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SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Towards a unified allometric and stoichiometric perspective in ecology:

Soil communities and decomposition in focus of the metabolic theory and the ecological stoichiometry

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Table of contents

Summary

Ecosystem functioning is maintained by the interplay of a multitude of species. However, in a time of global change there are high rates of species extinctions which can drastically reduce the functionality of natural ecosystems. Consequently, a mechanistic understanding of the relationship between biodiversity and ecosystem functioning becomes increasingly important. Diversity effects are mediated by complex interactions and impact multiple levels of biological organization. Changes in consumer-resource interactions at the individual level, for example, affect population densities, spreading across communities and ultimately scaling up to entire food webs. Hence, research at all of these levels is required to establish a comprehensive understanding how ecosystem functioning is maintained.

The metabolic theory of ecology and the theory of ecological stoichiometry both explore and describe various patterns ranging from species interactions to entire ecosystems. However, to date both theories focus on different perspectives: the conceptual idea behind the metabolic theory is allometry - non-linear scaling relationships of biological rates and processes with body mass and temperature. Ecological stoichiometry instead focuses on imbalances in elemental contents between units, such as consumers and their resources. However, the allometric and stoichiometric principles of the two theories are not mutually exclusive. Moreover, they should complement each other to form a more powerful, unified theory. This new theory would aid our understanding of the complexity of interactions amongst species within food webs. Surprisingly, to date these concepts have rarely been used in a combined framework.

In this thesis, I aimed to make an important step towards such a unified perspective of metabolic theory and ecological stoichiometry by studying the interplay of body mass, temperature and stoichiometry. The ecosystem function I focused on is decomposition, which directly influences nutrient cycling and thus is crucial for the ecosystem´s productivity. I concentrated on invertebrate species and communities of forest floors and studied possible direct and indirect effects on the process of litter decomposition. To disentangle the interplay of body mass and resource stoichiometry across several levels of organization, I conducted experiments and analyzed field data of natural environments.

"*A mechanistic understanding of how interactions between temperature and litter stoichiometry are driving decomposition rates is currently lacking*" (Ott *et al.* 2012). In Chapter 2, I "*filled this void by quantifying decomposer consumption rates*" in a

laboratory experiment (Ott *et al.* 2012). To realize this, I applied for the first time the concept of functional responses that consists of the parameters handling time and attack rate. In systematic variations of body masses of a woodlouse species, environmental temperature and the resource quality, I "*found that attack rates increased and handling times decreased (1) with body masses and (2) temperature*" (Ott *et al.* 2012). Notably, "*these relationships interacted with litter quality*" (Ott *et al.* 2012). Small woodlice possibly showed avoidance behavior of poor resource, whereas the consumption rates of large woodlice increased on the poor resource. This contrast suggests that larger woodlice have to compensate a higher metabolic demand with decreasing resource quality in relation to smaller woodlice. The combination of variables associated with "*metabolic theory and ecological stoichiometry provided significant mechanistic insights into how warming and varying litter quality may modify consumption rates*" of differently sized decomposers (Ott *et al.* 2012).

I investigated this interdependency of factors in different trophic levels of a forest floor community in Chapter 3. In a microcosm study, I manipulated horizontal (within a trophic level) and vertical (across trophic levels) diversity to examine multi-trophic diversity effects on the decomposition. While litter mass loss in general increased with total diversity (i.e., combined decomposer and predator richness), I found that this total diversity effect was driven by horizontal diversity. Moreover, effects of vertical diversity were surprisingly neutral to positive for ecosystem functioning, even though intra-guild predation likely could have released the decomposer prey from top-down pressure. I argue that the interplay between interference competition among decomposers and low top-down pressure by predators should be responsible for these results. Overall, I found interwoven effects of horizontal and vertical diversity on litter decomposition in forest ecosystems. As a possible stimulus for future research, my study provides an example how to systematically disentangle horizontal and vertical diversity effects on ecosystem functioning.

In Chapters 2 and 3, I combined effects of allometry and stoichiometry to consumer-resource interactions and multi-trophic mechanisms of diversity on decomposition in a small manipulated community. In Chapter 4, I extend the level of complexity to populations in soil food webs. "*Metabolic theory predicts variance in biomass density within communities in dependence of population average body masses, whereas the ecological stoichiometry*" considers resource stoichiometry to cause variation in density across communities via nutritional limitations on the consumers (Ott *et al.* 2014b). I

integrated these two theories into one novel framework to analyze biomass densities of "*populations of soil invertebrates across 48 forest sites*" (Ott *et al.* 2014b). Using linear mixed effects models, I investigated "*how the scaling of biomass densities with population-averaged body masses systematically interacts with stoichiometric variables*" (Ott *et al.* 2014b). The integrated model with allometric and stoichiometric predictors proved superior to the allometric null model. Moreover, the integrated model explained deviations from predicted allometric scaling while accounting for phylogenetic groups as co-predictor in the random structure of the model.

In Chapter 5, I applied the model concept developed in Chapter 4 to twelve phylogenetic groups of the same dataset separately. I "*investigated how the populations´ biomass densities of temperate forest soil communities depend on 1) the stoichiometry of the basal litter according to the ecological stoichiometry concepts and 2) the population average body mass as predicted by the metabolic theory*" (Ott *et al.* 2014a). "*Following various ecological stoichiometry hypotheses, I tested for effects of the carbon-to-element ratios of 10 elements*" (Ott *et al.* 2014a). "*Additionally, I included the abiotic litter characteristics habitat size, litter diversity and pH, as well as forest type as an indicator for human management*" (Ott *et al.* 2014a). For ten out of the twelve phylogenetic groups "*the biomass densities scaled significantly not only with population-averaged body masses but also with stoichiometric and abiotic co-variables*" (Ott *et al.* 2014a). Out of 14 predictors, "*the four most frequent co-variables were 1) forest type, 2) the carbon-to-phosphorus ratio, 3) the carbon-to-sodium ratio, and the carbon-to-nitrogen ratio*" (Ott *et al.* 2014a). While these results confirmed some element-specific hypothesis, I revealed that scaling relationships from taxa between functional groups (meso- and macrofauna) and trophic groups (decomposers and predators) were best predicted by the integrated model approach. In this comprehensive analysis, I demonstrated "*how the elemental stoichiometry of the litter as the basal resource constrains population densities across multiple trophic levels of soil communities*" (Ott *et al.* 2014a). Moreover, I confirmed the predictive power of the integrated model approach.

In Chapter 6, I extended the laboratorial (Chapters 2 and 3) and analytical (Chapters 4 and 5) approaches to situations under natural conditions on forest plots. I conducted a litter-bag study and examined several factors affecting litter decomposition. I examined: 1) litter quality using leaf litter of two tree species (maple and beech) that differed in litter stoichiometry; 2) the absence and presence of meso - and macrofauna compared to microorganisms alone; 3) land use via a gradient of intensive forest management; 4)

exclusion of living roots compared to an associated control on each plot; 5) species richness of the soil communities. I found significant interactive effects that yielded highest litter mass loss on maple litter, in presence of meso - and macrofauna and in most intensively managed forests. Summarizing, my study reports striking insights into how major components of the decomposition process interact with each other in managed forest ecosystems. Furthermore, the interactive effects of litter quality and with body mass (presence of meso-macrofauna) corroborate the finding from the previous chapters.

In a nutshell, I provide promising novel experimental solutions for measurements of interaction strengths of decomposers (Chapter 2) and for disentangling effects of multi-trophic diversity (Chapter 3). Moreover, the integrative model framework with interdependent allometric and stoichiometric variables successfully predicted population biomass densities superior to the allometric null model (Chapter 4 and 5). Due to its flexibility, this framework has much potential to be broadly applicable.

This thesis represents a highly promising step towards unifying metabolic theory and ecological stoichiometry. My results emphasize that a combination of body mass, temperature and stoichiometry yields superior predictive power on species interactions and population densities, which scale up to food webs. Ultimately, I demonstrate that a combination of metabolic theory and ecological stoichiometry provides a promising basis for future research on biodiversity and ecosystem functioning.

Author contributions and specific copyright of chapters

Chapter II.2

Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry

David Ott, Björn C. Rall and Ulrich Brose.

All authors designed the experiment. D.O. conducted the experiment and gathered the data. D.O. and B.C.R. conducted statistical analyses. All authors contributed to the text.

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Chapter II.3

Horizontal and vertical diversity interactively drive ecosystem functioning

David Ott, Miriam Achler, Björn C. Rall and Ulrich Brose.

The chapter is based on the Master Thesis written by M.A. entitled "*Effects of decomposer diversity on decomposition: Horizontal and vertical diversity drive ecosystem functioning.*", Georg-August-University Göttingen, Göttingen February 2013. This Master Thesis was conducted in the framework of the PhD Thesis by D.O. The authors re-analyzed the underlying data and all authors contributed to the new version embedded in this thesis: M.A., B.C.R., U.B. and D.O. designed the experiment. M.A. conducted the experiment and gathered the data with input and help from D.O. Statistical procedures were performed by M.A., B.C.R., U.B. and D.O. The text was written by M.A., U.B. and D.O with input from. B.C.R.

Chapter II.4

Unifying elemental stoichiometry and metabolic theory in predicting species abundances

David Ott, Christoph Digel, Björn C. Rall, Mark Maraun, Stefan Scheu and Ulrich Brose

U.B., M.M and S.S. designed the field experiment. D.O. and C.D. assembled the database. Statistical procedures were performed by D.O., B.C.R., C.D. and U.B. Text was written by D.O., B.C.R. and U.B. with input from M.M. and S.S.

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Chapter II.5

Litter elemental stoichiometry and biomass densities of forest soil invertebrates

David Ott, Christoph Digel , Bernhard Klarner , Mark Maraun , Melanie Pollierer , Björn C. Rall , Stefan Scheu , Gesine Seelig and Ulrich Brose.

U.B., M.M, and S.S. designed the field experiment. D.O., C.D., B.K., M.P. and G.S. assembled the database. D.O., C.D., B.C.R., G.S. and U.B. performed statistical procedures. Text was written by D.O., G.S. and U.B. with inputs from B.K., M.M., M.P., S.S. and B.C.R.

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Chapter II.6

Land use, decomposer community composition and leaf species interactively control litter decomposition

David Ott, Esra H. Sohlstroem and Ulrich Brose.

The chapter is based on the Bachelor Thesis written by E.H.S. entitled "*Effect of land use and animal diversity on the decomposition of two common leaf species.*", Georg-August-University Göttingen, Göttingen September 2013. This Bachelor Thesis was conducted in the framework of the PhD Thesis by D.O. The authors re-analyzed the underlying data and all authors contributed to the new version embedded in this thesis: D.O. and U.B. designed the experiment. D.O. prepared and conducted the experiment. E.H.S. and D.O. collected the data and conducted statistical procedures. The text was written by E.H.S., D.O. and U.B.

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Part I

General introduction

Chapter 1.

Introduction

1.1. Aims and scope

This thesis was inspired by two major theories: the metabolic theory of ecology (Brown *et al.* 2004) and the theory of ecological stoichiometry (Sterner & Elser 2002). Both theories claim to be applicable across multiple levels of organization that scale from "*individuals to whole ecosystems*" (Sterner & Elser 2002; Enquist *et al.* 2003; Brown *et al.* 2004; Woodward *et al.* 2010). The universal validity is based on the use of variables of fundamental importance "*rooted in first principles of thermodynamics and mass conservation*" (Woodward *et al.* 2010 after Brown *et al.* 2004 and Sterner & Elser 2002). The metabolic theory of ecology considers body mass and temperature as the main driver of biological rates (West, Brown & Enquist 1997; Brown *et al.* 2004). The theory of ecological stoichiometry on the other hand focuses on imbalances between the elemental contents and the according elemental ratios in consumers and their resources (Sterner & Elser 2002). However, concepts and predictors from both these bodies of theory will in principle complement each other to form a more powerful, unified theory and remarkably aid our understanding of the complexity of interactions amongst species and in food webs. They also serve as a starting point for future research. Even if such an unified approach has been called for in the past (Brown *et al.* 2004; Woodward *et al.* 2005, 2010; Allen & Gillooly 2009; Hillebrand *et al.* 2009), it has rarely been elaborated in research so far.

In the research chapters of this thesis, I aimed to make a major step towards such a unified perspective on population and community ecology by studying properties of soil ecosystems in dependence of body mass structures and stoichiometry. I concentrated on species and communities belonging to soil system that are directly or indirectly involved in the ecosystem functioning of litter decomposition and nutrient cycling. To disentangle the interplay of body mass structures and stoichiometry, I conducted laboratory experiments as well as analyzing field data of natural environments. I quantified the leaf-

litter consumption of a decomposer (Chapter 2) and disentangled soil animal diversity effects across trophic levels with an innovative application of study designs (Chapter 3). I developed a concept on how interactive effects of allometric and stoichiometric predictors affect biomass densities of populations in forest soil communities (Chapter 4) and examined how this concept applies to phylogenetic groups in the soil (Chapter 5). In a final step, I addressed effects of body mass and litter stoichiometry in combination with human management on litter decomposition in forests (Chapter 6).

1.2. Biodiversity and ecosystem functioning

We live in a time of global change, where mean global surface temperature, mean global sea level and emission of green-house gases (such as CO_2) reach higher levels and rise faster than in the last century or pre-industrial times (IPCC 2007). Moreover, the recent high rates of species extinctions are considered to be driven or at least intensified by anthropogenic induced threats (Gaston & Spicer 2003; Barnosky *et al.* 2011; Cardinale *et al.* 2012). Recently, extensive research sought mechanistic understanding of ecosystem services and how their underlying functions are maintained by each systems´ biodiversity (Chapin III *et al.* 2000; Loreau 2001, 2010; Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2012). These functions and services are of tremendous economic value for us (Costanza *et al.* 1997, 2011; Wilson & Carpenter 1999; de Groot *et al.* 2002). In theory, biodiversity and ecosystem functioning can be related in different ways (see e.g. Vitousek & Hooper 1994; Gaston & Spicer 2003), which has been addressed by a vast body of empirical work (summarized in the metastudy of Balvanera *et al.* 2006). Research at the end of the last century already demonstrated the drastic consequences of decreased diversity for ecosystem functioning (see e.g. Naeem *et al.* 1994). Now there is consensus that 1) in general the relationship between effects of biodiversity on ecosystem functioning (BEF) is non-linear and positive (Cardinale *et al.* 2012) and 2) declining diversity reduces functionality and resilience across ecosystems (Cardinale *et al.* 2006, 2012; Worm *et al.* 2006). However, the existing evidence that links biodiversity and decomposition is inconsistent and skewed towards some functions and services, such as for example the productivity in grasslands (Balvanera *et al.* 2006; Cardinale *et al.* 2012). Despite a good conceptional understanding of different effects of diversity, e.g. how species complement each other in maintaining a process or function (see e.g. Loreau *et*

al. 2001; Reiss *et al.* 2009), there is still a lack of a general concept capable of accurately describing the mechanisms behind these diversity effects.

Often body mass has been used as kind of a super-trait of species (Peters 1983; Brown *et al.* 2004) and is considered to have the potential to combine research on BEF with community ecology (Woodward *et al.* 2005; Loreau 2010). Independent of these approaches, Cardinale *et al.* (2009) combined perspectives of resource availability and nutrient ratios to BEF relationships. The metabolic theory of ecology and the theory of ecological stoichiometry are important theories that implement these considerations, i.e., how body size and resource availability and stoichiometry affect BEF relationships. Thus, both theories aim at exploring and describing various patterns that affect species interactions, population densities, complex food webs and whole ecosystems (Lotka 1925; Sterner & Elser 2002; Brown *et al.* 2004; Kaspari 2012).

1.3. Metabolic theory of ecology (MTE)

A striking feature of processes or biological rates (such as metabolism, fertility, mortality and consumption) is their parallel response in the scaling with body size (Peters 1983; Brown *et al.* 2004; Brown, Sibly & Kodric-Brown 2012). The metabolic theory of ecology (or simply metabolic theory[1]) describes the relationship between body size and biological rates. These relationships are non-linear in relation to body size, and are thus referred to as allometric (scaling) relationships - or simply as allometric scaling (Peters 1983). In principle, a biological characteristic (Y) scales with body mass (M) in a power-law of the form:

$$Y = Y_0 M^b \qquad (1.1),$$

where Y_0 is a normalization constant and b the (allometric) scaling exponent, both of which are empirically derived (Brown *et al.* 2004; Savage *et al.* 2004; Brown & Sibly 2012). The allometric scaling is non-linear unless b is zero or one (Peters 1983). The value of the exponent was debated heavily (Savage *et al.* 2004). Early work supported generally a scaling to the power of 2/3 (Rubner 1883).This was based on the proportion

[1] The metabolic theory of ecology is often referred to as the metabolic theory, even though other theories are abbreviated differently (theory of ecological stoichiometry, becomes ecological stoichiometry) and a similar abbreviation ("Metabolic Ecology", Sibly *et al.* (2012)) would also be possible. For clarity and convenience of the reader, I will use the notation metabolic theory throughout my thesis.

of body surface area to volume (Bergmann 1847), which is rooted in Euclidean geometry (Brown *et al.* 2004). However, later empirical studies suggested a 3/4 scaling exponent for metabolism (Kleiber 1932, 1947). West *et al.* (1997) reasoned that the scaling of the quarter-power metabolic derives from fractal like structures of branching networks in an organism. Metabolism does not only scale with body mass, but also with temperature (Peters 1983). To account for this, the original model from equation (1.1) was extended. The whole-organism metabolic rate follows a 3/4 power law with body size and scales exponentially with temperature, with an additional coefficient for the activation energy, E, of approximately - 0.65 eV (Gillooly *et al.* 2001; Brown *et al.* 2004):

$$B = B_0 M^{\alpha} e^{-E/kT} \qquad (1.2),$$

where B is the metabolic rate, B_0 a normalization constant that is independent of body size and temperature, M the body mass and α the allometric scaling exponent, which is 3/4 for whole-organism metabolic rate and - 1/4 for mass-specific metabolic rate (Brown *et al.* 2004, 2012; Brown & Sibly 2012). $e^{-E/kT}$ is the exponential Arrhenius function, where E is the activation energy of biochemical reactions (~ 0.65eV), k is Boltzmann's constant (8.62 x 10^{-5} eV K^{-1}), and T is the body temperature or the environmental temperature for ectotherms, in Kelvin (Gillooly *et al.* 2001; Brown *et al.* 2004; Meehan 2006b; Brown & Sibly 2012). This equation is the central basis of metabolic theory (Brown *et al.* 2012; Brown & Sibly 2012), of which Brown *et al.* (2004) stated that among all biological rates the "*metabolic rate is the most fundamental…because it is the rate of energy uptake, transformation, and allocation*" and "*it determines the rates of almost all biological activities*".

Allometric scaling does not only occur within individuals, but also within populations, where densities and abundances scale with body mass and temperature. Empirically, this was found for example in soil invertebrates (Meehan 2006a; Ehnes *et al.* 2014). The relationship between species abundance, (N), and body size (M) follows a negative three-quarter power law (Damuth 1981; Peters 1983; Woodward *et al.* 2005; White *et al.* 2007; Brown *et al.* 2012; Passy 2012; Mulder *et al.* 2013):

$$N = M^{-0.75} \qquad (1.3),$$

However, the universality of the actual exponent values in allometric scaling has been disputed much (Tilman *et al.* 2004; Glazier 2005, 2014; White *et al.* 2007; Isaac &

Carbone 2010; Price *et al.* 2012): allometric exponents or coefficients of activation energy occurred with differences among phylogenetic groups of soil organism (Meehan 2006b; Ehnes, Rall & Brose 2011).

1.4. From feeding rates to food webs

According to metabolic theory, feeding rates should follow allometric scaling relationships, just like the metabolic rate (Brown *et al.* 2004). One way to describe and measure feeding or consumption rates is the functional response (Holling 1959; Brose 2010), a measure of "*the magnitude of the effect of one species on the abundance of another*" (Berlow *et al.* 1999). More precisely, a functional response quantifies the *per capita* consumption rate of a consumer in dependence of the resource density (i.e., resource abundance) (Holling 1959; Brose 2010). Hereby, the functional response discriminates between two underlying mechanisms, the attack rate (the rate of successful search or attacks) and the handling time ("*the time the consumer needs to pursuit, ingest and digest a resource individual*; Brose 2010). Both these rates, and therefore the functional response as such, depend on body mass, consumer-resource body-mass ratios and temperature (Brose 2010; Vucic-Pestic *et al.* 2011; Englund *et al.* 2011; Rall *et al.* 2012). Indeed, interaction strengths were shown to scale with body size relationships (Berlow *et al.* 2004; Wootton & Emmerson 2005). This has far-reaching implications. Species must acquire resources to survive and reproduce (Brose *et al.* 2012) and are thus involved in interactions and connected to each other via direct feeding of a consumer on a resource (i.e., a trophic link). These trophic links exist building entire food webs across several trophic levels (Elton 1927; Paine 1980). Knowing the strength of trophic interactions in these food webs is a key towards understanding the dynamics of populations and communities (Scheu 2002). Moreover, a variation in the type of the functional response (due to altered scaling exponents) can stabilize food web dynamics (Williams & Martinez 2004; Rall, Guill & Brose 2008), which highlights the predictive power of this framework. Summarizing, body size related scaling laws can propagate from simple consumer-resource feeding interactions across entire food webs in ecosystems (Woodward *et al.* 2005; Petchey & Dunne 2012).

