss layer on the decomposer activity were also observed. Soil water content within the organic horizon was found to be higher in plots with the moss layer intact than in the plots where it had been removed. In addition, moss removal reduced the concentrations of extractable mineral N from the organic soil layer by 80% across the ten stands, while in the three youngest stands the microbial biomass in the organic soil layer was reduced by 40%. These results add to the findings of Paper I, showing that the effect of the mosses on decomposition is driven by the retention of water in the moss layer, which prevents the desiccation of litter that would otherwise limit decomposer activity. Similar effects of mosses have been seen in Mediterranean pine forests, where pine litter was found to have a higher moisture content and decompose faster when a moss layer covered the soil surface (Garcia-Pausas, 2004). In combination with the findings of this study they suggest that the role played by mosses in mediating moisture effects on decomposition may be common, and with widespread implications for carbon and nutrients cycling.

The decomposition of the leaf and needle litter was also found to be affected by its position in the moss layer during decomposition. After the one-year decomposition period, litter mass loss was on average 10% higher for the litter decomposed at the interface between the moss layer and the upper surface of the soil organic layer than on the surface of the moss layer. Similarly, mass loss was on average 6% higher for the litter inserted between the growing stems of the mosses than on the surface of the mosses. These observations are consistent with the water retentive capacity of the moss layer as the mechanism through which decomposer activity is promoted. In the absence of new moisture inputs, the moss layer loses water through evaporation, with drying starting at the upper surface and passing progressively down through the moss layer (Zotz & Kahler, 2007). In this way the microclimate deeper within the moss layer remains suitable for decomposer activity for longer periods of time. These observations, together with those made in Paper I also contradict findings from Canadian Boreal forests showing that the moss layer can retard decomposition processes by reducing soil temperatures below the moss layer and thereby potentially inhibiting microbial activity (Fenton *et al.*, 2010). While the capacity of the moss layer to buffer soil temperatures has long been

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identified as a potentially important effect (Vancleve *et al.*, 1991; Bonan & Shugart, 1989), in the Canadian study the decomposing litter was incubated at significantly greater depths than in the present study. As such, while lower temperatures may affect soil organic matter transformations deep beneath the moss layer, the results from this study show that in the upper moss layer where litterfall is intercepted and litter decomposition begins, the availability of water is the more limiting factor. Further, by retaining moisture the moss layer prolongs decomposer activity whereas, in the absence of moss cover, litter decomposing on the soil surface is more susceptible to desiccation.

The results also showed that the positive effect of the moss layer on the decomposition of the leaf and needle litter was consistent across all ten stands of the chronosequence. No differences in the magnitude of the moss effect on litter decomposition were observed among stands despite a more than two-fold increase in the depth of the moss layer. Contrary to our expectations that the increase in the depth of the moss layer might enhance the moss effect on decomposition, this result suggests that the simple presence of moss cover is sufficient to cause the observed changes in decomposer activity. This may be a consequence of the clonal nature of the growth of the feather moss *P. schreberi*, which spreads as a carpet across the forest floor. New individual shoots branch off from older ones in a tightly packed matrix. The density of growing shoots determines the capacity of the layer to retain moisture (Rixen & Mulder, 2005), which facilitates moss growth as well as processes driven by mosses such as litter decomposition and N_2-fixation. Overall the results from Paper II add to the findings of Paper I by confirming that under field conditions and using methodology suited to studying the fine spatial scale at which the processes under consideration operate, the moss layer in boreal forests plays a clear role in promoting the decomposition of intercepted leaf and needle litter from understory and canopy species. Further, the promotion of decomposition by mosses was surprisingly consistent across forests stands at different successional stages. This indicates that the effect of the moss layer on litter decomposition is widespread. Given the abundance of feather mosses in boreal forests (Nilsson & Wardle, 2005; Turetsky, 2003), they are therefore an ecologically important plant functional group that has an important influence on processes relevant to biogeochemical cycling in boreal ecosystems.

3.2   Functional traits and decomposition in temperate rainforests

3.2.1 Traits and decomposition of leaves and wood are decoupled

Paper III compared the patterns of functional trait variation and decomposability of leaves, twigs and wood material collected from across a