1.5. Theory of ecological (elemental) stoichiometry (ES)

From an ecosystem perspective, trophic links within food webs can be described as a flux of biomass and nutrients between consumers and resources (Woodward *et al.* 2005). It is thus reasonable that shortcomings in the resource supply constrain these interactions. This is known as Liebig´s Law of the Minimum (Liebig 1855), where the limiting nutrient is defined as the one shortest in supply relative to the demand. Despite some early concepts of supply rates of resources (Kaspari 2004), the metabolic theory of ecology generally does not account for such nutrient limitations (Allen & Gillooly 2009). The question hence remained how to "*deal with environmental deficits in elements*" from the perspective of metabolism (Kaspari 2004). The answer is the theory of ecological stoichiometry (or simply ecological stoichiometry), of which foundations and early approaches are summarized in the seminal work of Sterner and Elser (2002). Dating back to the first concept by Lotka (1925) and the extended approach by Reiners (1986), ecological stoichiometry is based on first principles of physics, chemistry and biology (Sterner & Elser 2002; Allen & Gillooly 2009). Elemental stoichiometry seeks to explain the strength of trophic interactions (Sterner & Elser 2002; Hillebrand *et al.* 2009) by analyzing the constraints of the mass balance of multiple chemical elements (Elser & Urabe 1999; Sterner & Elser 2002). Thus, the state variables are contents of elements or the according proportions of various elements to each other (Sterner & Elser 2002). Among the approximately 22 biologically relevant elements, carbon (C), nitrogen (N) and phosphorus (P) and carbon-to-nutrient ratios are traditionally highlighted (Sterner & Elser 2002; Kaspari 2012). The focus on these three elements of the major nutrient cycles was started by the groundbreaking research of Redfield (1958), who revealed a conserved ratio (C:N:P = 106:16:1) in oceanic ecosystems, known as the "*Redfield Ratio"* (Sterner & Elser 2002). Nevertheless, also other elements, such as sodium (Na), were found to play a critical role for abundance of soil invertebrates (Kaspari *et al.* 2009; Clay, Yanoviak & Kaspari 2014).

An important question is, how elements can exhibit such a critical role? In the same way, Frost (Frost *et al.* 2005b) asked what the physiological mechanisms behind the constraints on trophic interactions and the linkages between organism and ecological processes proposed by ecological stoichiometry are. To address these questions we need do to some considerations: First, and related to the *Redfield Ratio*, the elemental compositions of organisms and organismal subunits of different scale, e.g. ribosomes,

cells, or skeleton, are relatively fixed and conserved across taxa, known as the concept of stoichiometric invariance (Sterner & Elser 2002; Allen & Gillooly 2009). Second, despite this invariance, there is considerably difference in the elemental composition across the organizational scale, for example across molecules, organelles, cells, and organisms (Elser *et al.* 1996; Elser & Urabe 1999). Third, organisms need to maintain these elemental contents and compositions against changes of resource quality, which is the concept of homeostasis (Sterner & Elser 2002). This concept is based on negative feedback, which is the resistance to change the internal (organismal) stoichiometry with variation in external (resource) stoichiometry (Sterner & Elser 2002). Thus, if consumer stoichiometry remains constant or changes in constant proportions to resource stoichiometry there is no homeostasis (Sterner & Elser 2002). Fourth, physiological processes that exhibit control over organismal homeostasis are a) acquisition (e.g. feeding rate, food selection and assimilation efficiency), b) incorporation (e.g. bio-synthesis, gene expression, allocation and storage), and c) release (e.g. exudation and release) (Frost *et al.* 2005b). Fifth, there are fundamental differences in the flexibility in the elemental composition between autotroph and heterotroph organisms (Sterner & Elser 2002; Frost *et al.* 2005b; Persson *et al.* 2010). In general autotroph organisms are more flexible than heterotroph organisms (Sterner & Elser 2002; Frost *et al.* 2005b; Persson *et al.* 2010). These points are key to reveal "*nutritional requirements of organisms for survival, growth and reproduction, and for understanding how these processes, in turn, affect the flux, storage and turnover of elements in ecosystems*" (Allen & Gillooly 2009). In simple words, and to answer the question above: the structuring force of interactions are consequences of stoichiometric mismatches between consumers and their resources (Frost, Cross & Benstead 2005a). More generally, resource quality and stoichiometric constraints can occur in multiple ways: via limited nutrient supply for autotrophs (Elser *et al.* 2007), in different trophic groups, such as herbivores (Elser *et al.* 2000a) and decomposers (Hladyz *et al.* 2009) and across ecosystems (Elser *et al.* 2000a, 2007). These constraints affect higher trophic levels (Malzahn *et al*. 2007; Boersma *et al.* 2008) and exhibit different controls on individual and population level herbivory (Hillebrand *et al.* 2009).

A first empirical example reported stoichiometric constraints on the metabolism of differently sized species of water flees (Jeyasingh 2007): the allometric scaling exponent decreased with decreasing resource quality, i.e. increasing stoichiometric mismatch. This influence of stoichiometry on allometry highlights, that metabolic theory and ecological

stoichiometry are not mutually exclusive. Rather, it indicates that variation in the scaling exponent can be related to resource stoichiometry (Woodward *et al.* 2010). The idea of such a fusion in perspectives of metabolic theory and ecological stoichiometry itself is not new - Brown *et al*. (2004) discussed stoichiometric implications in the scaling of metabolic rates with body mass. Consequently, extensions of metabolic theory yielded a more complex model (Gillooly *et al.* 2002, 2005; Allen & Gillooly 2009), which refined the theoretical backbone and allowed a first integration of both theories. This model was capable to make impressively accurate predictions of growth rates under nutrient limitation, with model parameters based on the densities and masses of cellular and sub-cellular metabolic units, e.g. ATP and RNA (Allen & Gillooly 2009; Woodward *et al.* 2010). However, such a parameterization requires empirically derived estimates, e.g. on elemental contents of the subunits in consumers and resources, or needs to be based on assumptions. Thus, parameterization with estimates can be logistically very challenging, or the predictive power may be limited. Therefore, I developed in my studies a novel approach to combine metabolic theory and ecological stoichiometry in a way that overcomes the need of extensive parameterizations while still being accurate in predicting population densities in entire food webs.

1.6. Soil system and litter decomposition

In this thesis, I used the soil system, its specific animals and an ecosystem function (litter decomposition) to detect and address allometric and stoichiometric constraints on interaction strengths and population densities in entire communities, rather than aiming to explain the process of decomposition in its full complexity. Here, I provide some background knowledge of the soil system needed enable an adequate understanding and interpretation of my results.

The vast majority of net primary productivity reenters the soil system via dead organic material, e.g. litter fall, or root exudates (Swift, Heal & Anderson 1979; Cebrian 1999; Scheu & Setälä 2002; Cebrian & Lartigue 2004; Gessner *et al.* 2010). The process of decomposition reduces dead organic material to carbon dioxide and soil organic matter and warrants the release of nutrients for incorporation into soil food webs and the availability to plants (Swift *et al.* 1979; Wolters 2000; Moore *et al.* 2004; Coleman 2004). Consequently, soils and the associated organic matter, play an essential role for

functioning, decomposition and nutrient cycling, and are of crucial relevance to ecosystem productivity (Swift *et al.* 1979; Wolters 2000; Moore *et al.* 2004; Coleman 2004). Wall *et al.* (2010) stated that soils are "*the biologically active skin of our planet's land surface*". The decomposition process in and on the surface soils depends on the decomposer community, abiotic conditions (such as the pH, temperature or moisture availability) and leaf litter quality (Swift *et al.* 1979; Berg *et al.* 1993; Coûteaux, Bottner & Berg 1995; Aerts 1997; Hättenschwiler, Tiunov & Scheu 2005; Gessner *et al.* 2010), where leaf litter quality and can be indicated by the stoichiometry, i.e. carbon-to-element ratios (Swift *et al.* 1979; Enríquez, Duarte & Sand-Jensen 1993a; Anderson, Boersma & Raubenheimer 2004; McGroddy, Daufresne & Hedin 2004; Hladyz *et al.* 2009; Ågren *et al.* 2013). Moreover, resource quality and nutrient supply traditionally constrain abundances of species in the soil and entire food webs (Scheu & Schaefer 1998; Chen & Wise 1999; Salamon *et al.* 2006; Kaspari & Yanoviak 2009; Mulder *et al.* 2011). Soil food webs are very diverse in terms of community composition and species richness (Swift *et al.* 1979; Schaefer 1991; Giller 1996). Furthermore, soil food webs express a high level of complexity. They consist of several different functional groups with multi-trophic interactions above and below ground (Scheu & Setälä 2002; Wardle *et al.* 2004; Mulder *et al.* 2013). Since a major part of the interactions appear below ground the complexity is difficult to investigate (Wall *et al.* 2010).

Classically, soil organisms have been differentiated into coarse groups by their body width or length, including specific taxa (Swift *et al.* 1979; Scheu & Setälä 2002). These categories are the microfauna and microflora, including, e.g., bacteria, fungi and nematodes (Nematoda), the mesofauna, including, e.g., springtails (Collembola) and mites (Acari), and the macrofauna, including decomposers, e.g., woodlice (Isopoda), millipedes (Diplopoda), and earthworms (Lumbricidae), as well as predators, e.g., centipedes (Chilopoda) and spiders (Arachnida) (Swift *et al.* 1979; Scheu & Setälä 2002). The carbon and energy fluxes in the soil food webs are dominated mainly by fungi and bacteria, which thus function as the basis of the whole web (Swift *et al.* 1979; Swift & Anderson 1994; Scheu 2002 p. 20002; Mulder *et al.* 2013). Nevertheless, species belonging to the meso-and macrofauna contribute importantly to decomposition processes (Seastedt 1984; Coûteaux *et al.* 1995; Aerts 1997), via trophic and non-trophic interactions (i.e. stimulation of microorganism activity by litter fragmentation and pore formation, altered nutrient contents in faeces after gut passage) (Wolters 2000; Scheu & Setälä 2002; Hedde *et al.* 2007). Especially the macrofauna is capable of increasing leaf

litter mass loss (Hättenschwiler *et al.* 2005; De Oliveira, Hättenschwiler & Tanya Handa 2010; Vos *et al.* 2011). Consequently, studies that compared decomposition in the presence or absence of larger fauna, found higher mass losses when larger decomposers were able to access the leaf litter (Irmler 2000; Wall *et al.* 2008; Makkonen *et al.* 2012; Handa *et al.* 2014). Moreover, species belonging to the macrofauna accelerated decomposition in studies that investigated temperature effects in streams (Boyero *et al.* 2014) and subarctic conditions (van Geffen, Berg & Aerts 2011). Summarizing, a combined approach to study effects of allometry (emphasized for the macrofauna) and resource quality on decomposition is not only promising to elucidate our understanding of biodiversity on ecosystem functioning.

1.7. Project framework

This thesis was conducted in the subproject "*ModelWeb*" in the project of the Biodiversity Exploratories (Fischer *et al.* 2010). The Biodiversity Exploratories project is established as a large-scale and long-term research program (Fischer *et al.* 2010, www.biodiversity-exploratories.de) with the aim of examining the relationship between biodiversity and ecosystem functioning as influenced by human land use intensity (Fischer *et al.* 2010). A comprehensive summary of the overall design and arrangement of the field sites of the project can be found in Fischer *et al.* (2010). In collaborative work with the subproject "*Litter Links*", an impressive dataset on soil meso- and macrofauna was assembled after an intensive sampling and species identification process (Ehnes 2014; Klarner 2014; Ehnes *et al.* 2014). The gathered data represents species level information across 48 forest plots in three different landscapes and along a gradient of forest types that varied in management intensity (Ehnes 2014; Klarner 2014). I used this data in Chapter 4 and Chapter 5. The litterbag study presented in Chapter 6 was conducted on forest plots in two of the three regions.

1.8. Research objectives and chapter outline

In the research chapters of this thesis, I addressed the interplay of body mass and resource stoichiometry on different levels of complexity in food webs and how litter decomposition depended on these relationships. First, I examined decomposer-detritus (i.e. leaf litter) feeding interactions (Chapter 2). Second, I investigated if these patterns hold when species richness increases in and between trophic levels (Chapter 3). Third, I searched for allometric and stoichiometric constraints on whole communities using data of complex forest soil communities. I developed a concept of how population densities that follow the biomass - body mass scaling relationship, additionally correlate to and depend on litter stoichiometry (Chapter 4). Fourth, in subsequent analyses on several taxonomic groups, I addressed some element-specific hypothesis and importance of single carbon-to-element ratios (Chapter 5). Fifth and finally, I used litterbags to directly manipulate the effects of decomposer body mass and resource stoichiometry in the natural situation on forest plots (Chapter 6).

The simplest complexity level I studied was the direct consumer-resource feeding interaction of a macrofauna decomposer (a species of terrestrial isopods, i.e. woodlice) and leaf litter of two different tree species (Chapter 2). In a laboratory experiment, I introduced for the first time decomposer feeding rates in dependency of body mass, temperature (controlled on three different levels) and density and quality of the litter resource (as indicated by stoichiometric contents). In this context, I applied the functional-response framework to the feeding behavior of a decomposer, a concept that is traditionally used in studies examining predator-prey feeding interactions (Vucic-Pestic *et al.* 2010b; Lang, Rall & Brose 2011; Rall *et al.* 2011, 2012b; Kalinkat *et al.* 2013b). This enabled me to successfully quantify decomposer feeding rates and gain insights into the mechanisms of the decomposer functional response, i.e. attack rates and handling times (Holling 1959). These mechanisms can directly be compared to those on higher trophic level feeding interactions. Ultimately, this will lead to an increased predictive power of food-web models, when parameterization of model coefficients is empirically derived from lower trophic levels, too.

To have a look into more complex communities, I performed a microcosm study. In Chapter 3, I examined if and how relationships of the simple decomposer-detritus feeding interaction changed with increasing species richness, and how these possible changes

could alter decomposition rates. I used four different decomposer species of the macro- and mesofauna belonging to the same trophic level (i.e. horizontal diversity). However, while decomposer diversity was manipulated, I kept litter diversity constant and offered a litter mixture of four different leaf species. Additionally, I added a species of a higher trophic level (which is a vertical increase in species richness, i.e., vertical diversity) - either a predatory mite or a centipede. Centipedes were able to exert both intra- and interspecific predation pressure. In this study, I combined two promising designs for the first time into one innovative approach: 1) the random partitions design by (Bell *et al.* 2009), a stepwise linear-regression approach to disentangle diversity and species identity effects and 2) the allometric design by Schneider *et al.* (2012) and Schneider & Brose (2013) that calculates species abundances based on allometric scaling relationships with species specific average body masses (Damuth 1981; Peters 1983; White *et al.* 2007; Passy 2012) in dependence of temperature, principles of chemical reactions and trophic level (Gillooly *et al.* 2001; Meehan 2006a). Moreover, the final densities per species were calibrated to the abundance of the largest species in the experimental unit following the allometric scaling rules (Schneider *et al.* 2012; Schneider & Brose 2013). In summary, I tracked the effects of predictors belonging to metabolic theory or ecological stoichiometry for decomposition on lower trophic level diversity in presence of a higher trophic level.

In Chapter 4, I increased the level of complexity and scaled up to forest soil food webs. I used a dataset of complex soil invertebrate communities from 48 forests of the Biodiversity Exploratories, which consisted of nearly five thousand populations and measurements of leaf litter stoichiometry. As demonstrated in a previous study (Ehnes *et al.* 2014), density distributions in these communities follow allometric relationships, e.g. biomasses scale with population-averaged body masses (alternatively defined as the body-size spectra, Mulder & Elser 2009; Mulder *et al.* 2011, 2013, or the local size–density relationship, White *et al.* 2007). I developed a model framework to examine how this scaling relationship correlated to and depended on litter stoichiometry across the entire dataset including different trophic levels, functional and taxonomic groups. Furthermore, I examined how allometric scaling coefficients vary when litter stoichiometry is considered.

In Chapter 5, I applied the integrated approach of Chapter 4 to investigate population biomass densities in different functional, trophic and phylogenetic groups of the same dataset (Chapter 4). In addition to allometric and stoichiometric variables, I used habitat

characteristics like litter pH value, litter depth and forest type as predictor variables. While I addressed some specific hypothesis related to litter nutrient contents, I also obtained a general frequency ranking of carbon-to-element ratios and habitat related variables. This enabled us to reveal a pattern that shows the general importance of the predictor variables for density distributions across the considered animal groups.

In the final research Chapter 6, I manipulated the availability of resource stoichiometry by offering leaf litter of different quality from two tree species. This was done in a litterbag study on forest plots under natural conditions in two regions of the Biodiversity Exploratories as part of the collaborative root exclusion (trenching) experiment. I discriminated between decomposers of different body masses (i.e., body size or body diameter in this case) by two different mesh sizes of the litterbags: either both meso- and macrofauna was excluded (micro meshes) and decomposition was exerted by microorganisms only, or the larger fauna was allowed to access the leaf litter (macro meshes) leading to a decomposition that was processed by the full community. Moreover, a full- factorial combination of the different litterbags was distributed across all forest types assessing effects of different land use intensities. The response variable representing decomposition was litter mass loss in the litterbags. I related differences in litter mass loss to the manipulated factors and additionally to the available species data from the Biodiversity Exploratories (Chapters 5 and 6).

Part II

Research chapters

Chapter 2.

Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry

David Ott, Björn C. Rall and Ulrich Brose.

2.1. Abstract

Macrofauna invertebrates of forest floors provide important functions in the decomposition process of soil organic matter, which is affected by the nutrient stoichiometry of the leaf litter. Climate change effects on forest ecosystems include warming and decreasing litter quality (e.g. higher C:nutrient ratios) induced by higher atmospheric CO2 concentrations. While litter-bag experiments unraveled separate effects, a mechanistic understanding of how interactions between temperature and litter stoichiometry are driving decomposition rates is lacking. In a laboratory experiment, we filled this void by quantifying decomposer consumption rates analogous to predator–prey functional responses that include the mechanistic parameters handling time and attack rate. Systematically, we varied the body masses of isopods, the environmental temperature and the resource between poor (hornbeam) and good quality (ash). We found that attack rates increased and handling times decreased (i) with body masses and (ii) temperature. Interestingly, these relationships interacted with litter quality: small isopods possibly avoided the poorer resource, whereas large isopods exhibited increased, compensatory feeding of the poorer resource, which may be explained by their higher metabolic demands. The combination of metabolic theory and ecological stoichiometry provided critically important mechanistic insights into how warming and varying litter quality may modify macrofaunal decomposition rates.

2.1. Introduction

Two aspects of climate change (Brose *et al.* 2012), warming and elevated atmospheric CO2 concentrations, can both influence soil organisms and their critically important ecosystem function of litter decomposition (Swift *et al.* 1998). First, warming affects all levels of biological organization from individuals up to communities (Walther *et al.* 2002; Woodward *et al.* 2010), because it directly accelerates the metabolic rates and biochemical processes of organisms as conceptualized by metabolic theory (Gillooly *et al.* 2001; Brown *et al.* 2004). Eventually, this implies that warming should accelerate decomposition rates. Second, elevated atmospheric CO2 concentrations increase the carbon content of plant tissues (Swift *et al.* 1998). Ecological stoichiometry describes how the macroelements carbon (C), nitrogen (N) and phosphorus (P), and their ratios are critical for organisms to build biological structures and regulate physiological processes (Sterner & Elser 2002; Frost *et al.* 2005b). Interestingly, most animals need to maintain an elemental homeostasis, and thus stoichiometric mismatches between consumers and their resources, as caused by higher atmospheric CO2 concentrations, can lead to decreased (avoidance) as well as increased (compensatory) levels of herbivory (Hillebrand *et al.* 2009). Moreover, these stoichiometric mismatches can strongly interact with species' body masses in driving the strength of herbivory (Hillebrand *et al.* 2009). In consequence, the importance of ecological stoichiometry for decomposition processes was recognized (Martinson *et al.* 2008; Mulder & Elser 2009) and related to relationships between stoichiometric litter quality and decomposer abundance (Kaspari & Yanoviak 2009). However, mechanistic insights into how warming and modified litter stoichiometry interactively affect decomposition rates are still lacking (Martinson *et al.* 2008; Tylianakis *et al.* 2008).

The decomposition of litter depends on the interaction (trophic and non-trophic) of the microflora (bacteria and fungi) with primary and secondary decomposers (Wolters 2000; Scheu & Setälä 2002; Scheu 2002). Among these, the larger decomposers such as earthworms, millipedes and woodlice (macrofauna henceforth) contribute by consuming leaf litter (colonized by microflora), thereby shredding it into finer pieces and mixing the leaf fragments with other layers and components of the forest floor habitat (Wolters 2000; Scheu & Setälä 2002; Scheu 2002). These processes increase the leaf litter accessibility to the microflora and smaller decomposers (Wolters 2000; Scheu & Setälä 2002; Scheu

2002). Thus, the presence and activity of the macrofauna is crucially important for the energy transfer and decomposition speed of soil organic matter (Wolters 2000; Scheu & Setälä 2002; Zimmer *et al.* 2002; Hättenschwiler & Gasser 2005). Previous climate change studies on macroarthropods concentrated on behavior (Hassall *et al.* 2010), physiology (Schuler *et al.* 2011), life-history traits combined with resource quality (Hättenschwiler & Bretscher 2001; Zimmer 2002; David & Gillon 2009), population density and phenology (Zimmer 2004) or habitat specification and geographical distribution patterns (reviewed by David & Handa, David & Handa 2010). Quantitative predictions of how decomposer-feeding rates depend on warming and the lower stoichiometric quality of the litter resources have not been provided by previous studies.

In this study, we addressed how climate change alters decomposition rates by systematically varying temperature, decomposer body mass and litter quality in a laboratory experiment. By using the concept and methodology of nonlinear functional responses (nonlinear models relating feeding strength to resource density, see §2c) characterizing predator–prey interactions, we aimed to provide a novel mechanistic understanding of decomposer–litter feeding interactions. According to metabolic theory, we addressed whether consumption depends on (i) decomposer body mass, and (ii) temperature. While metabolic theory does not assume any relationship of feeding interactions with resource quality, stoichiometric theory suggests either compensation or avoidance if consumption rates on the poorer resource are increased or decreased, respectively. Furthermore, we aimed to address the entirely novel question of how these metabolic and stoichiometric constraints interact in determining decomposition. We used the parameters of the functional response, attack rate and handling time, to reveal a mechanistic understanding of decomposer feeding under the influence of climate change.

2.2. Methods

(a) Experimental design

We quantified the feeding rates of a common terrestrial woodlouse, *Oniscus asellus* L. (Isopoda: Oniscidae) across a full-factorial combination of three levels of environmental temperature (10°C, 15°C and 20°C) with a poor (hornbeam: *Carpinus betulus* L.) and a good litter resource (ash: *Fraxinus excelsior* L.). Litter quality was judged by the

stoichiometric contents of the leaf species (see §2b). For each of these combinations, 18 trials across a continuous size range from small to large isopods (11.1–130.4 mg) were established leading to a total of 108 experimental units. Full-factorially replicated control units without animals exhibited only minimal leaf decay. Hence, a significant influence of micro-organisms on the leaf decay in our feeding experiments could be excluded.

We used glass jars (6.3 cm diameter, 7.5 cm height) as experimental units. Each jar had a 2 cm layer of plaster at the bottom to provide constant moisture during the experiment. Jars were covered with gauze mesh (100 mm) to allow gas exchange. Habitat structure was provided by 1 g (dry mass) of artificial leaves made of plastic cloth. A pre-test assured that these artificial leaves were not consumed by woodlice. Our experiment ran for a total of 115 days with a day–night rhythm of 12 L : 12 D in thermostatically controlled incubators and a relative air humidity of 70 per cent (+10%). In spring 2011, woodlice were collected in a deciduous forest and kept in closed plastic boxes at 15°C. Woodlice were weighed before and after the experiment to calculate the average individual body masses for all experimental units. All weight measurements were performed with a precision scale (LE225D, d = 0.01 mg, Sartorius AG, Göttingen, Germany). Three woodlouse individuals were placed in each experimental unit. Individuals were distributed across experimental units to minimize within-unit variation of body mass while maximizing the range in body masses across experimental units. Moreover, we ensured that a similar body-mass range was realized for each treatment combination of temperature with litter quality. Pilot studies on woodlouse consumption allowed calculation of the initial litter biomasses per experimental unit depending on consumer body mass, temperature and resource quality. Thus, initial litter density differed across treatments, which was necessary to enable robust fits of functional-response models to data with initially strong declines and subsequently saturating decreases. However, effects of these initial differences on their parameters (attack rate and handling time) are unlikely (see §4). On the basis of these relationships, we started with different initial litter biomasses per treatment (a range of 9.8–145.6 g m^{-2} for ash and 7.1–60.1 g m^{-2} for hornbeam; variation according to temperature and woodlouse body mass).

Leaf litter and plaster were moistened with water every day. Experimental units were aligned in the incubators in a random rotation after daily moistening to avoid any blocking effects. Dead animals were replaced, and faeces were removed daily to ensure that litter consumption was not influenced by fluctuating isopod numbers, necrophagic or coprophagic feeding (Zimmer 2002). During the experiment, leaf litter weights were

measured every third day for each replicate independently to monitor the decay in litter biomass. Prior to weighing, experimental units were acclimatized for 1 h to the weighing room conditions that were held constant for the entire experimental time (relative air humidity 62 ± 3%, temperature 24.5 ± 1°C). All litter weights are fresh weights (litter was not dried prior to weighing), but note that it is not equivalent to the fresh weight of green leaf tissue.

(b) Litter material and quality

Litter material was obtained from deciduous forest stands located in the northeastern part of the Hainich National Park, Germany. Freshly fallen leaves were collected in autumn 2010. Litter was air-dried and separated into species. Woodlice prefer decomposed over freshly fallen leaf litter (Zimmer 2002, and citations therein). Thus, the sorted leaf material was exposed to natural conditions for eight weeks in open plastic vats (aperture: 0.29 m^2) to ensure abiotic conditioning, including leaching and physical breakdown. Subsequently, the leaf litter was defaunated for 3 days at 60°C and stored at room conditions before usage.

Analyses of litter quality were based on two samples per species, each sample pooled three randomly taken leaves. Leaf sample preparations and analyses of initial nutrient concentrations were carried out according to published protocols (Jacob *et al.* 2009).Concentrations were measured as millimol per gram dry weight. A recent study demonstrated that woodlouse abundance is positively correlated to litter contents of calcium (Ca) (Kaspari & Yanoviak 2009). Thus, we analyzed the contents of carbon (C), nitrogen (N), phosphorous (P) and calcium (Ca).

In our study, nutrient concentrations in ash were: N = 1.37, P = 0.03 and Ca = 0.66 (mmol g^{-2}). These contents were higher than those in hornbeam: N = 0.80, P = 0.02 and Ca = 0.59 (mmol g^{-2}). The corresponding ratios to carbon (C) contents were 27.24 C:N and 1176.84 C:P for ash versus 47.10 C:N and 1816.55 C:P for hornbeam. Together, these stoichiometric data indicated that ash should be a better resource than hornbeam. Several studies suggested that other chemical compounds of leaf litter such as lignin, cellulose and phenolic contents may affect the accessibility of leaf resources to decomposer animals (Zimmer *et al.* 2002; Hättenschwiler & Jørgensen 2010). Thus, it might be anticipated that decomposer feeding rates could respond to these leaf characteristics. However, contents of lignin or polyphenols in ash and hornbeam are so low (Hendriksen

1990; Hättenschwiler & Gasser 2005; Hladyz *et al.* 2009) that differences among the two resources should be negligible in our study. Moreover, isopods are well adapted to tolerate phenolic litter contents (Zimmer *et al.* 2002; Zimmer 2002). Hence, these non-stoichiometric characteristics of the leaf resources should not account for the results presented here, though our approach would be flexible enough to incorporate these additional indicators of litter quality.

(c) Functional responses as mechanistic models of nonlinear interaction strengths

The functional response describes the per capita consumption rate F_{ij} of a consumer i in dependence of the density, N_j, of its resource j:

$$F_{ij} = \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \qquad (2.1)$$

where a_{ij} is the per capita attack rate (also instantaneous rate of successful capture) and h_{ij} is the handling time needed to ingest and digest a resource unit (Holling 1959). Here, we extend this concept to decomposer– detritus interactions and replace resource abundance by biomass density of litter to predict quantitative decomposition rates. Many biological rates such as attack rate, a_{ij}, and handling time, h_{ij}, follow power–law relationships with organism body mass, m_i (gram fresh weight), and exponential relationships with temperature, T (K) (Gillooly *et al.* 2001; Brown *et al.* 2004), expressed as an extended Arrhenius term (Vasseur & McCann 2005; Rall *et al.* 2010):

$$h_{ij} = h_0 m_i^{sh} e^{\frac{-E_h (T - T_0)}{k T T_0}} \qquad (2.2)$$

and

$$a_{ij} = a_0 m_i^{sa} e^{\frac{-E_a (T - T_0)}{k T T_0}} \qquad (2.3)$$

where h_0 and a_0 are normalization constants at temperature T_0 (15°C = 288.15 K equal to the average of our temperature gradient), s_h and s_a are the allometric scaling exponents for handling time and attack rate, respectively, E_h and E_a are the activation energies (eV) for handling time and attack rate, respectively, k (1/ eV) is Boltzmann's constant (8.62 10^{-5} eV K^{-1}) and T (K) is the absolute temperature. This allometric concept of species

interactions has been implemented in simple model systems (Vucic-Pestic *et al.* 2010b; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011) and complex ecological networks (Brose 2010).

(d) Statistical procedures

Data were analyzed using the statistical program R (version 2.14.0) (R Development Core Team 2011) with the additional package "emdbook" (Bolker 2008). Instead of varying the resource density similar to a traditional functional-response experiment, we used only one initial litter density per replicate and kept track of the decomposer feeding by measuring a highly resolved time-series. The statistical procedure, however, was the same as in traditional functional-response experiments using Rogers "random predator equation" (Rogers 1972) as the integrated form of the functional response while correcting for decreasing prey density during the time of the experiment:

$$N_e = N_j\left(1 - e^{a_{ij}\left(N_e h_{ij} - P\tau\right)}\right) \qquad (2.4)$$

where *Ne* [Ind$_j$ m^{-2}] is the density of prey *j* eaten during the experiment, *P* is predator *i*'s density [Ind*i* m^{-2}], τ is the experimental time [d], N_j is the initial prey density [Ind*j* m^{-2}], a_{ij} is the attack rate [m² d^{-1} Indi^{-1}] and h_{ij} is the handling time [d Ind$_i^{-1}$]. Note that in our case N_e and N_i are expressed in mass [g *FW*] instead of individuals.

We solved the recursive function (eqn. 2.4) using non-linear least square-regressions (function "nls" in R) yielding:

$$N_e = N_j - \frac{\omega\left(a_{ij}h_{ij}N_j e^{-a_{ij}\left(P\tau - h_{ij}N_j\right)}\right)}{a_{ij}h_{ij}} \qquad (2.5)$$

where ω is the *Lambert W* function (see Bolker 2008 and references therein for a detailed description). We applied the power-law and exponential relationships of handling time (h_{ij}) and attack rate (a_{ij}) with body mass and temperature, respectively, as described in equations (2.2) – (2.5). We began by fitting the full functional-response model with all parameters (the scaling exponents of body mass and temperature in equations (2.2) and (2.3) dependent on litter quality. Hence, the full model included different allometric exponents and activation energies for the two leaf resources, ash and hornbeam. Subsequently, we systematically simplified this model according to the lowest Akaike information criterion (AIC) (Bolker 2008) by removing the dependency of the

parameters on litter quality. These AIC values (ΔAIC) describe the equality of models: models with ΔAIC 2 are not distinguishable; ΔAIC values of 4 – 7 indicate slightly different models and models with ΔAIC 10 are severely different (Burnham & Anderson 2004; Bolker 2008).

Table 2.1: Parameters of the functional-response model for decomposer interactions with a good (ash) and a poor resource (hornbeam): all parameters except for the mass-scaling exponent of handling time, s_h, depended on litter quality. Estimates of handling time, h_0 (d ind^{-1}) and attack rate, a_0 (m^2 d^{-1}), allometric exponents, s_a and s_h, activation energies, E_a and E_h and their standard errors (SE) were obtained by fitting the functional response model (eqn. (2.5) including equations (2.2), (2.3)).

litter species	parameter	estimate	SE	significance level
ash (*F. excelsior*)	mass-scaling exponent of handling time (s_h)	-17.5	4.83	$p < 0.001$
	normalization constant for handling time (h_0)	$2.07*10^{2}$	$2.61*10^{1}$	$p < 0.001$
	activation energy of handling time (E_h)	-1.36	$3.53*10^{-2}$	$p < 0.001$
	normalization constant for attack rate (a_0)	$2.74*10^{-4}$	$4.46*10^{-5}$	$p < 0.001$
	mass-scaling exponent of attack-rate (s_a)	$2.01*10^{-1}$	$5.30*10^{-2}$	$p < 0.001$
	activation energy of attack rate (E_a)	$2.30*10^{-2}$	$6.71*10^{-2}$	$p > 0.1$
hornbeam (*C. betulus*)	normalization constant for handling time (h_0)	$5.10*10^{2}$	$6.59e*10^{1}$	$p < 0.001$
	activation energy of handling time (E_h)	-87	$4.77*10^{-2}$	$p < 0.001$
	normalization constant for attack rate (a_0)	$1.18*10^{-3}$	$3.55*10^{-4}$	$p < 0.001$
	mass-scaling exponent of attack-rate (s_a)	$7.45*10^{-1}$	$8.42*10^{-2}$	$p < 0.001$
	activation energy of attack rate (E_a)	$2.74*10^{-1}$	$9.47*10^{-2}$	$p < 0.01$

2.3. Results

(a) Litter decay

The amount of leaf litter exhibited a continuous and saturating decay in our experiment, which was terminated after 76 days for ash (figure 2.1a, c, e) and 115 days for hornbeam (figure 2.1b, d, f). As our control units without woodlice did not show a similar decay, we could assign these decreases in litter biomass to consumption by decomposers. Our experiment included a continuous body-mass spectrum of the woodlice (shown in discrete size classes as the three rows in figure 2.1 for clarity of presentation) and three different temperature levels (10°C, 15°C and 20°C; figure 2.1). This nonlinear decay in leaf litter resulting from feeding by woodlice was quantified by fitting type II functional-response models to the data (curves in figure 2.1). In general, the decline of litter mass became steeper with warming (e.g. red compared with blue curves, figure 2.1) and decomposer body mass (lower to upper row of figure 2.1), and it was shallower for the poor resource hornbeam (figure 2.1b, d, f) than for the good resource ash (figure 2.1a, c, e).

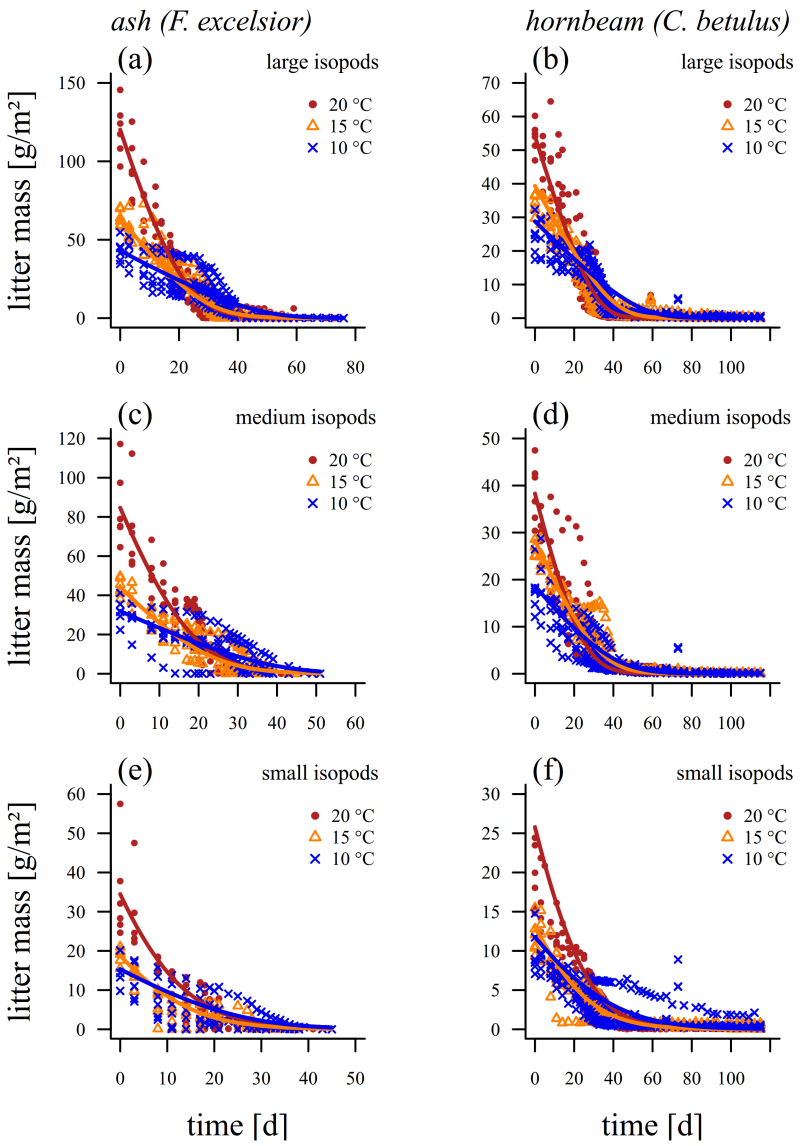

Figure 2.1: Time-series of litter mass loss resulting from isopod consumption. Curves are based on the best-fitting functional response model of isopods feeding on ash (a, c, e) and hornbeam (b, d, f) plotted as litter mass loss (g m22) against time (day). We plotted panels with differently sized isopods: large (70 – 130 mg, (a, b)), medium (40 – 70 mg, (c, d)) and small (11 – 40 mg, (e, f)) to disentangle the size range of the isopods. (a – e) The overall trends for the three temperatures (blue line: 10°C, orange line: 15°C, red line: 20°C) are fitted to the six associated replicates. Note that we fitted a single model to the data while disentangling the data in this figure for clarity of presentation. See table 2.1 for model parameters.

(b) Choice of functional-response model

The lowest AIC value was achieved by the model with the mass-scaling exponent of the handling time, s_h, set independent of litter quality (table 2.1). Thus, this model has the same allometric exponent (s_h) for both litter resources (ash and hornbeam) and is more parsimonious than the full model. All other possible model simplifications were not warranted (ΔAIC < 2), suggesting that (i) attack rates and handling time depend on decomposer body mass and temperature, and (ii) litter stoichiometry affects the allometric and temperature relationships of attack rates, but only the temperature dependency of handling time. The subsequent results are based on this model.

(c) Functional-response parameters

Consistent with our expectations, the most adequate functional-response model suggested significant dependencies of decomposer attack rates and handling times on decomposer body mass, environmental temperature and resource quality (table 2.1). The attack rates increased significantly with increasing isopod body mass (figure 2.2a) feeding on the good resource ash (power-law exponent: $s_a = 0.201 \pm 0.053$, $p < 0.001$, table 2.1) as well as on the poor resource hornbeam ($s_a = 0.745 \pm 0.084$, $p < 0.001$, table 2.1). These differences in attack rates between the two litter types are significant: the model with a single attack rate on both resources performed significantly worse (ΔAIC = 37.57, F-test for model comparison $p < 0.001$). Interestingly, the attack-rate curves across the isopod body mass gradient intersect. This is because the allometric exponent for the poor resource is roughly 3.7 times larger than for the rich resource (figure 2.2a). While the attack rate on the poor resource (hornbeam) was lower than the attack rate on the good resource (ash) for isopods of small body masses, it was higher at higher body masses (figure 2.2a). This points to a compensatory feeding of large isopods, whereas small isopods seem to avoid the poor resource (hornbeam).

Following our expectations, attack rates increased with warming when feeding on the poor resource (hornbeam; activation energy $E_a = 0.274 \pm 0.095$, $p < 0.01$, figure 2.2b and table 2.1). In replicates with the good resource (ash), however, attack rates did not increase significantly ($E_a = 0.023 \pm 0.067$, $p < 0.1$, figure 2.2b and table 2.1). More generally, the attack rate on the poor resource (hornbeam; figure 2.2b) was higher than the attack rate on the good resource (ash; figure 2.2b). This difference increased with warming, suggesting accelerated compensatory feeding on the poor resource (hornbeam).

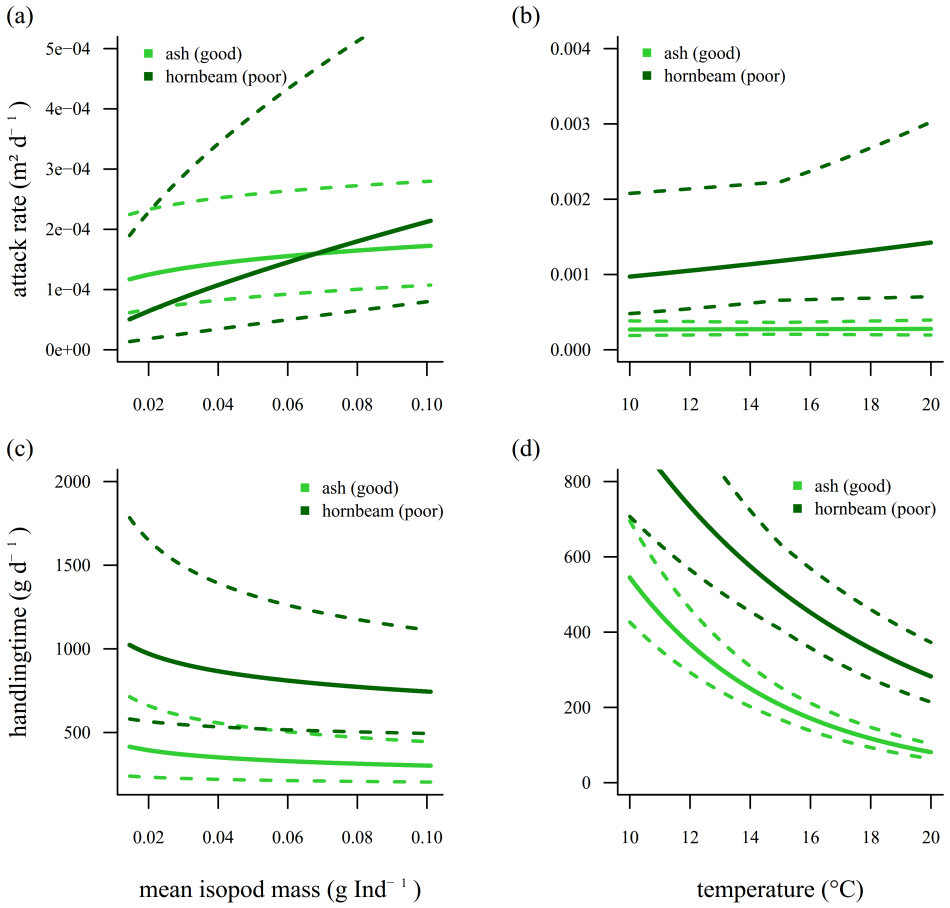

Figure 2.2: Scaling of functional-response parameters: attack rates depended on isopod masses (a) and temperature (b); handling times depended on isopod masses (c) and temperature (d). The different leaf resources are indicated in light green (good) and dark green (poor). 95% CIs are shown by dashed lines. See table 2.1 for model parameters.

Together, these results illustrate that effects on attack rates of consumer body mass, temperature and resource stoichiometry are not independent of each other. Moreover, handling times decreased significantly with increasing isopod body mass (figure 2.2c). The power-law exponent of body mass was independent of litter species (s_h = 20.165 ± 4.827, $p < 0.001$, figure 2.2c and table 2.1). However, the normalization constants for handling time (parameter h_0 in equation (2.2) and table 2.1) differed for the litter species (figure 2.2c). Handling time decreased with warming (figure 2.2d). The activation energies characterizing the strength of these relationships differed between litter types (good resource (ash): E_h = 21.363 ± 0.035, $p < 0.001$; poor resource (hornbeam): E_h = 20.860 ± 0.048, $p < 0.001$, table 2.1). In consequence, across our gradients in isopod body

mass and temperature, we found that the handling time was higher on the poor resource (hornbeam; figure 2.2c, d) than the handling time on the good resource (ash; figure 2.2c, d). This was consistent with expectations, and the difference became more accentuated with warming (figure 2.2d).