wide range of temperate rainforest tree species in New Zealand. Green leaf and litter material from 27 co-occurring tree species, including angiosperms and gymnosperms, was used to characterize the variation across these species for a suite of functional traits. Traits were chosen to reflect both the ecological strategies of the trees as well as the quality of their litter. Subsamples of the leaf, twig and wood litters were then decomposed under controlled conditions to assess the relative decomposability of the litter for each litter type from each species. Analyses of the functional trait data revealed coordination between the green leaves and leaf and twig litter, in the patterns of trait variation across the tree species. For each of these structures, both nutrient and structural traits varied along a common axis of trait covariation, consistent with the leaf economic spectrum (LES), which represents a well described tradeoff in how plants acquire and use resources (Freschet *et al.*, 2010; Wright *et al.*, 2004). In addition, these axes of trait covariation were strongly correlated with each other. In contrast, the pattern of variation in N and P content of the wood litter was not related to how structural traits of wood varied across species. Further, only the variation across species in the nutrient content of the wood was correlated with the axes of trait covariation of the other structures. Consequently, variation in the structural traits of wood across species was unrelated to the trait variation of the green leaves, or of the leaf and twig litter. These results build on the findings of several prior studies, with implications for the integration of resource strategies between the structures of whole plants.

Previous work involving analysis of a large database of functional traits of tree species has also revealed positive correlations between the variations in the N and P contents of leaves, stems and roots across species (Kerkhoff *et al.*, 2006). Further, a large trait data base for neotropical trees showed that variation in the structural traits that form the wood economic spectrum (WES) was unrelated to the pattern of structural and nutrient trait variation for the LES (Baraloto *et al.*, 2010). These observations in combination with the results in this study suggest that partial coupling of trait variation between plant structures may occur for trees and woody species. However, this contrasts with the more complete coupling of both structural and nutrient trait variation between the leaves, fine stems and roots found for wide range of plant species in the Swedish subarctic (Freschet *et al.*, 2010). Correlations between traits of the LES and WES have also been observed in a study conducted on the Pacific Bonin Islands (Ishida *et al.*, 2008). Overall, these observations and the findings in this study indicate that functional traits and thus potentially the resource strategies of plants, may be at least partially coordinated between plant structures. However, further work is required to establish for which species and contexts trait coupling does occur.

Overall, the relative decomposability of the litter from the trees was not coordinated between the leaf, twig and wood litter. In other words, those species with the more rapidly decomposing leaf litter did not in turn have twig litter and wood that decomposed more rapidly relative to the tree species. This was apparent for the mass loss of the litter and the loss of N and P from the litter. There were a few exceptions for which coordination in decomposition was observed, but these were related to contrasting responses of the angiosperm and gymnosperm species. The lack of coordination in the decomposition for the three litter types can be explained least in part, by examining which traits were most closely related to the decomposition of each of the litters. The decomposition of both the leaf and twig litter was consistently correlated with the C/P and lignin/N ratios of these structures, both of which were shown to be closely associated with the LES in these structures. These results are consistent with the many reports of litter decomposition being driven by the chemical composition of litter and in particular C/N and lignin/N ratios (Aerts, 1997; Couteaux *et al.*, 1995). The lack of coordination of decomposition for these two litter types is thus surprising, in particular because trait variation was coordinated between these two structures. An immediate explanation for this contradiction was not apparent, but may be explained by potential interactions of litter quality with the decomposer community. Leaf and twig litter differ considerably in proportions of specific compounds known to require specialist decomposers (Schwarze, 2000) and thus the community of decomposers can be more adapted to one type of litter over another (Strickland *et al.*, 2009). The assembly history of the decomposer community also has strong impacts on decomposition (Fukami *et al.*, 2010), and may differ between species litters types.

In contrast to the leaf and twig litter, the decomposition of the wood litter was correlated only with the structural traits of the wood and in particular with wood density. Prior studies have shown that wood density is closely associated with decomposition rates of wood in South American forests (Chave *et al.*, 2005; Chambers *et al.*, 2000), and with standing stocks of undecomposed coarse woody debris (Chao *et al.*, 2009). Wood density is also considered as a trait of central importance to the WES, and one that is related to both the structure and functions of wood. Further, both in this study and in previous work, variations across species in wood density and other structural traits of wood have been shown to be decoupled from the traits of the LES (Baraloto *et al.*, 2010). As such, this study provides evidence that across a broad range of tree species, wood decomposition is decoupled from the decomposition of leaf and twig litter and that this is primarily because the traits driving wood decomposition are themselves unrelated to those driving the decomposition of

leaf and twig litter. As such, traits of the LES are not suitable predictors of the contributions of plant structures other than leaves to ecological processes such as decomposition. Further explicit consideration of the functional traits of plant organs other than leaves should greatly improve the effectiveness of ecological models describing carbon and nutrient cycling in forest ecosystems.