2.4. Discussion

For the first time, this study successfully quantified consumption rates of terrestrial decomposers in the context of a consumer–resource functional response. Our analyses unraveled significant effects of decomposer body mass, temperature and resource quality on attack rates and handling times. Strikingly, litter quality interacted with metabolic constraints of body mass and temperature in driving decomposer feeding rates, suggesting a synthesis of ecological stoichiometry and metabolic theory. This synthetic theory will be at the heart of obtaining a generalized understanding of how climate change will affect decomposition rates across ecosystems.

Consistent with metabolic theory (Gillooly *et al.* 2001; Brown *et al.* 2004), we found that attack rates increased and handling times decreased with (i) isopod body mass, and (ii) temperature. However, we also found surprising and entirely novel interactions with litter quality. Our results demonstrated higher handling time of the poorer resource, confirming assumptions that poorer resources require more time for digestion owing to longer biochemical processing of carbon-rich resources (Hättenschwiler & Bretscher 2001). Moreover, we found a shift from possible avoidance of the poor resource by small isopods to compensatory feeding by large isopods, indicated by higher attack rates on the poor resource. However, lower attack rates of the small isopods on the poor resource might also be influenced by the limited foraging behavior of the juveniles (e.g. slower moving speed or resource detection). Compensatory feeding implies increased feeding of poor resources to balance nutritional requirements for elements (e.g. N, P and Ca) that are necessary for the structural components of their body tissues. In addition to that, the resource quality (i.e. litter species) influenced the mass and temperature dependence of attack rates and the temperature dependence of handling times. These results imply an interplay among metabolic and stoichiometric constraints of decomposer feeding.

The power-law and exponential relationships with body mass and warming are consistent with similar scaling relationships found in predator–prey studies (Vucic-Pestic

et al. 2010b; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). Moreover, similar relationships drive metabolic rates of invertebrates (Ehnes *et al.* 2011). The inverse of handling time, the maximum consumption rate, describes consumers' ability to balance their metabolic demands (Rall *et al.* 2012a). Consequently, we can compare handling times directly to the scaling of metabolic rates because they follow similar relationships (Brown *et al.* 2004; Dell, Pawar & Savage 2011). The metabolism of isopods exhibits an activation energy E_i = 0.686 (Ehnes *et al.* 2011) which is substantially lower than the activation energies of handling times in our study when absolute values are considered (ash: E_h = 1.363; hornbeam: E_h = 0.86). This indicates that woodlouse consumption of both resources should increase more strongly with warming than metabolism. The resulting net energy gain suggests that warming may cause population growth of decomposers. These findings are contrary to predator–prey systems: a new meta-study on predator–prey functional responses reported that the activation energy of handling times for terrestrial invertebrates (E_h = 20.3) (Rall *et al.* 2012a) is lower than that of metabolism (E_i ranging from 0.38 to 0.8) (Ehnes *et al.* 2011). Hence, the increase in decomposer feeding rates with warming exceeded that of metabolism, whereas predators failed to cover their increasing metabolic demands with warming. Together, this may lead to increased population growth of decomposers owing to accelerated feeding and reduced top down pressure.

As for any laboratory study, potential caveats have to be discussed. We used initial litter densities that differed across treatments, which were necessary to enable robust fits of functional-response models. This came at the cost of potentially confounding temperature treatments with initial litter densities, and some of the conclusions drawn concerning effects of high temperature might have been driven by high initial litter density. However, this alternative explanation has the unlikely implication that higher consumption rates at high litter density (prior to intersection of curves in figure 2.1) would preclude saturation and lead to continuously higher consumption rates at low litter density (after intersection of curves in figure 2.1). Instead of this mechanistically dubious explanation, we interpret the steeper decreases in litter density at higher temperatures as a consequence of the increased metabolism of isopods forcing them to higher consumption.

Conclusions

Our results indicate an important interaction between decomposer body mass and compensatory feeding behavior that may be explained by varying metabolic constraints. Small decomposers with a low metabolic rate exhibited lower attack rates on the poorer resource that can be interpreted as avoidance behavior. By contrast, large decomposers showed compensatory feeding behavior with a higher attack rate on the poorer resource. This may imply that small decomposers can avoid poor resources, whereas their substantially higher metabolic rate drives large decomposers into compensatory feeding behavior. This argument is supported by the accelerated compensatory feeding on the poorer resource that is caused by warming. Ultimately, our results imply that metabolic theory and ecological stoichiometry interact with each other to constrain decomposition rates. Our results provide an important step towards an "overarching framework" that integrates "from individuals to ecosystems" (Woodward 2009) thus linking metabolic theory and ecological stoichiometry to a single synthetic theory. This multitrophic perspective will become critically important for predicting warming effects on population stability, species coexistence (Binzer *et al.* 2012; Rall *et al.* 2012a) and organic matter fluxes in food webs (Moore *et al.* 2004; Nielsen *et al.* 2011).

Since decomposition and climate change are multifactorial processes, other factors such as litter mixtures, species interference, moisture availability and dispersal should be of main concern in future studies testing the macrofaunal functional responses with warming (Swift *et al.* 1998; Scheu & Setälä 2002; Hättenschwiler & Gasser 2005; Aerts 2006). Interestingly, warming may yield range shifts of macrofauna decomposers leading to increased invasions of prior-permafrost ecosystems of the cold biomes (Aerts 2006). Contingently, our results suggest warming may accelerate decomposition rates, which could fuel carbon turnover and CO2 release. Together, these findings suggest a possible positive feedback loop between warming and decomposition with the potential to push the world's ecosystems faster towards melting point.

2.5. Acknowledgements

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Chapter 3.

Horizontal and vertical diversity drive ecosystem functioning

David Ott, Miriam Achler, Björn C. Rall and Ulrich Brose

3.1. Abstract

Understanding the relationship between biodiversity and ecosystem functioning becomes increasingly important as anthropogenic stressors strongly impact the structure and diversity of natural communities. While most studies of diversity-functioning relationships were restricted to manipulations of specific functional group, anthropogenic impacts on natural communities spread across trophic levels. A systematic understanding how changes in horizontal (within a trophic level or functional group) and vertical (across trophic groups) diversity interact is thus rendered critically important. In a multi-trophic diversity experiment, we manipulated horizontal diversity (four decomposer species) and vertical diversity (two predator species) to examine decomposition (leaf litter mass loss) as the ecosystem functioning (four different leaf litter species). We used litter stoichiometry to discuss differences in quality of leaf litter types. For the first time, we used a combination of the random partitions design (Bell *et al.* 2009) - manipulating horizontal diversity - and an allometric design (Schneider *et al.* 2012) - manipulating vertical diversity. This enabled to successfully monitor the complex effects and interactions in this multi-trophic system. We found that ecosystem functioning increased with total diversity (i.e., combined decomposer and predator richness). Disentangling this overall diversity effect yielded strong effects of horizontal diversity (decomposer richness) on decomposition, whereas effects of vertical diversity (predator richness) were mostly neutral to –surprisingly- slightly positive. Our systematic combination of designs provided mechanistic insights suggesting that the interplay between interference competition among decomposers and low top-down pressure by predators should be responsible for these results. These findings were related to intra-guild-predation among

predator species and the substantial habitat structure provided by the leaf litter layer. Overall, our study enabled insights into the interwoven mechanisms of horizontal and vertical diversity driving litter decomposition in forest ecosystems. Moreover, our study provides an example how to systematically disentangle horizontal and vertical diversity effects on ecosystem functioning, which may trigger further multi-trophic biodiversity studies.

3.2. Introduction

Biodiversity on Ecosystem Functioning (BEF)

Under the risk of a new wave of species' extinctions (Barnosky *et al.* 2011) the correlation between ecosystem functioning and biodiversity (species richness) has received increasing scientific attention (Loreau *et al.* 2001; Naeem & Wright 2003; Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2012; Reiss *et al.* 2009; Loreau 2010). While several hundred studies addressed biodiversity effects on ecosystem functioning (Balvanera *et al.* 2006), few of them focused on decomposition as the ecological function (Hooper *et al.* 2005; Balvanera *et al.* 2006). Moreover, studies manipulating diversity across multiple trophic levels are extremely scarce (Balvanera *et al.* 2006; Duffy *et al.* 2007; Srivastava *et al.* 2009a; Reiss *et al.* 2009). In this vein, species diversity can be distinguished further into horizontal and vertical diversity (Duffy *et al.* 2007; Reiss *et al.* 2009; Gessner *et al.* 2010). Horizontal diversity is defined as an increase of species richness within a trophic level or an increase of species within a functional group (Duffy *et al.* 2007; Reiss *et al.* 2009; Gessner *et al.* 2010). In contrast, vertical diversity describes the increase in diversity across trophic levels and functional groups, which is often quantified as predator diversity (Duffy *et al.* 2007; Reiss *et al.* 2009; Gessner *et al.* 2010). In this study, we use forest litter communities as an example to compare effects of total diversity to those of horizontal (decomposers) and vertical diversity (predators) on the decomposition of four leaf species.

Decomposition

Decomposition - which includes nutrient cycling as an ecosystem service - is among the most important ecosystem functions (Hooper *et al.* 2005; Balvanera *et al.* 2006; Reiss *et al.* 2009; Gessner *et al.* 2010), because the major amount of the net primary productivity (NPP) - with up to 90% in forest and shrub ecosystems - enters the decomposer system via dead organic material or root exudates (Cebrian 1999; Cebrian & Lartigue 2004; Srivastava *et al.* 2009a; Gessner *et al.* 2010). Beside the effects of decomposers (see below), leaf litter decomposition depends under constant climatic conditions on the chemical and physiological properties of the leaf species (Berg *et al.* 1993; Coûteaux *et al.* 1995; Aerts 1997; Hättenschwiler *et al.* 2005). The quality of leaf litter (i.e., palatability for the decomposers) ranks according to the fractions of carbon (C) (Aber, Melillo & McClaugherty 1990; Hättenschwiler & Jørgensen 2010; Hättenschwiler *et al.* 2011) and the content of elements such as nitrogen (N) and phosphorous (P) (Aber *et al.* 1990; Aerts 1997; Ågren *et al.* 2013). Differences in leaf litter quality can be indicated by the nutrient stoichiometry, i.e. carbon-to-element ratios (Enríquez *et al.* 1993a; Anderson *et al.* 2004; McGroddy *et al.* 2004; Hladyz *et al.* 2009; Ågren *et al.* 2013). Decomposition thus varies strongly across different leaf litter types (Hättenschwiler & Gasser 2005; Hättenschwiler *et al.* 2005; Gessner *et al.* 2010; Ott, Rall & Brose 2012; Makkonen *et al.* 2012; Handa *et al.* 2014).

Horizontal diversity (decomposer richness)

Decomposers maintain important steps of the decomposition process (Seastedt 1984; Coûteaux *et al.* 1995; Aerts 1997). Over the last decade, progress has been made in disentangling the roles of litter diversity and diversity of both - microbial decomposers and invertebrate detritivores - for decomposition in complex, multi-trophic system (Scheu & Setälä 2002; Gartner & Cardon 2004; Hättenschwiler *et al.* 2005; Srivastava *et al.* 2009a; Gessner *et al.* 2010), but the results concerning the relationship between biodiversity and ecosystem functioning remained variable (Scheu & Setälä 2002; Gartner & Cardon 2004; Hättenschwiler *et al.* 2005; Gessner *et al.* 2010). However, an increase in horizontal decomposer diversity (Srivastava *et al.* 2009a; Gessner *et al.* 2010) and functional group dissimilarity (Heemsbergen *et al.* 2004) generally increases ecosystem functioning. Recent studies integrating across ecosystems provide strong support for the general perspective of positive horizontal diversity effects: enhanced decomposition rates

were found when the complete decomposer community had access to leaf litter (Makkonen *et al.* 2012; Handa *et al.* 2014) and when higher taxonomic richness was present (Wall *et al.* 2008). Mechanistically, however, such diversity effects can arise from pure additivity of decomposers, but they can also include indirect interactions leading to over- or underyielding (Gessner *et al.* 2010). Simple additivity would occur if the effects of all decomposer species were independent of each other, and consequently the decomposition in the polycultures with multiple decomposer species equaled the sum of the decomposition rates of the same species' monocultures. In contrast, systematically higher decomposition rates in polycultures would suggest overyielding (Gessner *et al.* 2010), which can be a consequence of facilitative interactions among decomposers (Cardinale, Palmer & Collins 2002; Jonsson & Malmqvist 2003; Bruno, Stachowicz & Bertness 2003; Heemsbergen *et al.* 2004; Kéfi *et al.* 2012), whereas systematically lower decomposition rates indicate underyielding that is potentially caused by exploitative or interference competition interactions among decomposers (Jonsson & Malmqvist 2003; McKie *et al.* 2008; Bastian, Pearson & Boyero 2008). In conclusion, increasing decomposer diversity can increase or decrease decomposition depending on whether facilitation or competition dominate, but interactions of these processes with the vertical diversity of the predator communities have not been addressed yet.

Vertical diversity (predator richness)

It is well documented that not only horizontal diversity but also vertical diversity (predator richness) modifies ecosystem functioning (Finke & Denno 2004, 2005; Duffy *et al.* 2007; Bruno & Cardinale 2008; Schneider & Brose 2013). Increasing predator diversity can cause trophic cascades that strongly dampen the density and process rates at the trophic level below, which reduces herbivore pressure and thus fosters ecosystem functioning (Finke & Denno 2004, 2005; Otto *et al.* 2008). However, intra-guild predation among predators can dampen trophic cascades thus diminishing or removing their effects on ecosystem functioning (Finke & Denno 2004, 2005; Schneider & Brose 2013). While an increase in predator diversity can thus have positive and negative effects on ecosystem functioning (Bruno & Cardinale 2008), more recent work demonstrated the importance of predator body masses and their constraints on feeding strengths (Schneider *et al.* 2012). Predator feeding strength generally follow a hump-shaped exploitation curve with an optimum prey size, often characterized by prey that is one order of magnitude

smaller, and decreases in the efficiency at which smaller or larger prey consumed (Brose *et al.* 2008; Rall *et al.* 2011; Kalinkat *et al.* 2013b). Consequently, small predators may predominantly exert top-down control on lower trophic levels, whereas larger predators may also impose strong intra-guild predation pressure on smaller predators, which can lead to a positive net effect on lower trophic levels (Schneider *et al.* 2012; Schneider & Brose 2013). Interestingly, this simple concept was able to predict the effects of predator diversity on ecosystem functioning in a microcosm experiment (Schneider *et al.* 2012). Prior studies thus documented a general positive effect of decomposer richness (horizontal diversity) on decomposition (Heemsbergen *et al.* 2004; Wall *et al.* 2008; Srivastava *et al.* 2009a; Gessner *et al.* 2010), and strong, size-dependent effects of predator richness (Schneider *et al.* 2012; Schneider & Brose 2013), whereas the interplay of these effects has not been addressed yet.

Study overview and questions

In this study, we established laboratory microcosms of forest litter communities comprising four decomposers, two predators and four leaf types (figure 3.1). We systematically varied decomposer richness according a random partitions design (Bell *et al.* 2005, 2009) and replicated the series according to a full-factorial manipulation of predator combinations. This allowed addressing (1) effects of total diversity (decomposers and predators), horizontal diversity (decomposers) and vertical diversity (predators) on ecosystem functioning (leaf litter mass loss). More specifically, we also tested for additivity, over- and underyielding effects in these relationships. Furthermore, we disentangled mass loss effects across different leaf litter species that vary in their quality according to ratios of carbon (C) to nitrogen (N) or phosphorus (P). Subsequently, we examined (2) if effects of species identities drive the diversity effects on ecosystem functioning. Finally, we investigated (3) if intra-guild predation among predators modified the biodiversity-ecosystem functioning relationships.

3.3. Methods

Experimental units

The experiment ran for seven weeks in late summer 2013 in laboratory microcosms (20x20x10 cm) made of acrylic glass and tightly sealed with gauze (45 µm mesh size). Prior to the experiment, the bottom of the microcosms was covered with plaster (approx. 2 cm) which was mixed with a small amount of activated charcoal for coloring and to prevent fungal growth. The hardened plaster was saturated with water for one hour 72 hours before the onset of the experiment. The layer of plaster allows to control for constant air humidity in the microcosms (Vucic-Pestic *et al.* 2010b). The microcosms were stored in climate chambers with controlled conditions (15 °C, ≥ 60 % rH and a day-night-rhythm adjusted to 12:12 hours). Each microcosm was placed on a small platform in a water bath. The water bath received liquid soap to reduce surface tension. In this way, together with the gauze cover, we aimed to prevent predatory mites from escaping and contaminating other microcosms. The leaf litter was placed into the microcosms 40 hours before the onset of the experiment and sprayed with 20 milliliter of water. During the duration of the experiment the microcosms were moistened thrice a week with approximately ten milliliter of water. All microcosms were initially placed and ordered after each moistening process in random rotation across the climate chambers to avoid blocking effects.

We used leaf litter of the four tree species *Fraxinus excelsior* (Linnaeus, 1758; ash), *Acer pseudoplatanus* (Linnaeus, 1758; maple), *Tilia ssp*. (Linnaeus, 1758; lime) and *Fagus sylvatica* (Linnaeus, 1758; beech) as a basal resource (figure 3.1). Approximately two gram (dry weight) of each leaf species were randomly distributed in the microcosms yielding a total of eight gram of leaf litter per microcosm. The animal community of the experiment consisted of six different species, four decomposer and two predator species (figure 3.1). The largest predators, centipedes (Chilopoda: Lithobiidae), and the decomposers *Glomeris marginata* (Villers, 1789; Diplopoda; pill millipede) and *Oniscus aselllus* (Linnaeus, 1758; Isopoda; woodlice) were collected in the surrounding forest of the city Göttingen, Germany ("Göttinger Wald"). Since our sampling of centipedes yielded insufficient amounts to enable the use of only a single centipede species in our experiment, we used centipedes of different species (i.e., *Lithobius forficatus* (Linnaeus, 1758), *Lithobius mutabilis* (Koch, 1862) and *Lithobius piceus* (Koch, 1862). However we

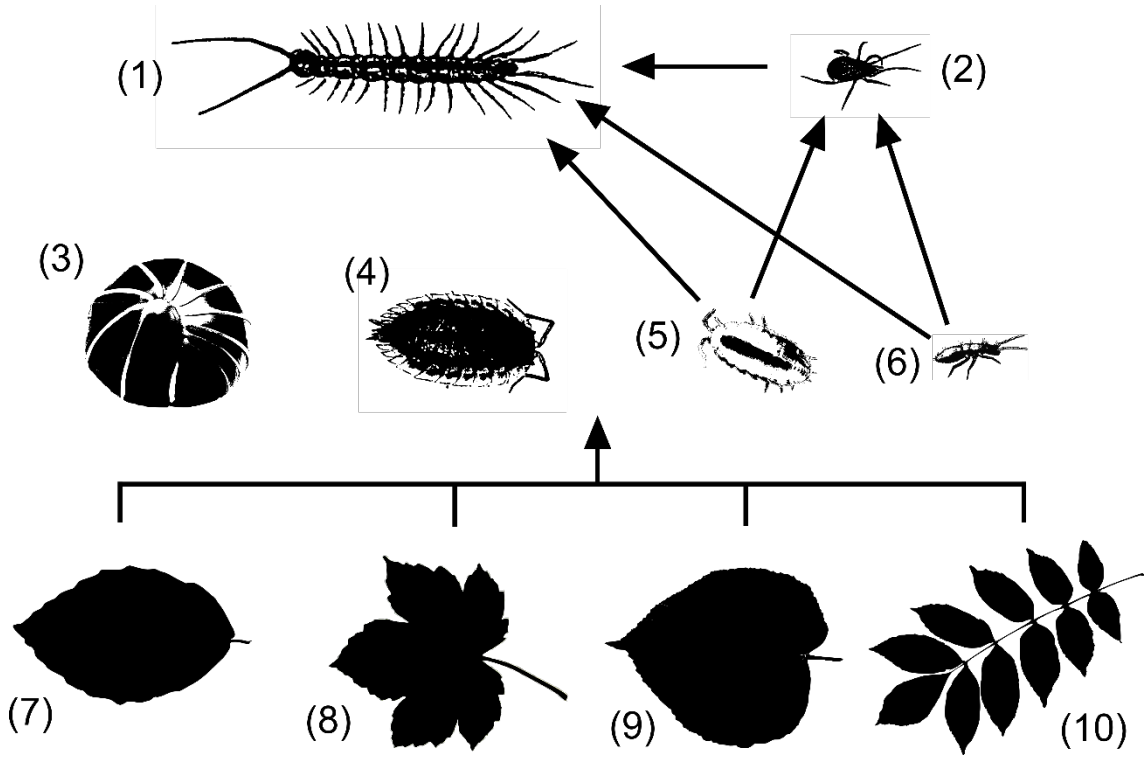

Figure 3.1: Experimental food web: The predator level consisted of centipedes (1) and predatory mites (2). Pill millipedes (3), large (4) and small (5) isopod species as well as springtails (6) were used on the decomposer level. Litter of the four leaf species beech (7), maple (8), lime (9) and ash (10) built the basal resource level. The arrows symbolize energy flux by feeding interactions.

treated these different centipede species as a common centipede predator and assumed all three species to oppose equal predation pressure and feeding habits in the experimental setup (hereafter referred to as *Lithobius ssp.*). All other animals of the experimental community, i.e. the second predator *Hypoaspis miles* (Berlese, 1892; Acari: Mesostigmata; mite) and the decomposers *Trichorhina tomentosa* (Budde-Lund, 1893; Isopoda; white woodlice) and *Sinella curviseta* (Brook, 1882; Collembola; springtails), were ordered from an online-shop (www.terraristika-express.com). All animals, the sampled and the ordered ones, were kept or reared at least on week in the laboratory prior to the experiment to determine species identity and to assure good fitness of organisms. For nutrition of the animals we used different organisms or litter material than used in the experiment to avoid feeding adaption. The decomposer species were combined in different richness levels according to the random partitions design (see below) and their abundances followed an allometric design (see below). Predator treatments were established one day (24 hours) after the start of the experiment: treatments without predators, treatments with either centipedes or predatory mites and treatments with both predators in combination. At the end of the experiment, all animals were removed from

the microcosms, counted and weight with a precision scale (LE225D, d = 0.01 mg, Sartorius AG, Göttingen, Germany). Leaf litter mass loss was used as an indicator of ecosystem function (see below).

Leaf litter

The leaf litter used in this study was collected in 2010 in the Göttinger Wald (maple) and in the Hainich National Park, Thuringia, Germany (beech, ash and lime). The leaf litter has been pre-conditioned and stored dry until further usage (Ott *et al.* 2012). Prior to the experiment, leaf litter was heated (three days at 60°C or until no further weight loss was observed) to ensure a similar dryness of all leafs and defaunation. Subsequently, leaf litter was allowed to adjust one day (24h) to the weighing-room conditions (air humidity 37% and temperature 22°C) before the weighing took place. Measurements of initial concentrations of total carbon (C), nitrogen (N) and phosphorous (P) in the leaf litter were conducted with two samples of a mix of three randomly taken leaves of each species (Ott *et al.* 2012). From each sample, 55 mg powder material was used for chemical analyzes according to published protocols (Jacob *et al.* 2009). We calculated carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P) ratios to estimate the quality of the leaf litter species (Berg *et al.* 1996; Aerts 1997; Ågren *et al.* 2013). We ranked the leaf species from ash with the best quality to beech with the lowest quality (table 3.S1). At the end of the experiment, the remaining leave litter was cleaned from faeces and sorted into species. For the estimation of leaf litter mass loss, dry weights were measured following the same procedure as at the beginning of the experiment, and final dry weights were subtracted from the initial ones.

Experimental design – random partitions.

A requirement of experiments that address the question of biodiversity effects on ecosystem functioning is to be able to disentangle species richness effects from community composition, i.e., effects of species identities (Bell *et al*. 2005, 2009; Byrnes & Stachowicz 2009). Addressing this with a combination of the common additive and substitutive approaches (Byrnes & Stachowicz 2009), or even a full factorial realization of treatments, has its limits in the amount of logistically feasible units, when the number of species of the community in focus gets larger (Bell *et al.* 2009). The random partitions

design (Bell *et al.* 2005, 2009) aims to differentiate between the effects of species richness and species identities without a realization of all species combinations on each richness level (Bell *et al.* 2005, 2009). Furthermore, the species richness effect is separated into contrasts of a linear ("*i.e., richness treated as a linear, untransformed, continuous variable*", Bell *et al.* 2009) and a non-linear part ("*nonlinear species richness treated as a categorical variable*", Bell *et al.* 2009), see Bell *et al*. (2009) for more details. More specifically, each species is drawn from the species pool without replacement at all richness levels independently (Bell *et al.* 2009); table 3.S2). A full set of richness levels derived by this random drawing is called a partition series (Bell *et al.* 2009). Replication is derived by newly random drawing for each richness level, starting again from the full species pool and yielding another partition series (Bell *et al.* 2009). In our study, we used four decomposer species. According to the random partitions design a partition series contained three levels of decomposer richness: one (monocultures), two or four species (table 3.S2). We applied the random partitions selection only to the decomposer community. Thus, a full partition series consisted of seven microcosms with different decomposer treatments. In addition to the partition series that contained only decomposers (i.e., a predator richness of zero), we extended the manipulation on the horizontal diversity gradient by adding vertical diversity (i.e., predator richness). The full factorial extension of the random partitions design yielded additional partition series containing centipedes, predatory mites, or the combination of both predators (table 3.S2). We established two partition series at each level of predator manipulation, i.e. eight partition series, which summed up to 56 microcosms (table 3.S2). Together with 16 controls without animals, we obtained a total of 72 microcosms (table 3.S2).

Experimental design - allometric combination of abundances

Larger animals are less abundant than smaller ones, because the relationship of population density (N) and body size (M) follows a power function $N = M^b$, with b as the scaling exponent at about -0.75 (White *et al.* 2007; Passy 2012; Ehnes *et al.* 2014). A recent study showed that predator size is important for the predator's effect on ecosystem functioning, i.e. spiders, centipedes and mites differed in their amount of prey demand (Schneider *et al.* 2012). Further they considered that an increase of predatory diversity resulted mostly in predator species with different body masses (Schneider *et al.* 2012). Both facts led to the establishment of the allometric design (Schneider *et al.* 2012). This design allows

Table 3.1: Empirical variables used to calculate the abundance of each species per experimental unit.

Variable	Symbol	Value	Unit
Normalization factor	α/η_0	31.15	[g Cyr-1 g body mass-b]
Activation energy	E	0.71	[eV]
Boltzmann´s constant	k	8.62*10-5	[eV/°K]
Temperature	T	15	[°C]
Constant	a	1.03	
Exponent	b	0.72	
Euler´s number	e	2.72	
Proportion of metabolic energy	ε	2.68	

Abbreviations: C indicates carbon, yr is year, eV indicates electron Volt, K is Kelvin, C is Celsius and g is gram.

balancing effects of (predator) diversity (the number of predator species) and predator density (the number of predator individuals) by mimicking natural density-mass relationships. Following this approach, we calculated the initial abundance of each invertebrate species per experimental unit according to:

$$N_0 = \left(\frac{\alpha}{n_0}\right) NPP^a M^b \mathrm{e}^{E/k(T)} \varepsilon^{(L-1)} \qquad (3.1),$$

where N_0 is the abundance of each species [individuals per microcosms] depending on the net primary production, here defined as 200 [mg C/(m^2/h)], M is the mean body mass [mg] of the given species and L is the trophic level of the species (decomposer 1.5; predator 2.5) (Meehan 2006a). Other parameters are the normalization factor, $\alpha/\eta 0$, the activation energy , E, the Boltzmann´s constant , k, the temperature , T, Euler´s number , e, scaling exponent , b, and the proportion of metabolic energy, ε, all of which were empirically parameterized (Meehan 2006; table 3.1 this study). In a final step, abundances of each species were adjusted to the size of the experimental units (table 3.2).

Table 3.2: Number of invertebrates per species. Calculated after equation 3.1. Depicted are the values for the defined species specific body mass (mean values of a sample).

Animals*	Functional group	Body mass [mg]	Cosm area[m²]	Abundance [Ind/Cosm]
springtails	decomposer	0.09	0.04	156
small isopods	decomposer	2.16	0.04	16
large isopods	decomposer	40	0.04	2
pill millipedes	decomposer	80	0.04	1
centipedes	predator	30	0.04	1
predatory mites	predator	0.16	0.04	7

* springtails = *Sinella curviseta*, small isopods = *Trichorhina tomentosa*, large isopods = *Oniscus asellus*, pill millipedes = *Glomeris marginata*,

Data analyses

Analyses were performed with the statistical software GNU R version, 3.0.2 (R Development Core Team 2014). The R-code which was used for the analyses was modified after Bell *et al*. (2009), Appendix B. We used Pearson product-moment correlation coefficients to investigate correlations between all combinations of the mass loss of the single leaf species and the total leaf litter mass loss (table 3.S3). Since total leaf litter mass loss was significantly correlated to the mass loss of the single leaf species (table 3.S3), we ran all analyses for each leaf species separately.

We used linear regression models to examine the effects of species richness (continuous predictor variable) on ecosystem function (continuous response variable). Litter masses were $\log_{10}$ transformed and some outliers were eliminated (four data points of beech, two of maple, one of lime and one of ash; table 3.S4) after raw data fitting and residual inspection to increase normality and homogeneity. In the first step of the analyses (addressing question 1), we tested for effects of total species richness (decomposers and predators) on ecosystem functioning. We included the controls without animals in the richness gradient, and thus richness ranged from zero to six species. Furthermore, we analyzed the effect of horizontal (decomposer richness) and vertical (predator richness) diversity as separate variables (continuous predictors) with interactions between them. This was done in two ways: (1) we entered decomposer richness before predator richness into the linear model and (2) vice versa. In this way, we obtained the variance explained by one richness parameter while controlling for the other. Thus, we aimed to support the results of the overall species richness model when examining if the explanatory power increases by disentangling horizontal and vertical richness effects. In these regression analyses, an additive effect of predators is indicated by a slope of one (increases in diversity are followed by a proportional increase in functioning), whereas over- and underyielding are indicated by slopes that are significantly larger or smaller, respectively.

In the second step of the analyses (addressing question 2), we followed the stepwise approach of the random partitions design (Bell *et al.* 2009) and used linear models with the residuals of the previous model (with decomposer and predator diversity as two independent variables) as the dependent variable and decomposer identity variables (presence absence for each species independently) as the independent variables. Additionally, we followed the random partition designs analyses (Bell *et al.* 2009) by also analyzing non-linear richness effects with total species richness as a factor using the

residuals of the second step (linear models testing for identity effects). We found no evidence of non-linear richness effects (table 3.S5) suggesting that richness effects on ecosystem functioning in our experiment were adequately described by the linear models employed under step 1.

In the third step of the analyses (addressing question 3), we tested for effects of the predators and intra-guild predation on litter decomposition. Similar to step 1, we employed linear models with litter decomposition as the dependent and decomposer diversity as the independent variable. The decision to include only decomposer diversity as the continuous independent variable was based on the results obtained under step 1 (see below). The full-factorial design of the predator treatments allowed adding the effects of the two predator species (representing their identity effects) and their interaction term (indicating intra-guild predation) as factorial co-variables to the linear model.

3.4. Results

The average mass loss across all experimental units was highest for ash (0.355 ± 0.073 g) suggesting that on average only 17.3 % of the initially about two gram per leaf species per microcosm were consumed. This results was followed by 10.2 % (0.21 ± 0.045 g) on average for lime and 7.8 % (0.16 ± 0.043 g) for maple. The lowest mass loss was obtained for beech, with an average of 4.6 % (0.095 ± 0.034 g). Thus, the total leaf litter mass loss did not exceed an overall average of approximately 10 % (0.82 ± 0.123 g) and had a maximum of 13.8 % (1.11 g) of the eight gram total initial litter mass per microcosm. These results follow our ranking of the leaf litter quality according to leaf stoichiometry (table 3.S1) suggesting that leaf litter mass loss and thus decomposer consumption are positively correlated with the nitrogen and phosphorous contents of the leafs.

Step 1: diversity effects on ecosystem functioning

Detailing the overall effect of total leaf litter mass loss into those for single leaf litter types yielded significantly positive effects of total species richness on beech ($F_{1, 66}$ = 17.64***, R^2 = 0.21; table 3.3, figure 3.2a), lime ($F_{1, 69}$ = 6.18*, R^2 = 0.08; table 3.3, figure 3.2c) and ash ($F_{1, 69}$ = 13.54***, R^2 = 0.16; table 3.3, figure 3.2d), whereas the result for the subset maple was positive but not significant (table 3.3, figure 3.2b).

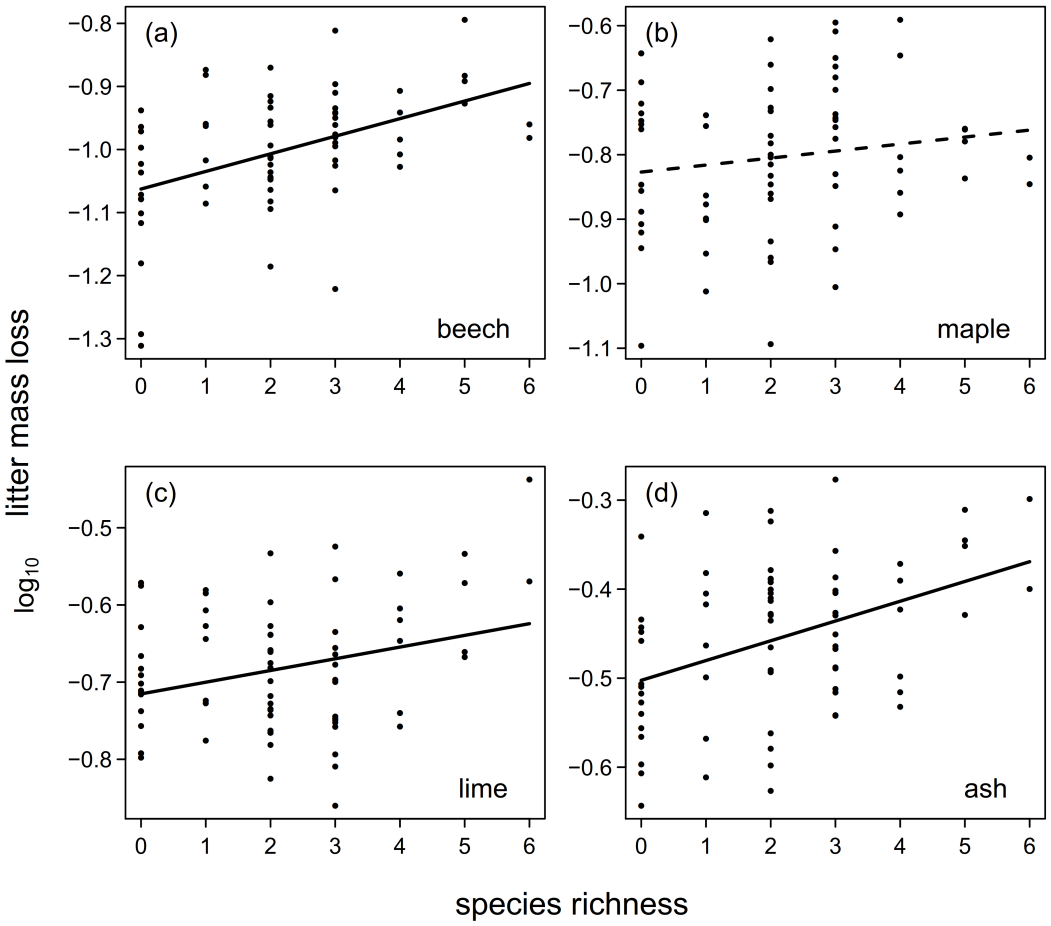

Figure 3.2: Effects of total species richness on the leaf litter mass loss [log_{10} (mg) dry weight]. Total diversity is the number of species (ranging from zero to six on the x-axis) including decomposers and predators. Litter mass loss is shown for the different leave species beech (a), maple (b), lime (c) and ash (d). The solid lines represent significant relationships, whereas an insignificant relationship is illustrated with the dashed line. Regressions estimates of the linear model are given in table 3.3. Black dots indicate a single microcosms.

Table 3.3*: Results of the linear model testing total species richness on litter mass loss (step 1).*

Leaf species	Parameter	Estimate	Std.error	t-value	p-value	
Beech	Intercept	-1.06	0.02	-60.25	<0.001	***
	Slope	0.03	0.01	4.20	<0.001	***
	R^2	0.21				
	F-statistic (1,66)	17.64				
Maple	Intercept	-0.83	0.02	-36.09	<0.001	***
	Slope	0.01	0.01	1.26	0.212	
	R^2	0.02				
	F-statistic (1,68)	1.59				
Lime	Intercept	-0.72	0.02	-44.18	<0.001	***
	Slope	0.02	0.01	2.49	0.015	*
	R^2	0.08				
	F-statistic (1,69)	6.18				
Ash	Intercept	-0.50	0.02	-31.38	<0.001	***
	Slope	0.02	0.01	3.68	<0.001	***
	R^2	0.16				
	F-statistic (1,69)	13.54				

*Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.*

Table 3.4: Results of linear regression model testing horizontal and vertical diversity effects on leaf litter mass loss (step 1). Predator and decomposer richness (p-rich and d-rich, respectively) were tested in sequential procedure, i.e. how much variance is explained by one richness parameter when the other richness parameter was entered first in the mode. Effects of decomposer richness was tested after accounting for predator richness (Horizontal : Vertical diversity) and predator richness was tested after accounting for decomposer richness (Vertical : Horizontal diversity).

Horizontal : Vertical diversity								Vertical : Horizontal diversity						
Response	Predictor	DF*	SSq†	MSq‡	F-value	p-value		Predictor	DF*	SSq†	MSq‡	F-value	p-value	
Beech	d-rich	1	0.12	0.12	16.44	<0.001	***	p-rich	1	0.05	0.05	6.57	0.013	*
	p-rich	1	0.01	0.01	1.63	0.207		d-rich	1	0.09	0.09	11.51	<0.01	**
	p x d	1	0.01	0.01	1.69	0.198		p x d	1	0.01	0.01	1.69	0.198	
	error	64	0.48	0.01				error	64	0.48	0.01			
Maple	d-rich	1	<0.01	<0.01	0.37	0.547		p-rich	1	0.04	0.04	2.88	0.094	.
	p-rich	1	0.03	0.03	2.51	0.118		d-rich	1	<0.01	<0.01	<0.01	0.966	
	p x d	1	<0.01	<0.01	0.01	0.943		p x d	1	<0.01	<0.01	0.01	0.943	
	error	66	0.86	0.01				error	66	0.86	0.01			
Lime	d-rich	1	0.06	0.06	10.56	<0.01	**	p-rich	1	<0.01	<0.01	0.19	0.660	
	p-rich	1	<0.01	<0.01	0.45	0.504		d-rich	1	0.06	0.06	10.82	0.002	**
	p x d	1	0.02	0.02	4.05	0.048	*	p x d	1	0.02	0.02	4.05	0.048	*
	error	67	0.40	0.01				error	67	0.40	0.01			
Ash	d-rich	1	0.09	0.09	14.84	<0.001	***	p-rich	1	0.02	0.02	3.10	0.083	.
	p-rich	1	<0.01	<0.01	0.27	0.608		d-rich	1	0.08	0.08	12.00	<0.001	***
	p x d	1	<0.01	<0.01	0.01	0.908		p x d	1	<0.01	<0.01	0.01	0.908	
	error	67	0.43	0.01				error	67	0.43	0.01			

* Degrees of freedom, † Sum of squares, ‡ Mean squares. Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

Table 3.5: Regression estimates of the models testing horizontal and vertical diversity effects on leaf litter mass loss (step 1). Decomposer richness is indicated with d-rich and predator richness is indicated with p-rich. Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

Leaf species	Parameter	Estimate	Std.error	t-value	p-value	
Beech	Intercept	-1.07	0.02	-54.86	<0.001	***
	d-rich	0.04	0.01	3.35	<0.01	**
	p-rich	0.04	0.02	1.82	0.073	.
	p x d	-0.02	0.01	-1.30	0.198	
	R^2	0.20				
Maple	Intercept	-0.83	0.03	-32.31	<0.001	***
	d-rich	< -0.001	0.02	-0.02	0.986	
	p-rich	0.03	0.03	0.97	0.335	
	p x d	<0.01	0.02	0.07	0.943	
	R^2	<0.01				
Lime	Intercept	-0.70	0.02	-40.42	<0.001	***
	d-rich	0.01	0.01	1.01	0.318	
	p-rich	-0.04	0.02	-1.97	0.053	.
	p x d	0.02	0.01	2.01	0.048	*
	R^2	0.15				
Ash	Intercept	-0.50	0.02	-28.06	<0.001	***
	d-rich	0.03	0.01	2.60	0.012	*
	p-rich	0.01	0.02	0.42	0.675	
	p x d	< -0.01	0.01	-0.12	0.908	
	R^2	0.15				

Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

For each of the single leaf species regression models, we analyzed the effects of decomposer and predator richness separately while also including the interaction between them (i.e., horizontal and vertical diversity effects, table 3.4). The analysis with decomposer richness entered first in the regression equations yielded a significant scaling of leaf litter mass loss with decomposer richness for beech, lime and ash ($F_{1, 64} = 16.444^{***}$, $F_{1, 67} = 10.559^{**}$, $F_{1, 67} = 14.837^{***}$, respectively; table 3.4), whereas effects of predator richness were not significant (table 3.4). The interaction of decomposer and predator richness affected leaf litter mass loss significantly in lime ($F_{1, 67} = 4.046^{*}$; table 3.4), but it was not significant in all other cases. In the other sequence, we first entered predator richness and subsequently decomposer richness in the regression models. In this case, predator richness affected leaf litter mass loss significantly in beech treatments ($F_{1, 64} = 6.567^{*}$; table 3.4), but this effect was not significant for the other litter types. Contrasting, decomposer richness yielded significant effects on leaf litter mass loss in beech, lime and ash treatments ($F_{1, 64} = 11.506^{**}$, $F_{1, 67} = 10.816^{**}$, $F_{1, 67} = 12^{***}$, respectively; table 3.4) after accounting for explained variance by predator richness. Results for the interaction between predator richness and decomposer richness were the

same as in the first sequence (i.e., only slightly significant effects on leaf litter mass loss in the lime treatment, see above), since the interaction terms are not affected by differences in the variable sequence – their position stays the same in the sequential testing in the two sequences. Summarizing, in both sequences we found strong support for horizontal diversity effects by decomposer richness that were thus independent of predator richness effects, whereas predator richness effects were marginal even when entered first into the model. Hence, in our further analyses we focused on the model including only decomposer diversity as the independent variable to test for additional effects of decomposer species identity effects (step 2) and predator identity and intra-guild predation effects (step 3).

Interestingly, we found that all slopes of the linear regression models relating increases in decomposition to increases in total diversity or decomposer diversity were substantially lower than one (table 3.3, table 3.5). As one was outside the range of one standard error around the estimated slopes in all cases, this result suggests that systematic underyielding occurred in our experimental communities, whereas additivity of decomposer effects (implying a slope of one) or overyielding (causing a slope systematically higher than one) can be ruled out.

Step 2: decomposer identity effects on ecosystem functioning

We analyzed species identity effects with the residuals of the (above described) regression models that tested leaf litter mass loss against decomposer and predator richness (note that the residuals of both models are exactly the same). In these analyses, we found no support for identity effects of decomposer species (table 3.6). This implies that the diversity results described above are unlikely to be driven by sampling effects of a dominant decomposer species. In contrast, each of the decomposers should contribute similarly to the litter decomposition in our experiment. Hence, we did not include decomposer identity effects in the third step of our analyses.