3.2.2 Within-species trait variation and decomposition are unrelated

Paper IV examined within- and between-species variation in the leaf and leaf litter traits, and in leaf litter decomposability, of leaf litter from 16 co-occurring temperate rainforest species in New Zealand. Leaf and litter was collected from 32 forest stands representing a strong gradient of soil nutrient availability. The contribution of trait variation within individual species to the variations in litter decomposition was assessed by decomposing litter under standardized conditions. In addition, the contributions of the two sources of trait variation to community level trait measures and decomposition at the stand level were assessed using a weighted traits approach. Significant within-species variation in the leaf and litter traits was observed for all 16 species in the study. On average, the magnitude of the within-species variation of the leaf and litter traits were approximately 50% of that observed between species. This observation is consistent with the few recent studies that have expressly quantified intra-specific trait variation (eg. Albert *et al.*, 2010b; Messier *et al.*, 2010). Further, for two-thirds of the species in the study, the pattern of variation in leaf and litter traits within individual species, resembled the pattern of variation across species. As such, LDMC, SLA, and the N and P contents of the leaves within each of these species all covaried along a common axis of trait variation that collectively explained between 53% and 70% of the total within-species trait variation. This pattern of within species variation conforms to the patterns shown for the LES across species, which represents a well-known tradeoff in leaf economic strategy (Freschet *et al.*, 2010; Wright *et al.*, 2004). Similar patterns of trait variation within species have also been shown for a handful of species in alpine perennial shrubs (Albert *et al.*, 2010a), which together with the present results indicate that the same constraints that give rise to the LES also operate within species. However, this was not the case for all of the species in the study, and further work will be required to confirm how widely across different species an identifiable within-species leaf economic spectrum occurs.

Across most of the species, within-species trait variation was also observed to be correlated with the changes in soil nutrient status across the 32 forest stands. Of all the traits, the nutrient contents and C to N and C to P ratios of the leaves and leaf litter were most strongly associated with the soil nutrients.

Between 17% and 58% of the within-species variation in the C/N and C/P of the leaves was explained by variation among plots in soil C/N and C/P ratios. This result adds to a growing number of studies showing that leaf traits clearly respond at the within-species level to various environmental factors including temperature, rainfall, disturbance, and soil nutrients (Lagerström *et al.*, 2012; Fajardo & Piper, 2011; Lepš *et al.*, 2011; Albert *et al.*, 2010a; Jung *et al.*, 2010; Messier *et al.*, 2010; Wardle *et al.*, 2009). Further analyses of the trait variation at the community level revealed that within-species trait variation made a significant contribution to the relationships between the community level trait measures and the changes in soil nutrients. While this contribution was secondary to the effects of between-species trait variation resulting from species turnover across plots, it indicates that intraspecific trait variation can be an important component of how plant communities respond to environmental drivers (Albert *et al.*, 2010a; Messier *et al.*, 2010).

Considerable within-species variation in the decomposition of the leaf litter of individual species was also observed. On average across the 16 species, the coefficient of variation for the variability of mass loss within individual species was 14%. This was marginally lower than the level of variability of leaf and litter traits within species, but was nonetheless substantial in comparison with the variation in mass loss between species. Contrary to expectations, few significant relationships were observed between the variations in decomposition and leaf and litter traits within-species. The overall absence of a link between traits and decomposition within species contradicts a number of previous findings (eg. Lecerf & Chauvet, 2008; LeRoy *et al.*, 2007; Sariyildiz, 2003). As such, the results of this study indicate that variation in traits of the LES do not drive litter decomposition within species, in contrast to the predictable trait-decomposition relationships seen between species in this and other studies (Freschet *et al.*, 2012; Cornwell *et al.*, 2008; Santiago, 2007). Accordingly, predictions of community level measures of litter decomposition were not improved by the integration of within-species trait variation. Instead, species mean trait values were equally good if not better predictors of how litter decomposition at the stand level varied across the soil nutrient gradient. Overall, the findings of this study indicate that leaf functional traits respond to environmental drivers in much the same way within species as between species, and within-species variation can make significant contributions to the responses of whole plant communities to variations in environmental conditions. As such, explicit consideration of within-species trait variation is necessary to improve plant trait-based assessments of plant communities and their responses to environmental conditions. However, at the within-species

level leaf and litter traits associated with the LES do not drive litter decomposition.