Table 3.6: Step 2 - decomposer identity effects on residuals of the linear model that tested horizontal and vertical diversity effects on leaf litter mass loss (1st step). Identities of species are indicated for springtails (*Sinella curviseta*), small isopods (*Trichorhina tomentosa*), large isopods (*Oniscus asellus*), pill millipedes (*Glomeris marginata*).

		Residuals of the 1st step					
Response	Predictor	DF*	SSq†	MSq‡	F-value	p-value	
Beech	large isopods	1	<0.01	<0.01	0.19	0.668	
	springtails	1	<0.01	<0.01	0.17	0.681	
	pill millipedes	1	<0.01	<0.01	0.35	0.558	
	small isopods	1	<0.01	<0.01	0.08	0.779	
	Residuals	64	0.47	0.01			
Maple	large isopods	1	0.01	0.01	0.81	0.372	
	springtails	1	0.02	0.02	1.42	0.237	
	pill millipedes	1	<0.01	<0.01	0.18	0.671	
	small isopods	1	0.02	0.02	1.62	0.208	
	Residuals	66	0.81	0.01			
Lime	large isopods	1	<0.01	<0.01	0.55	0.460	
	springtails	1	0.01	0.01	1.49	0.226	
	pill millipedes	1	0.01	0.01	1.83	0.181	
	small isopods	1	0.02	0.02	3.82	0.055	.
	Residuals	67	0.36	0.01			
Ash	large isopods	1	<0.01	<0.01	0.57	0.455	
	springtails	1	0.01	0.01	1.59	0.211	
	pill millipedes	1	0.01	0.01	1.31	0.257	
	small isopods	1	0.02	0.02	2.82	0.098	.
	Residuals	67	0.39	0.01			

* Degrees of freedom, † Sum of squares, ‡ Mean squares. Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

Step 3: Effects of predator identities and intra-guild predation

As in our analyses under step 1, we found systematic effects of decomposer diversity on litter decomposition for all leaf types except maple (table 3.7). For the two leaf types of the highest quality, ash and lime, we did not find any additional effects of predators or intra-guild predation (table 3.7). In contrast, we found predator effects of the centipedes on maple and the mites on total leaf litter decomposition. For the leaf type of the lowest quality, beech, we found a significant three-way interaction term between centipedes, mites and decomposer diversity (table 3.7). This indicates an intra-guild predation effect (centipedes feeding on mites) on the slope of the relationship between decomposer diversity and beech decomposition (table 3.8). Intra-guild predation thus reduced decomposition of the stoichiometrically poorest resource, whereas the higher quality resources were not affected by predator identities or intra-guild predation.

Table 3.7: Horizontal diversity and predator identity (step 3): effects of centipedes (C), i.e. *Lithobius ssp.*, and predatory mites (M), i.e., *Hypoaspis miles*, on the leaf litter mass loss. Indicated are their single effects, the predator interaction (C:M) or interactions with decomposer richness (d-rich).

Response	Predictor	DF*	SSq†	MSq‡	F-value	p-value	
Beech	d-rich	1	0.03	0.03	5.61	0.022	*
	C	1	<0.01	<0.01	0.63	0.433	
	M	1	<0.01	<0.01	0.03	0.859	
	d-rich : C	1	<0.01	<0.01	0.21	0.650	
	d-rich : M	1	0.01	0.01	1.45	0.235	
	C : M	1	0.01	0.01	2.38	0.130	
	d-rich : C : M	1	0.04	0.04	6.52	0.014	*
	Residuals	45	0.25	0.01			
Maple	d-rich	1	<0.01	<0.01	0.35	0.555	
	C	1	0.08	0.08	6.68	0.013	*
	M	1	<0.01	<0.01	0.01	0.909	
	d-rich : C	1	<0.01	<0.01	0.13	0.725	
	d-rich : M	1	<0.01	<0.01	0.38	0.540	
	C : M	1	<0.01	<0.01	0.02	0.902	
	d-rich: C : M	1	0.01	0.01	0.41	0.526	
	Residuals	47	0.58	0.01			
Lime	d-rich	1	0.06	0.06	9.63	0.003	**
	C	1	<0.01	<0.01	0.02	0.894	
	M	1	<0.01	<0.01	0.15	0.699	
	d-rich : C	1	0.02	0.02	2.87	0.097	.
	d-rich : M	1	<0.01	<0.01	0.65	0.424	
	C : M	1	0.01	0.01	1.36	0.250	
	d-rich : C : M	1	<0.01	<0.01	0.27	0.608	
	Residuals	48	0.31	0.01			
Ash	d-rich	1	0.04	0.04	5.75	0.020	*
	C	1	<0.01	<0.01	0.08	0.785	
	M	1	<0.01	<0.01	0.05	0.829	
	d-rich : C	1	<0.01	<0.01	0.46	0.500	
	d-rich : M	1	0.01	0.01	2.09	0.155	
	C : M	1	<0.01	<0.01	0.30	0.585	
	d-rich : C : M	1	<0.01	<0.01	0.46	0.503	
	Residuals	48	0.31	0.01			

* Degrees of freedom, † Sum of squares, ‡ Mean squares. Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

Table 3.8: Regression estimates of the model horizontal diversity with predator identity (step 3): decomposer richness (d-rich), centipedes (C) and predatory mites (M) are indicated.

Leaf species	Parameter	Estimate	Std.error	t-value	p-value	
Beech	Intercept	-0.98	0.04	-24.20	<0.001	***
	d-rich	<0.01	0.02	0.23	0.820	
	C	-0.12	0.06	-2.11	0.040	*
	M	-0.08	0.06	-1.48	0.145	
	d-rich:C	0.06	0.03	2.14	0.038	*
	d-rich:M	0.03	0.03	0.98	0.332	
	C:M	0.23	0.08	2.98	0.005	**
	d-rich:C:M	-0.10	0.04	-2.55	0.014	*
	R^2	0.16				
Maple	Intercept	-0.87	0.06	-15.07	<0.001	***
	d-rich	0.01	0.03	0.45	0.655	
	C	0.07	0.08	0.79	0.435	
	M	0.01	0.08	0.08	0.938	
	d-rich:C	0.01	0.04	0.21	0.836	
	d-rich:M	<0.001	0.04	0.01	0.990	
	C:M	0.06	0.12	0.49	0.630	
	d-rich:C:M	-0.04	0.06	-0.64	0.526	
	R^2	0.02				
Lime	Intercept	-0.68	0.04	-16.28	<0.001	***
	d-rich	0.01	0.02	0.56	0.578	
	C	-0.06	0.06	-1.09	0.282	
	M	-0.04	0.06	-0.74	0.461	
	d-rich:C	0.02	0.03	0.83	0.410	
	d-rich:M	0.01	0.03	0.21	0.838	
	C:M	0.01	0.08	0.16	0.875	
	d-rich:C:M	0.02	0.04	0.52	0.608	
	R^2	0.13				
Ash	Intercept	-0.45	0.04	-10.75	<0.001	***
	d-rich	0.01	0.02	0.48	0.634	
	C	-0.01	0.06	-0.10	0.923	
	M	-0.09	0.06	-1.56	0.124	
	d-rich:C	< -0.001	0.03	< -0.01	0.997	
	d-rich:M	0.04	0.03	1.50	0.141	
	C:M	0.07	0.08	0.86	0.393	
	d-rich:C:M	-0.03	0.04	-0.68	0.503	
	R^2	0.04				

Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

3.5. Discussion

In laboratory microcosms, we manipulated the diversity levels of decomposers (horizontal diversity) in a random partitions design (Bell *et al.* 2009) and the predator richness (vertical diversity) full-factorially atop of decomposer richness and monitored the decomposition rates of leafs varying in their stoichiometry and thus nutritional quality. We found that an increase in total diversity (i.e., combined decomposer and predator richness) had a positive effect on ecosystem functioning. Disentangling this overall diversity effect into the two richness components yielded strong effects of horizontal diversity (decomposer richness) on the leaf litter mass loss, whereas vertical diversity (predator richness) only exerted marginal effects. These results suggest that the total diversity effects in our study were mainly driven by horizontal decomposer diversity effects. These horizontal diversity effects were not driven by decomposer identity effects, and we found evidence for systematic underyielding suggesting that the polycultures of decomposers were less effective in decomposing the leaf litter than expected based on extrapolations of the monocultures. Furthermore, we found some evidence for interactions between centipedes and predatory mites, indicating intra-guild predation, affecting the decomposition of the stoichiometrically poorest resource. The novel combination of the random partitions design (Bell *et al.* 2009) and the allometric predator diversity design (Schneider *et al.* 2012) in our study enabled us to successfully disentangle horizontal and vertical diversity effects in the relationship between biodiversity and the ecosystem function litter decomposition.

Ecosystem functioning: leaf litter mass loss

In our study, litter decomposition was the ecosystem function, and we used four different leaf litter species. Concerning leaf litter quality, we found the highest mass losses for ash litter, which was the best litter quality ranked according to C:N ratios. More generally, we found an increase of leaf litter mass loss with decreasing C:N ratios. This suggests that decomposer species distinguished among litter of different nutritional quality and preferred leaf species with a relative high amount of nitrogen compared to the amount of carbon which is consistent with prior studies demonstrating food preferences of decomposers (Hättenschwiler & Bretscher 2001; Hättenschwiler & Gasser 2005; Vos *et al.* 2011). Additionally, our results show that on average 17.3 % or less of a single leaf

litter species was consumed, which has several implications for the interpretation of our study. First, litter resources were available in high densities during the entire experimental time thus preventing effects of resource limitation on decomposers. These high litter densities are consistent with the conditions in natural habitats (Digel *et al.* 2014; Klarner *et al.* 2014). Second, these litter densities ensured that a realistic habitat structure was present thus preventing excessive and unrealistically high top-down pressure in experimental units without habitat structure (Vucic-Pestic *et al.* 2010a; Kalinkat, Brose & Rall 2013a). Overall, the ecosystem functioning - litter decomposition - depended on differences in litter stoichiometry between the leaf types, and the low overall decomposition rate across these leaf types ensured a realistic resource density and habitat structure during our experiment.

Partitioning total diversity into horizontal decomposer and vertical predator richness - more than an horizontal perspective

While our study thus follows the general pathway of BEF research (Duffy *et al.* 2007; Reiss *et al.* 2009), we additionally distinguished between horizontal (decomposer richness) and vertical (predator richness) diversity. There is an ongoing discussion of how (horizontal) diversity drives ecosystem functioning with a particular focus on diversity per se or the number of functional groups (Heemsbergen *et al.* 2004; Loreau 2010). Moreover, vertical diversity (predator richness) also modifies ecosystem functioning (Finke & Denno 2004, 2005; Bruno & Cardinale 2008; Schneider & Brose 2013), but the sign of this effect can be positive or negative (Bruno & Cardinale 2008; Schneider *et al.* 2012; Schneider & Brose 2013). In our study, the splitting of total diversity into the two richness components of the functional groups decomposers and predators revealed strong effects of horizontal diversity (decomposer richness): increasing horizontal diversity (decomposer richness) increased ecosystem functioning significantly in the majority of cases. Compared to these strong decomposer richness effects, the vertical diversity (predator richness) was only marginally significant when analyzed prior to horizontal diversity effects. In general, predator diversity studies found cascading effects of increasing vertical diversity on plant mass as an indicator of ecosystem function: either production increased or herbivory decreased (Finke & Denno 2004, 2005; Balvanera *et al.* 2006; Otto *et al.* 2008). Theoretically, the increase of vertical diversity in our experiment should thus result in a reduction of decomposer abundance leading to a lower

amount of leaf litter mass loss due to reduced decomposer consumption. In our case, a reduced leaf litter mass loss, i.e. lower decomposition rates, equals a lower ecosystem functioning. Thus, the effect of vertical diversity on the ecosystem functioning should be negative. Contrasting, we found a slightly positive effect of vertical diversity (predator richness) on the ecosystem functioning for the leaf mass loss of beech litter and neutral relationships for the other litter types. These results could be caused by strong intra-guild predation interactions among predators (Finke & Denno 2004, 2005; Duffy *et al.* 2007), which are generally imposed by the largest species (the centipedes in our experiment) that form an additional trophic level and invert the trophic cascade (Schneider *et al.* 2012). Alternatively, the negative top-down effects of predator diversity on decomposer density could also be compensated by the resulting release of competition among decomposers. The relative importance of these two alternative but not mutually exclusive explanations will be discussed below. Together, these results suggest that the total diversity effect on litter decomposition in our experiment was driven by the strong effect of horizontal diversity of decomposers, whereas intra-guild interactions among predators or strong competition among decomposers prevented negative effects on lower trophic levels and functioning.

Nevertheless, the question arises whether the strong positive horizontal diversity effect arises from pure additive effects of species or from over- or underyielding (Gessner *et al.* 2010). Our results provide strong support for systematic underyielding, because all slopes of the diversity-functioning relationships were significantly lower than one and thus lower than expected based on extrapolations of the feeding amount in the monocultures. Hence, we can rule out that facilitation or other positive effects (Cardinale *et al.* 2002; Jonsson & Malmqvist 2003; Heemsbergen *et al.* 2004; Kéfi *et al.* 2012) that are wide-spread across natural communities and soil ecosystems (Wall *et al.* 2008; Makkonen *et al.* 2012; Handa *et al.* 2014) were important in our study. Instead, the reduction in per species decomposition rates in polycultures compared to monocultures can be explained by interference or exploitative competition between different species of decomposers (Jonsson & Malmqvist 2003; McKie *et al.* 2008; Bastian *et al.* 2008). Exploitative competition is an indirect competition between two species that feed on a limited resource (Moorhead, Westerfield & Zak 1998). However, our experimental set-up prevented resource limitation with an initial total of eight gram of leaf litter, which was not fully exploited during the experimental time (maximum total leaf litter mass loss equaled 13.8 %) thus rendering effects of exploitative competition unlikely. Therefore, it is more likely

that interference competition between the decomposer species was responsible for the reduced feeding and decomposition rates in the polycultures. We increased the total number of decomposer individuals by increasing the horizontal diversity, but the number of individuals of each decomposer species stayed the same. Thus, the amount of intraspecific interactions did not increase, whereas the number of interspecific interactions increased with increasing horizontal diversity. Therefore, we assume that it was more likely that interspecific interference prevented the decomposers from feeding (Jonsson & Malmqvist 2003; McKie *et al.* 2008; Bastian *et al.* 2008). Interestingly, this interference competition, that led to strong underyielding, may also explain the positive effects of predator diversity on ecosystem functioning: despite reduction in decomposer densities, increased predation by higher predator diversity and density yielded a strong release of interference competition, which may have caused an inverted trophic cascade. This interpretation is consistent with other ecosystems in which behavior – mediated trophic cascades have strong effects on ecosystem functioning (Schmitz, Beckerman & O'Brien 1997; Schmitz 2003). In summary, we obtained positive effects of horizontal diversity, but the occurrence of interference competition likely caused systematic underyielding and positive effects of predators on decomposition.

Decomposer identity effects

We found evidence for the importance of interference competition among decomposers in our study, but many other studies suggested identity effects of decomposer species on the litter decomposition process (Heemsbergen *et al.* 2004; Hättenschwiler & Gasser 2005; Vos *et al.* 2011; Boyero *et al.* 2014). For instance, the presence of millipedes changed the decomposition process of poor leaf resources significantly, whereas earthworms changed the decomposition process of high quality resources significantly (Hättenschwiler & Gasser 2005). In our study, however, we found no evidence of decomposer identity effects on leaf litter types across a strong gradient in nutrient stoichiometry. Per definition identity effects are properties of specific species and their interactions with others and the environment, which prevents general conclusions. For our study, however, we can rule out that identity effects have driven the relationship between diversity and litter decomposition.

Predator identity and intra-guild predation effects

Increasing predator diversity can cause trophic cascades with negative effects on the trophic level below (here: decomposers) thus reducing their feeding rates (here: decomposition of leaf litter). These expected (here: negative) effects of predator diversity on ecosystem functioning can be dampened by intra-guild predation (Finke & Denno 2004, 2005). In this vein, previous studies demonstrated that intra-guild interactions between centipedes, predatory mites and wolf-spiders altered the abundance of their springtail prey significantly (Schneider *et al.* 2012) leading to significant predator identity and intra-guild predation signatures in predator-diversity experiments (Schneider & Brose 2013). Hence, we expected intra-guild predation effects on ecosystem functioning across all leaf litter species, because the centipedes were able to include the predatory mites in their feeding range thus dampening their strong top-down control of springtails (Schneider *et al.* 2012; Schneider & Brose 2013). In contrast to this expectation, we found that this effect only cascaded down to the beech litter, whereas the other litter densities were independent of intra-guild-predation effects. Several factors may contribute to an explanation of this disparity. First, the decomposer community of our study was more diverse and included pill millipedes, large and small isopods in addition to springtails (see figure 3.1 for the food-web). Two of these decomposer species, pill millipedes and large isopods, are invulnerable to predator attacks due to their large size and their thick exoskeletons. As in natural communities (Digel *et al.* 2014), these primary decomposers live in "predator-free space" and changes in predator diversity and density are unlikely affect their density or feeding rates. Second, our microcosms were characterized by a substantial habitat structure provided by the litter layer (see above). This litter layer generally limits the top-down control of predators on lower trophic levels (Vucic-Pestic *et al.* 2010a; Kalinkat *et al.* 2013a). Certainly, our experimental design may thus be questioned, but we stress that both components of our experiment, primary decomposers in predator-free space and a thick litter layer limiting top-down control, are entirely consistent with natural conditions in forest litter habitats (Brose & Scheu 2014). Additionally, similar results indicating limited predatory top-down control have also been found in experiments with natural soil cores (Lang *et al.* 2014). Third, increasing top-down control of springtails and small isopods may have been compensated by increased feeding rates of the remaining decomposers that were released from intra- and interspecific interference competition (see above). Overall, our results concerning the

limited predator diversity, identity and intra-guild predation effects on ecosystem functioning may thus be characteristic for the habitat conditions and community characteristics of forest litter ecosystems. In addition, they may also represent other ecosystems with substantial habitat structure, low trophic level species that are invulnerable to predation and subject to strong intra- or interspecific interference competition.

Caveats

We aimed at finding effects of diversity on ecosystem functioning with a reduced set of experimental units compared to a standard full factorial design. Bell *et al.* (Bell *et al.* 2009) pointed to the problem of sufficient replication on levels of diversity, which is necessary to enable the discrimination of effects that are driven by species identity and the effects driven by species diversity (species richness), while keeping the amount of experimental units feasible when the species pool increases. Their proposed random partitions design is capable to solve this problem (Bell *et al.* 2009). When we applied this design here, it came at the cost of losing species combinations at the two-species and three-species richness level. While we were able to examine decomposer identity effects, we were not able to examine particular interactions among the decomposers. Thus, we are lacking detailed statistical analyses of decomposer interactions that would support our discussion on the importance of interference competition. While all our results, including those on systematic underyielding, point in this direction, future studies will need to unravel the exact mechanisms leading to these patterns. Second, we examined vertical diversity effects and added predators in a full-factorial fashion atop of the decomposer diversity series. This combination of vertical and horizontal diversity manipulation under the constraint of logistically feasible experimental units came at the cost of limiting the predator diversity levels. This somewhat low predator diversity in our experiment may reduce the representativeness of our results for natural ecosystems comprising substantially higher predator diversity (Digel *et al.* 2014). However, the combination of the random partitions design for decomposer diversity with a full-factorial allometric design for predator diversity provided mechanistic insights how predators can modify biodiversity-ecosystem functioning relationships at lower trophic levels.

Conclusion

With this study, we shed light on the effects of increasing biodiversity for ecosystem functioning particular in a multi-trophic decomposer system and demonstrated the importance and contribution of functional groups for total diversity. We contributed to the scarce knowledge of the interplay between horizontal and vertical diversity and showed a positive effect of increasing diversity on EF. We highlight interwoven mechanisms of (1) top down control for dampening interference competition and (2) intra-guild predation for reducing predation pressure. These mechanisms led to initially unexpected patterns that vertical predator diversity had neutral to positive effects on decomposition by the decomposer species they feed on. While some of the results of our study may be specific to the habitat conditions and community characteristics of forest litter ecosystems, our approach also illustrates a novel combination of experimental designs, which should stimulate progress in research examining the relative importance of horizontal and vertical diversity effects on ecosystem functioning in multitrophic communities.

3.6. Acknowledgements

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Chapter 4.

Unifying elemental stoichiometry and metabolic theory in predicting species abundances

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4.1. Abstract

While metabolic theory predicts variance in population density within communities depending on population average body masses, the ecological stoichiometry concept relates density variation across communities to varying resource stoichiometry. Using a data set including biomass densities of 4959 populations of soil invertebrates across 48 forest sites we combined these two frameworks. We analyzed how the scaling of biomass densities with population-averaged body masses systematically interacts with stoichiometric variables. Simplified analyses employing either only body masses or only resource stoichiometry are highly context sensitive and yield variable and often misleading results. Our findings provide strong evidence that analyses of ecological state variables should integrate allometric and stoichiometric variables to explain deviations from predicted allometric scaling and avoid erroneous conclusions. In consequence, our study provides an important step towards unifying two prominent ecological theories, metabolic theory and ecological stoichiometry.

4.2. Introduction

The density of organisms, measured as the number of individuals or the biomass of a population per spatial unit, is the most commonly used state variable in population ecology (Nichols & MacKenzie 2004; Noon *et al.* 2012; Passy 2012). Variance in density is used as an indicator of population interactions with other species or the abiotic environment, and it indicates the success or failure of species' establishment in ecological

communities. In separate realms, two prominent ecological theories unraveled constraints on population densities: the metabolic theory of ecology predicts how the density of populations within communities scales with population average body masses (Damuth 1981; West *et al.* 1997; Brown *et al.* 2004, 2012) and the ecological stoichiometry concept explains density variation across communities by varying resource stoichiometry (Reiners 1986; Elser *et al.* 1996; Sterner & Elser 2002; Kaspari & Yanoviak 2009). Despite their substantial predictive success, these two theories have rarely been systematically combined in a unifying framework to predict population density (Hillebrand *et al.* 2009; Kaspari 2012). In this study, we present novel concepts of combined metabolic-stoichiometric analyses and illustrate their consequences employing data of forest soil communities.