3.3 Summary and conclusions

The regulation of litter decomposition is driven by the interaction of three principal factors: environmental conditions; litter quality; and the decomposer community. This thesis explores two contrasting pathways by which plants and plant diversity can interact with these factors to influence litter decomposition rates in forested ecosystems. In the first half of the thesis, the indirect effect of a single functional group of plants on litter decomposition through the mediation of the availability of moisture was explored. The results from that work demonstrated a previously unrecognized role of feather mosses in driving the decomposition of vascular leaf litter in boreal forests. The highly abundant feather mosses typically cover the forest floor in a continuous mat. The structure of this moss layer results in the interception of much of the litterfall from vascular plant species such that the decomposition of the litter occurs in direct association with the feather mosses. The moss layer is also capable of retaining significant amounts of moisture from incoming rainfall. In a first step, by experimentally manipulating the patterns of rainfall inputs to the moss layer, the mosses were shown to mediate the impacts of moisture availability on litter decomposition. The patterns of moisture inputs and in particular the frequency of inputs was shown to be a major driver of both litter decomposition and the moss-associated process of cyanobacterial N_2-fixation. However, under conditions of limited moisture availability the mosses promoted the decomposition of leaf litter embedded within the moss layer by preventing the desiccation of the litter and maintaining decomposer activity. In this way the effect of the moss layer was dependent on the prevailing moisture conditions. In a second step, the effect of the moss layer on decomposition was shown to occur widely under natural conditions. The presence *vs.* absence of the moss layer was manipulated in experimental plots along a successional gradient of ten boreal forest stands. When intact, the moss layer was shown to significantly promote the decomposition of vascular leaf litter in a manner remarkably consistent across a 360 year successional gradient. This is despite a large increase in the depth of the moss layer and concomitant changes to the ecosystem properties of the forests as succession proceeded. Together, these results highlight that feather mosses are critical in determining how temporal variations in rainfall influence litter decomposition, and thus carbon and nutrient cycling at the forest stand scale. Importantly, the results also suggest

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that the role played by feather mosses will be particularly sensitive to alteration in precipitation patterns driven by global climate change.

In the second half of this thesis, the more direct influence of plants through their impact on the quality of litter entering the decomposer subsystem was examined. Plants are the main sources of dead organic matter entering the decomposer subsystem in terrestrial ecosystems. Plant species vary widely in the functional characteristics or traits of their leaves and other organs. Many of these functional traits in turn determine the substrate quality of dead plant organic matter for decomposer organisms. In this way, the differences between plant species in the functional traits of their leaves and leaf litter are widely used as indicators of the quality of their litter and to predict the rates of decomposition of that litter. In separate studies, two poorly explored aspects of trait-decomposition relationships were explored: the links between the traits of leaves and other plant organs including twigs and wood and the decomposability of these organs; and the potential for the variability of functional traits within species to drive litter decomposition. The results from these studies revealed that the decomposition of leaf, twig and wood litter of 27 co-occurring temperate rainforest tree species was largely uncoordinated. The lack of coordination in the decomposition of the wood with the two other organs was because wood decomposition was driven largely by wood density, which itself was unrelated to the chemical traits driving leaf and twig litter decomposition. The traits driving the decomposition of the leaf and twig litter were coordinated but this did not lead to coordination in the decomposition of the two organs. Together, these results indicate that plant functional traits commonly used as indicators of leaf litter quality are insufficient to either describe the traits or predict the decomposability of other plant organs. Therefore, explicit consideration of the functional traits of other plant organs is needed to improve models of C and nutrient cycling in forest ecosystems. The results also revealed that the functional traits of leaves and leaf litter of 16 co-occurring temperate rainforest species all showed considerable within-species variation. For the majority of species, leaf and litter traits varied predictably in response to variability in soil nutrient availability, and patterns of trait covariation within these species showed similar patterns to that commonly seen between species. Considerable within-species variation in leaf litter decomposition was also observed. However, unlike the well-described relationships documented between interspecific trait variation and litter decomposition, intraspecific variation in the leaf and litter traits was largely unrelated to the variations in litter decomposability within species. Consequently, intraspecific variability in leaf and litter traits were shown to make a significant contribution to how trait measures at the whole plant

community responded to differences in soil nutrient availability among plots, but were unable to predict litter decomposition rates at the whole community level. These results highlight intra-specific trait variation is an important component of plant community responses to environmental drivers but this trait variation is unrelated to the decomposition of leaf litter within species.

Overall, the results of this thesis illustrate the important and contrasting impacts plants have on litter decomposition, and contribute to the understanding of the complex interactions between the multiple factors regulating litter decomposition in forest ecosystems. They show that a single functional group of plants can have a major impact on the decomposer subsystem in forests ecosystems, largely independent of other plant species and despite representing only a small fraction of the total standing biomass. They also highlight the importance of understanding the combined influence of biotic and abiotic drivers on decomposition in order to make clear predictions of how changing climatic conditions will affect ecosystem processes. The results further suggest that efforts to model C and nutrient cycling in forest ecosystems should take into consideration the functional traits of other plant organs in addition to those of leaves to more accurately represent the effects of whole plants on key ecosystem processes like decomposition. Finally, they reveal that the identity and relative abundance of plant species are major drivers of litter decomposition at the community level. As a consequence, changes to plant community composition caused by biodiversity loss, shifting species distributions due to climate change, eutrophication and changing land use all have the potential to significantly alter litter decomposition and nutrient cycling.

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