Generally and across ecosystems, natural communities comprise a high number of small organisms and a low number of large organisms (Cohen, Jonsson & Carpenter 2003; Woodward *et al.* 2005; Ehnes *et al.* 2014). A mechanistic explanation for this pattern is provided by metabolic theory predicting that abundance follows a ¾ power-law scaling with population-averaged body mass as the inverse of the metabolic scaling relationship (West *et al.* 1997; Brown *et al.* 2004). Consequently, this yields a predicted quarter power-law scaling of biomass with body mass. These opposite scaling relationships of abundance and metabolism yield an equal population energy use (number of individuals x individual metabolic rate) for small and large species, which is known as the energetic equivalence rule (Damuth 1981; White *et al.* 2007; Ehnes *et al.* 2014). However, these predicted scaling relationships are based on the assumption of equal resource supply for all populations, which does not hold for multi-trophic communities, where the resource supply decreases with trophic levels due to assimilation losses (Hechinger *et al.* 2011). When populations across trophic levels are pooled scaling relationships within trophic levels exhibit ¾ power laws, but the intercepts decrease systematically with trophic levels due to lower resource supply. Together with systematic increases in body size with trophic levels (Riede *et al.* 2011) this yields shallower overall biomass scaling relationships, often with an exponent of zero (Brown & Gillooly 2003; Cohen *et al.* 2003; Hechinger *et al.* 2011). In soil ecosystems as in our study, however, the body mass range of low trophic level decomposers is similar to that of the high trophic level predators. For instance, decomposers in our data do not only span a similar body size range as predators, some groups such as earthworms were even larger than predators

(see Methods for more details). This suggests the quarter-power scaling of biomasses as the most appropriate metabolic prediction.

Ecological stoichiometry describes how the varying ratios of multiple chemical elements in the body tissues of organisms in combination with stoichiometry of their resources determine cellular processes, individual consumer-resource interactions, population densities, and community and ecosystem patterns (Reiners 1986; Elser *et al.* 1996; Sterner & Elser 2002; Frost *et al.* 2005b; Hillebrand *et al.* 2009). Predominantly, this approach is focused on three elements, i.e., carbon (C), nitrogen (N) and phosphorus (P), but other biologically relevant elements may be equally limiting for population densities (Reiners 1986; Sterner & Elser 2002; Frost *et al.* 2005b; Kaspari & Yanoviak 2009). In this framework, the rate of biomass accumulation is always constrained by the most limiting element as predicted by Liebig's law of the minimum (Allen & Gillooly 2009; Kaspari 2012).

While metabolic theory allows separating population densities across populations that vary in the average body size of their individuals as it typically occurs within communities, ecological stoichiometry predominantly explains differences across communities with different basal stoichiometry. In this vein, only some studies provided steps to integrate the predictions of both theories (Allen & Gillooly 2009; Hillebrand *et al.* 2009; Mulder & Elser 2009; Sinsabaugh, Hill & Follstad Shah 2009; Mulder *et al.* 2011). In a combined perspective, the metabolic rate determines how the individual uptake and loss rates of elements depend on body size thus constraining the same processes that balance and maintain elemental homeostasis of organisms (Sterner & Elser 2002; Frost *et al.* 2005b; Persson *et al.* 2010). Hence, energetic and stoichiometric constraints interactively determine metabolic activity (Jeyasingh 2007) and consumption rates of organisms (Hillebrand *et al.* 2007; Ott *et al.* 2012), which should ultimately affect population densities. A fundamental understanding of ecological population densities should thus be based on all processes including the uptake of resources from the environment, and their transformation and allocation to maintenance, growth and reproduction, which all depend to different extents on metabolic and stoichiometric characteristics of the populations and their environments (Allen & Gillooly 2009).

Following conceptual integrations of metabolic theory with ecological stoichiometry (Allen & Gillooly 2009), recent pioneering studies showed that abiotic conditions and the density of macroelements can impose constraints on the allometric scaling of population densities (Mulder & Elser 2009; Mulder *et al.* 2011, 2013). We extended this approach

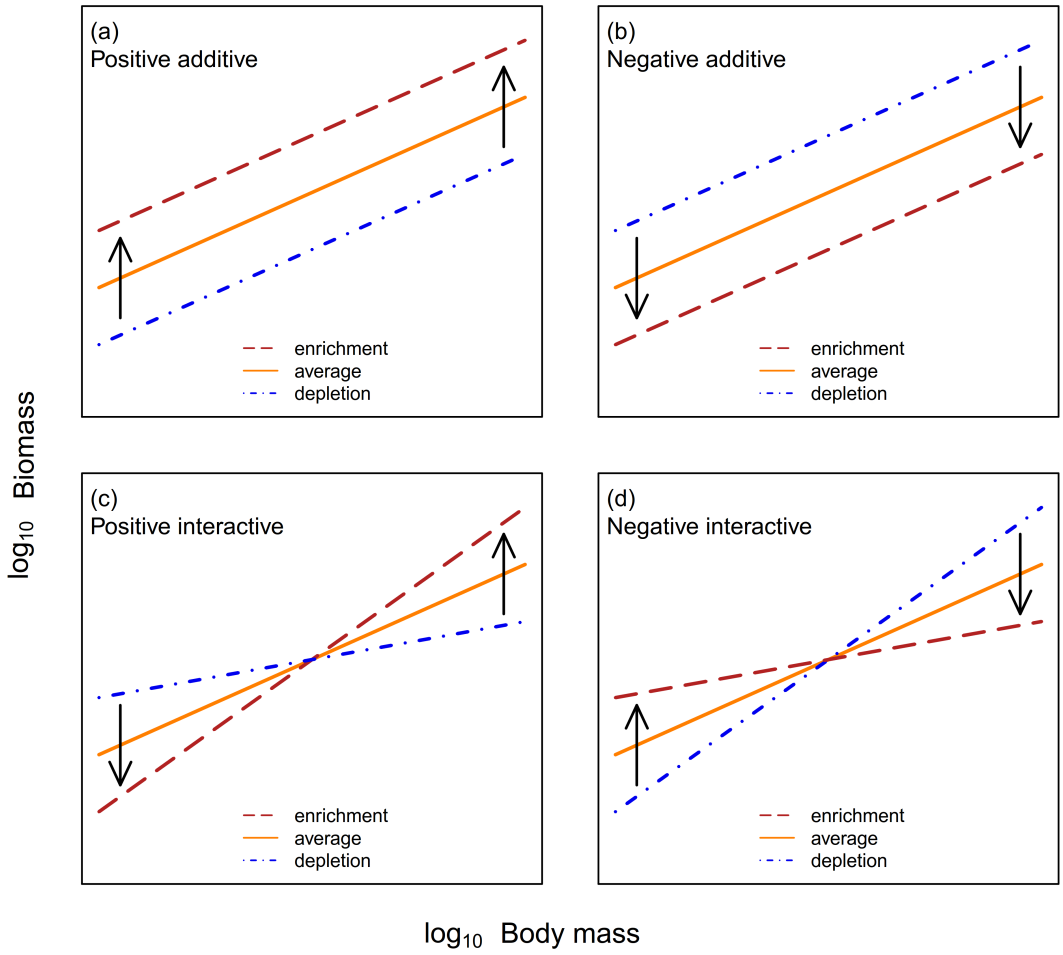

Figure 4.1: Conceptual overview how stoichiometry can interact with allometric scaling of biomass densities: (a) positive additive effect, (b) negative additive effect, (c) positive interactive effect, and (d) negative interactive effect. In each panel, three regressions show the allometric relationship according to metabolic theory for average contents of an element or carbon-to-element ratios (orange line), and for scenarios with enrichment (high contents or low C:X ratios, red line) or depletion (low contents or high C:X ratios, blue line).

employing data of 48 forest soil communities with multiple trophic groups (i.e., predacious, detritivorous and omnivorous species) to analyze the biomass – body mass scaling relationships in combination with the basal litter stoichiometry. Our analyses started from the null model of simple allometric scaling of population densities without effects of elemental stoichiometry (orange lines in figure 4.1). Note that we performed analyses in log-log space to follow previous allometric scaling studies (Brown *et al.* 2004; Mulder *et al.* 2013). Possible effects of stoichiometry on the scaling relationships were analyzed with carbon-to-element ratios, but additional sensitivity analyses were performed with contents of single elements. We interpreted a low carbon-to-element ratio

(or a high content of an element) as enrichment (red lines in figure 4.1) and a high carbon-to-element ratio (or a low content of an element) as depletion (blue lines in figure 4.1). Hypothetically, interactions between metabolic scaling and elemental stoichiometry can occur in four ways. The effect can be additive when the power-law exponent of the allometric scaling relationship is not affected, where enrichment can increase (positive additive, figure 4.1a) or decrease the intercept (negative additive, figure 4.1b). In both cases, stoichiometry and body masses impose entirely independent effects on population densities. In contrast, changes in the scaling exponent can also be positive (positive interactive, figure 4.1c) or negative (negative interactive, figure 4.1d), suggesting that the metabolic and stoichiometric effects on population densities should not be analyzed separately (Brown *et al.* 2004; Allen & Gillooly 2009). Employing a large forest-soil data set, our analyses illustrate this concept and document whether and how population densities across trophic levels and habitats are, additively or interactively, determined by body mass and elemental stoichiometry.

4.3. Methods

Field sites and data sampling

The study sites of the integrative Biodiversity Exploratories research platform (www.biodiversity-exploraties.de, Fischer *et al.* 2010) were located in the UNESCO Biosphere Reserve Schwäbische Alb in the south-west of Germany, in central Germany in the National Park Hainich and the surrounding Hainich-Dün region, and in the north-eastern part of Germany in the UNESCO Biosphere Reserve Schorfheide-Chorin. Characteristics of the study sites and regions are given by Fischer *et al.*(Fischer *et al.* 2010). Every exploratory region includes different forest management types. From all forest types, four representative stands were chosen at each exploratory yielding 16 stands per region and 48 sampling sites in total.

The fauna dwelling on the forest floor and the soil was sampled during spring 2008 and 2011 on each of the 48 sampling sites. A combination of four different methods enabled sampling of differently sized taxa across several phylogenetic groups: meso- and macrofauna was sampled with small and large soil corers, mustard solution was applied for earthworm extraction, and larger mobile macrofauna was collected by litter sieving.

Since all methods covered differently-sized sample areas, we converted all measurements into the units of abundance per square meter, which allowed pooling population densities for each site across sampling methods. Finally, the abundances were averaged across sampling dates. Details of the sampling methods used and species determination are provided by Ehnes *et al.* (2014) and references therein. After species determination we divided some species (114 of the 730 species in our study) with co-occurring adults and juveniles into distinct ontogenetic life stages. Additionally, we divided some species with high variability in their body mass (difference more than factor 10) into size classes yielding a total of 872 species (which sometimes represent size classes of the same taxonomy) across the 48 sites (table 4.S1 in supporting information. These size classes as well as the life stages of the same taxonomic species predominantly represent trophically separate species with different diets. For the sake of simplicity, we will subsequently use the term populations to differentiate different species as well as different life stages or size classes of a species.

All populations were characterized by averaged body masses (arithmetic mean of individuals [mg fresh weight]) that were calculated for each plot independently using log mass versus log length regressions (Ehnes *et al.* 2014). After exclusion of herbivorous species that do not depend on litter resources from our analyses, we used 4959 populations of 817 species for the analyses. For each population, these data included abundance [individuals/m²], population-averaged body mass [mg], and biomass [mg/m²]. In our dataset, the body mass of predators ranged from 0.0012 mg (dry weight) of the smallest species (Mesostigmata: Epicrius sp. (juv)) to 1290.95 mg of the largest species (Coleoptera: Carabidae sp. (juv.)) with an average of 12.02 mg (± 67.74). The body mass of decomposers, as the second dominant group, ranged from 0.0007 mg (dry weight) of the smallest species (Oribatida: Oribatida sp. (juv)) to 11060 mg of the largest species (Oligochaeta: *Lumbricus terrestris*, Linnaeus 1758) with an average of 89.59 mg (± 521.06).

Litter stoichiometry

We took four randomly chosen litter subsamples of the leaf litter from each experimental site and mixed them subsequently to ensure homogeneity (i.e., the data represent the average conditions of the site) as well as comparability to the ascertainment of animal data set (see above). The litter samples were dried at 60°C until no further mass loss and

ground to fine powder with a ball mill (Retsch Mixer Mill MM200, Haan, Germany). The subsequent elementary analyses were conducted based on 55 mg of dried mixed leaf litter material from each site (concentrations of 13 elements in [mg/g] dry mass, figure 4.S1, supporting table 4.S2 in supporting information) at the Albrecht-von-Haller Institute for Plant Sciences in Göttingen according to standard protocols (Jacob *et al.* 2009). Total carbon and nitrogen contents were analyzed by an automated CHNSO analyzer (Elementar Vario EL III, Elementar Analysensysteme GmbH, Hanau, GE) using five milligram (mg) powder material. The remaining 50 mg of powder material of each sample was with two ml of 65% nitric acid (HNO3) in teflon containers. The material in the teflon containers was pressure digested up to nine h at 185 °C (6-AM autoclave system, Loftfields Analytical Solutions GbR, Neu Eichenberg, GE). Samples were filtered and rinsed quantitatively with double distilled H_2O into 50 ml volumetric flasks and analyzed by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) (Optima 5300 DV, PerkinElmer Inc., Wellesley, MA, USA). We excluded the elements copper (Cu) and zinc (Zn) from further analysis, because the measured values of samples where in the range of the standard deviation of blank controls between ICP-OES runs and thus close to the detection threshold of the machine. Our analysis included the elements total carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), iron (Fe), aluminium (Al), manganese (Mn), sodium (Na), potassium (K), sulphur (S) and magnesium (Mg). For statistical analyses we used contents of elements expressed in milligram per gram dry weight. Carbon-to-element ratios were calculated from these contents.

Statistics

We analyzed the dependence of population biomasses on (1) the population-averaged body masses (i.e., allometric scaling of densities), (2) the leaf litter quality indicated by the carbon- to-element ratios (i.e., independent additive explanatory covariable effects on densities) and (3) interactions between body masses and each of the co-variables (i.e., interactive allometric scaling – co-variable effects on densities). Data were analyzed using the statistical program R, version 3.0.2 (R Core Team 2013). The continuous explanatory co-variables were $\log_{10}$ transformed to improve normality and homoscedasticity and all variables other than body mass were standardized to a mean of zero and unit variance. We tested for collinearity (function “cor.test” with Pearson´s product-moment correlation, hereafter “Pr” for coefficients) and checked for variance

inflation factors of the co-variables (i.e., VIF; function "corvif", Zuur *et al.* 2009). We found a high correlation between iron and aluminium (also between their carbon-to-element ratios) and high variance inflation factors for these variables (Pr > 0.75, VIF > 5, (Zuur *et al.* 2007; supporting tables 4.S3 & 4.S4 in supporting information). We could not judge which of these two elements should be excluded from further analyses. Thus, we tested the explanatory effects of those elements or their corresponding ratios with carbon in two alternative model selection sequences and chose the better fitting model (supporting table 4.S5 in supporting information).

We used linear mixed effects models (function "lme", Pinheiro *et al.* 2012) with the region (i.e., the "exploratories") set as a random effect. This random intercept model was chosen according to Akaike's information criterion (AIC) after testing for different random structures (i.e. random effects, random intercept or random intercept and slope, Zuur *et al.* 2009). For the fixed effects, we applied four different model types: As starting points we created a null model which includes only the biomass – mass scaling without any co-variables and a full model including all two-way interaction terms of body mass with the carbon-to-element ratios. Subsequently, we applied an automated step algorithm (function "stepAIC", Venables & Ripley 2002) with forward and backward selection in order to obtain the best model by using AIC. Thus, we obtained two additional models - an increase model (stepAIC function used on the null model) and a decrease model (stepAIC function used on the full model).

As a restricted maximum likelihood is not defined for the stepAIC function, we ran the linear-mixed effect models with unrestricted maximum likelihood (method = ML). After model selection procedure, we applied the restricted maximum likelihood method (method = REML) to the best model in order to obtain correctly estimated model coefficients (Zuur *et al.* 2009). Generally, we favored models with the lowest AIC. If the delta AIC (ΔAIC) between two models was smaller than two, and these models can be seen as not distinguishable by AIC (Burnham & Anderson 2004; Bolker 2008), we used the simpler model containing less terms.

In addition to these analyses, we applied two alternative mixed effects model procedures to ensure the reliability and generality of our results. In a previous study, we demonstrated differences in the biomass- body mass scaling among phylogenetic groups (Ehnes *et al.* 2014). Furthermore, we sampled individuals of species of these phylogenetic groups with different methods. These factors possibly impair the general scaling relationship across groups of the full data set used in this study. Thus, we first built an

alternative model that also used carbon-to-element ratios as co-variables but accounted for different phylogenetic groups of the populations in the random structure by hierarchically nesting the phylogenetic groups into the sampling method and the region (random effect: region/sampling/phylogeny). Second, we used models with the elemental contents (X) instead of the C:X ratios. This enabled us to compare if combined effects of stoichiometry and allometric scaling are affected by (1) the pooling of sampling methods and species of different phylogenies or (2) the type of dependent stoichiometric variables. Furthermore, our data set includes species of different trophic levels. As predators – in contrast to decomposers – do not directly feed on the leaf litter, we analyzed populations of predatory species as a subset of the data to ensure that our results are not entirely driven by decomposers. Moreover, we used other multiple regression approaches (i.e. linear models (OLS regression) and generalized linear models) in comparison with the original linear-mixed effects null model to examine, how sensitive the exponent of the slope (i.e., the body mass coefficient) changes by simply the choice of the regression model.

4.4. Results

The simple null model excluding stoichiometry showed significant decreasing scaling relationships of abundance and increasing scaling relationships of biomass density with population- averaged body masses (table 4.1, figure 4.2). The null model predicting biomass exhibited an exponent of 0.32 (± 0.01 standard error [SE], table 4.1), which is slightly higher than the ¼ power law predicted by the metabolic theory (Brown *et al.* 2004).

Table 4.1: Simple null models predicting the scaling of $\log_{10}$ abundance or $\log_{10}$ biomass density with the $\log_{10}$ of population-averaged body mass.

Model		Estimate	SE*	df†	t-value	p-value	low.ci‡	up.ci§
Abundance	Intercept	1.48	0.01	4955	140.4	0	1.46	1.50
	Slope (mass)	-0.68	0.01	4955	-101.8	0	-0.69	-0.67
Biomass	Intercept	1.48	0.01	4955	140.4	0	1.46	1.50
	Slope (mass)	0.32	0.01	4955	47.7	0	0.31	0.33

*Standard errors, †denominator degrees of freedom, ‡lower and §upper 95% confidence intervals. Units were [$\log_{10}$ (mg)] for body mass, [$\log_{10}$ (mg/m²)] for biomass and [$\log_{10}$ (ind/m²)] for abundance (please see methods for details).

Table 4.2: The best model predicting $\log_{10}$ population biomass densities by $\log_{10}$ body masses and normalized carbon-to-element ratios.

	Estimate	SE*	df†	t-value	p-value	low.ci‡	up.ci§
Intercept	1.45	0.01	4945	138.2	0	1.43	1.47
Body mass	0.30	0.01	4945	45.4	0	0.29	0.32
C:N	-0.03	0.01	4945	-2.5	0.01	-0.06	-0.01
C:P	0.04	0.01	4945	3.1	<0.01	0.01	0.07
C:Ca	-0.05	0.01	4945	-3.9	<0.01	-0.08	-0.03
C:K	-0.01	0.01	4945	-1.0	0.32	-0.03	0.01
C:Mn	-0.01	0.01	4945	-0.7	0.50	-0.03	0.02
Mass x C:N	-0.01	0.01	4945	-0.8	0.45	-0.02	0.01
Mass x C:P	-0.01	0.01	4945	-0.8	0.41	-0.02	0.01
Mass x C:Ca	-0.08	0.01	4945	-9.4	0	-0.10	-0.07
Mass x C:K	-0.02	0.01	4945	-2.6	<0.01	-0.03	< -0.01
Mass x C:Mn	0.02	0.01	4945	2.0	0.04	<0.01	0.03

This result was consistent across different regression methods (i.e., 0.32 (± 0.01 SE) for simple linear methods with and without the block factor region included, and 0.30 (± 0.01 SE) for a generalized linear model where the region was accounted for in the correlation subfunction of the model). The more complex models including stoichiometric parameters were superior to the simple biomass null model (ΔAIC_{Null1} = 193.72, $\Delta AIC_{Decrease1\text{-}Fe} = 0$, $\Delta AIC_{Decrease1\text{-}Al} = 1.67$; table 4.S5); suggesting that the decrease model initially including iron (Fe) instead of aluminium (Al) was the best model. This decrease model (from now on referred to as the best model) included the explanatory variables body mass, the five carbon-to-element ratios C:N, C:P, C:Ca, C:K and C:Mn and their interactions with log body mass (table 4.2, figure 4.3).

Detailed analyses of this best model exhibit several findings. First, the biomass–body mass relationship in the best model exhibited an exponent of 0.3 (± 0.01 SE) at average stoichiometry levels (table 4.2, orange lines in figure 3). Second, these interactions between body mass and stoichiometry were negative for the C:Mn ratio (figure 4.3e, table 4.2) and positive for the C:N, C:P, C:Ca and C:K ratios (figure 4.3a - d, table 4.2). These interaction terms caused shallower (negative interactions) and steeper (positive interactions) allometric scaling relationships with increasing carbon-to-element ratios, which implies variable effects on small and large-bodied species (figure 4.3). These variable effects are illustrated by comparing depletion (i.e., the highest value of this carbon-to-element ratio in our data: blue lines in figure 4.3) and enrichment (i.e., lowest highest value of this carbon-to-element ratio: red lines in figure 4.3). Overall, our results provide strong evidence that interactive effects of body mass and resource

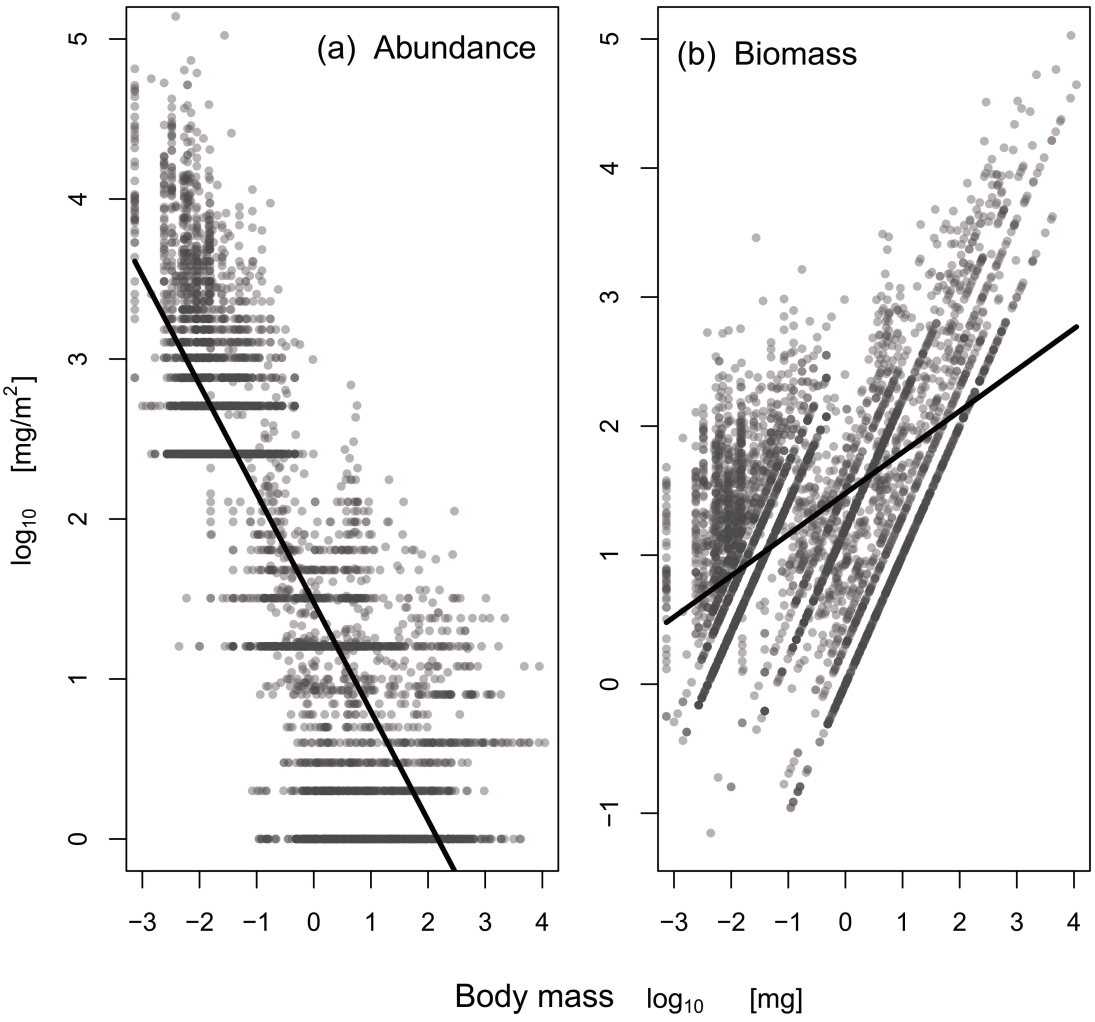

Figure 4.2: Soil community scaling relationships with body masses. (a) abundance - body mass and, (b) biomass – body mass scaling relationship of the forest soil communities. Grey points represent populations per plot and increasing intensity of grey points symbolizes differences in density of the data. Regressions are based on parameters according to table 4.1. Note that the emerging horizontal lines in (a) represent singletons and doubletons in subsamples with different sampling methods and thus different sampling areas. Converting these densities to individuals per m² yields multiple horizontal lines (e.g., one horizontal line of singletons for each method). Conversion into biomasses yielded the diagonal lines in (b).

stoichiometry on population densities characterize the forest soil communities studied, whereas additive effects are of limited importance.

In sensitivity analyses, we investigated whether our results are affected by pooling different phylogenetic groups (Ehnes *et al.* 2014) and sampling methods in our data. Hence, we added these factors in addition to the factor region to the random part of the linear-mixed effects models. Additionally, we also tested how the use of elements instead of carbon-to-element ratios changes the results (tables 4.S6, 4.S7 in supporting information, respectively).

The allometric exponent increased in the models with the complex random structure [i.e. changed to 0.76 (± 0.01 SE) and 0.75 (± 0.01 SE) in the null model and the model with stoichiometric co-variables, respectively]. In our analyses including single elements instead of carbon-to-element rations, however, the exponents were consistent with those reported here [0.32 (± 0.01 SE) and 0.3 (± 0.01 SE)] in the null model and the model with stoichiometric co-variables, respectively). Additionally, the best model with phylogeny as a random factor did not include C:Mn ratio as an explanatory variable (figure 4.S1, table 4.S6). Moreover, the best model that contained the contents of the elements instead of the C:X ratios included iron (Fe) as an additional explanatory variable (figure 4.S2, table 4.S7). Despite these differences, the results of these alternative analyses support our conclusion that stoichiometric and allometric effects on biomasses are generally interactive.

Our data set also pooled different trophic groups such as decomposers and predators. As predators do not use the litter as their direct resource, they could also be largely independent of litter stoichiometry unless the effects of resource stoichiometry are propagating up the food chains. However, we replicated our analyses for predatory species and found that their biomass is constrained by similar interactive scaling relationships (table 4.S8) including the same stoichiometric co-variables (table 4.S9).

4.5. Discussion

Our analyses of a large dataset of soil communities (Ehnes *et al.* 2014) with litter stoichiometry did not generally support the expected quarter-power scaling of biomass densities with population-averaged body masses, and they also showed systematic interactions of this scaling with stoichiometric variables. Interestingly, interactive effects of stoichiometry and body mass on population densities (as illustrated in figure 4.1c, d) dominated over simple additive effects. These results did not only hold across models in which we tested for differences between element availability and carbon-to-element ratios as predictors influencing allometric scaling exponents, they were also consistent in analyses accounting for phylogenetic groups of the populations. Our findings provide

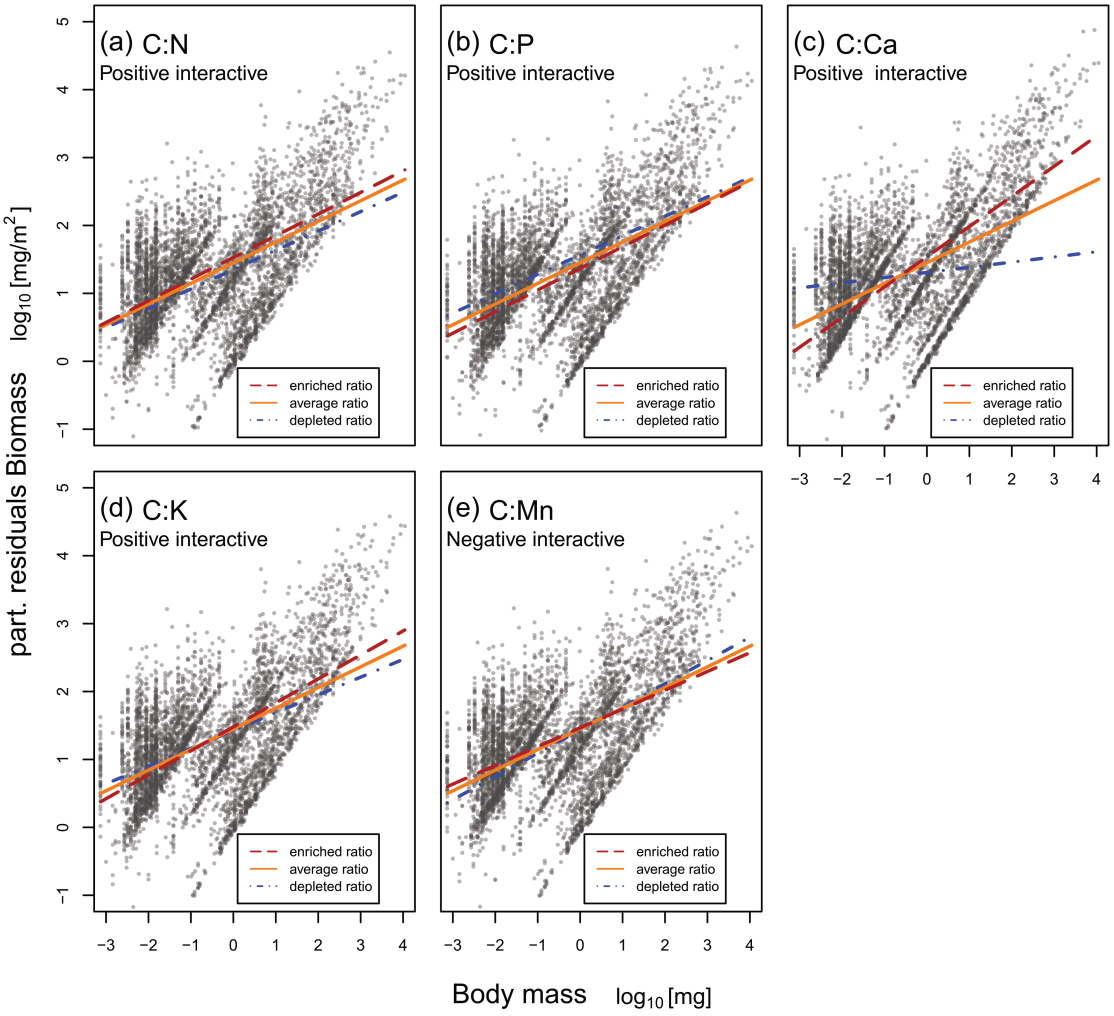

Figure 4.3: Interactive effects of stoichiometry and body masses on population biomass densities. Each panel shows the partial residuals for a single covariable after accounting for effects of the other co-variables in the best linear-mixed effects model (i.e., the decrease model with initially including iron, table 4.2). Regressions represent co-variable effects on the scaling of biomass densities depending on population-average body masses assuming average carbon-to-element ratios (average ratio, orange solid lines). Alternative scaling relationships are shown with either the lowest (enriched ratio, red dashed lines) or the highest (depleted ratio, blue dot-dashed lines) C:X ratios. Regressions are based on parameters according to table 4.2. Increasing intensity of grey points symbolizes differences in density of the data. For explanation of diagonal lines see fig. 4.2.

strong evidence that understanding of natural communities will profit tremendously from integration of metabolic theory with ecological stoichiometry.

We found a positive interactive effect of C:N and C:P enrichment on the biomass scaling relationships. Consistently, "bottom-up" effects of higher phosphorous availability were documented in a range of ecosystems (Kaspari & Yanoviak 2009; Mulder *et al.* 2011). This suggests a pattern that holds across ecosystems, which may be explained by the growth-rate hypothesis linking organismal phosphorus demands to ribosomal RNA and

protein production (Elser *et al.* 1996, 2006; Sterner & Elser 2002; Gillooly *et al.* 2005; Allen & Gillooly 2009): while organisms grow they have an increased demand for the relative availability of growth-limiting elements such as phosphorous. Despite decreases in per unit biomass growth rates with body masses, shifts in RNA versus tissue phosphorous pools during ontogeny yield a constant phosphorous demand per unit biomass and unit time of individuals during lifetime irrespective of their body size (Gillooly *et al.* 2005). Building up the biomass of large species thus integrates across a larger size range than for small-bodied species, and – together with the constant per unit biomass phosphorous demand during ontogeny – this requires a higher total phosphorous demand per unit biomass over lifetime. This should cause large organisms to be more phosphorous limited than small organisms. Hence, increasing the total P pool and thus decreasing the C:P ratio should support a higher density of large-bodied species. Consistent with this expectation, we found that phosphorous enrichment in the litter (low C:P) specifically fosters biomass densities of large species. Similarly, our results also reflect the general importance of nitrogen for nucleic acids and structural components, such as proteins, silk and chitin (Finke 2007; Kaspari & Yanoviak 2009; Kaspari 2012). Thus, the usage of C:N and C:P ratios as indicators for the three major elements C, N and P built the baseline for a stoichiometric perspective (Elser *et al.* 1996; Sterner & Elser 2002) that is crucially important for decomposition processes and the functioning of ecosystems (Enríquez *et al.* 1993a; Ott *et al.* 2012). Overall, our results demonstrate that the nitrogen and phosphorous availability fosters the biomass densities of large species thus supporting concepts integrating metabolic theory and ecological stoichiometry (Allen & Gillooly 2009).

In the same vein, we also found significant positive interactions of the elements calcium and potassium with their C:X ratios with the allometric scaling relationships. Calcium and potassium are of electro-chemical importance (Sterner & Elser 2002; Kaspari 2012). Furthermore, calcium acts as an enzymatic cofactor and a structural element (Reiners 1986; Sterner & Elser 2002; Kaspari 2012). Positive correlations between population densities and calcium were also documented for isopods of tropical forests (Kaspari & Yanoviak 2009), which is potentially caused by the high calcium content in their exoskeletons (Steel 1993) restricting their growth and thus limiting the biomasses of larger individuals. Potentially, our results indicate that high environmental supply with calcium relative to carbon may be particularly important for supporting the

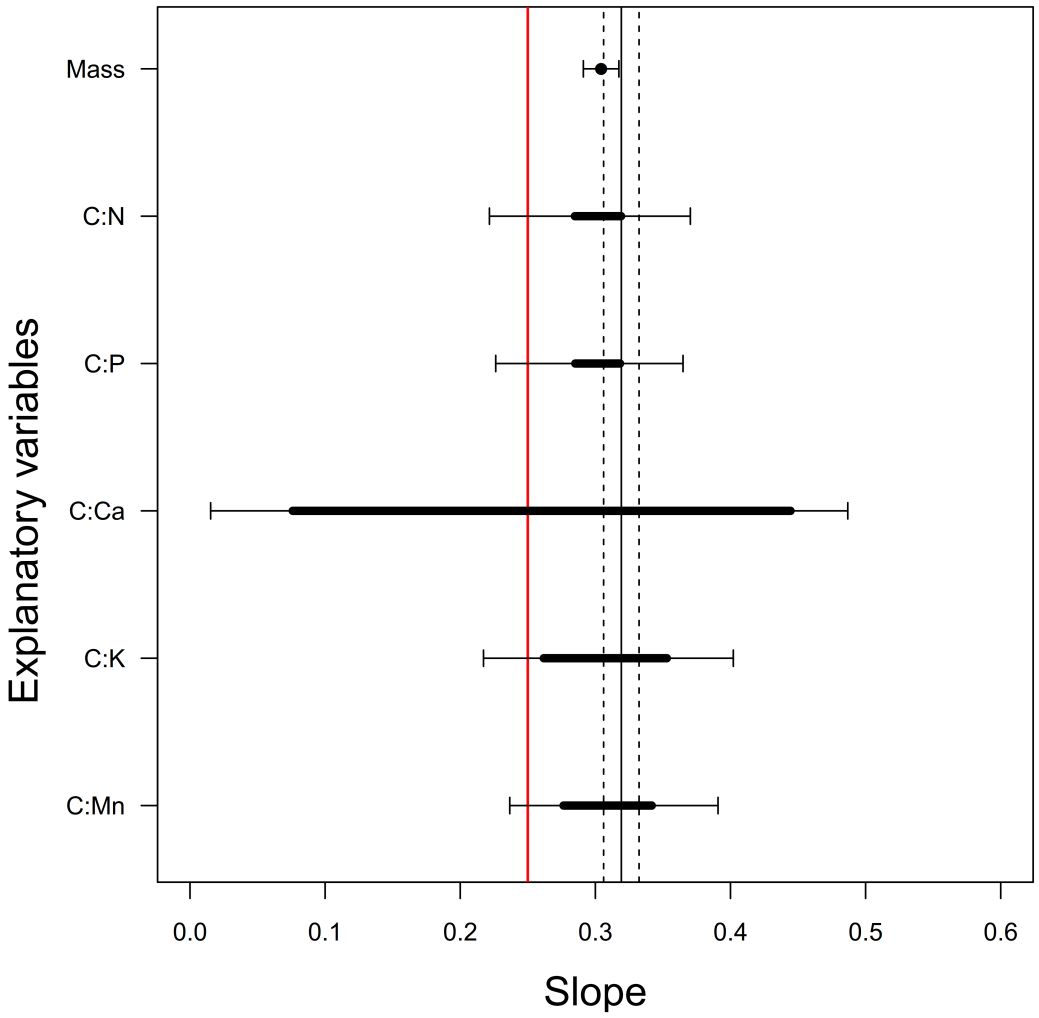

Figure 4.4: Allometric exponents of the biomass scaling relationships. Black bars represent the mass scaling exponents of the best model either independent of stoichiometry (Mass) or dependent on the carbon-to-element ratios (C:N, C:P, C:Ca, C:K, C:Mn). The range of the black bars resembles the distributions of the exponents from the lowest to the highest values of Carbon-to-element ratios of our data (table 4.2, table 4.S4). Error bars represent 95% confidence intervals (table 4.2). The red line shows the quarter-power scaling predicted by metabolic theory. The solid black line indicates the mass exponent of a simple biomass null model independent of stoichiometry.

structural components that are necessary to build large bodies, whereas small-bodied species depend less on this element. In turn, this leads to the positive interactions between the allometric scaling and calcium. These results suggest that for many invertebrate groups, the importance of calcium for large-bodied species is similar to those of phosphorous and nitrogen and can also be explained by the extended growth-rate hypothesis (Allen & Gillooly 2009).

Many of these stoichiometric effects may find their explanation in the specific physiology and body structure of the animal groups included, whose analyses is beyond

the scope of the present study. Our analyses focused on the general variation in biomass-mass scaling relationships depending on elemental stoichiometry resulting in wide ranges of allometric exponents (figure 4.4, black bars). These can greatly deviate from simple allometric models without stoichiometry effects (figure 4, black line). Interestingly, the simple allometric analyses of biomass scaling (figure 4.4, black line) rejected the metabolic theory predictions, whereas the integrated allometric-stoichiometric model documented ranges in exponents that most often include the predicted quarter-power scaling (figure 4.4, red line). These results suggest that simple allometric analyses may lead to erroneous rejections of quarter-power scaling, whereas including stoichiometric variation across sites does not support this conclusion. Accounting for the phylogenetic substructure of our dataset yielded higher allometric exponents than in the general models without phylogeny (supporting figure 4.S1 and table 4.S6 in supporting information). This mirrors the differences in allometric exponents of individual phylogenetic groups as the values fall into the range between the lowest exponent for isopods (0.27 ± 0.08 SE) and the highest exponent for gastropods (0.97 ± 0.05 SE) reported in a previous study (Ehnes *et al.* 2014). At the same time, the overall scaling exponent of the allometric relationship is the same as derived by the null model in our study (i.e., 0.32 ± 0.01 SE in Ehnes *et al.* 2014). While we focused on combining allometric and stoichiometric predictors in the same multiple regression approach to reveal variations in these scaling relationships, these results highlight the importance of including phylogenetic groups variables to obtain specific predictions of scaling exponents. Future studies should thus integrate phylogeny with the stoichiometric-allometric approach of our study. Additionally, the ranges in allometric exponents caused by different elemental stoichiometry might explain variation in allometric exponents across studies and ecosystems (Reuman *et al.* 2008). Hence, integrating stoichiometry with allometric scaling approaches could elucidate general patterns and processes across natural ecosystems.

Our results demonstrate that ignoring stoichiometric or body mass constraints on biomass densities as in traditional approaches (Kaspari & Yanoviak 2009; Hechinger *et al.* 2011; Ehnes *et al.* 2014) could lead to inaccurate rejections of (1) the predicted quarter-power scaling (when ignoring stoichiometry) or (2) stoichiometry effects (when ignoring interactions with body mass). For instance, analyzing stoichiometry effects on biomasses for subsets of our data set including either small or large-bodied species will lead to opposite conclusions in case of interactive effects. Moreover, stoichiometry analysis

without accounting for body mass effects suggests negligible effects on biomass densities, and allometric scaling without stoichiometry imprecisely leads to a rejection of the predicted quarter-power scaling. We integrated metabolic theory and ecological stoichiometry to explain variation in allometric scaling relationships of biomass densities, which implies that metabolism and stoichiometry interactively constrain the processes of growth, reproduction, interaction and death that determine biomasses (Allen & Gillooly 2009; Hillebrand *et al.* 2009; Ott *et al.* 2012).

However, this study included only resource (litter) stoichiometry, whereas consumer (animal) stoichiometry was not assessed. Hence, our conclusions are based on the assumption of stoichiometry invariance of consumers (Allen & Gillooly 2009) reflecting the general contrast of a relatively fixed body stoichiometry of heterotroph consumers compared to the flexible stoichiometry of their (autotroph) resources (Frost *et al.* 2005b; Persson *et al.* 2010). This assumption rests on the general pattern that the variation in nitrogen and phosphorous consumer body contents within and across trophic levels (Martinson *et al.* 2008; González *et al.* 2011) as well as intraspecific variation (Bertram *et al.* 2008; Abbas *et al.* 2014) appears to be minor compared to the larger difference to the stoichiometric content of plant litter (e.g., our study: N = 1.46 ± 0.19%, P = 0.07 ± 0.01%, mean ± SD). Nevertheless, our approach ignores variations in the body stoichiometry across the invertebrate communities, which leads to equal constrains of litter stoichiometry on the densities of different trophic levels and phylogenetic groups. Despite this we have added population average body masses as an explanatory co-variable, which may account for some of the differences across trophic levels and phylogenetic groups. Nevertheless, future studies will need to integrate our allometric approach with variability in the response of phylogenetic groups and the stoichiometry of their body tissues to varying resource stoichiometry. Future extensions of our approach should thus include consumer tissue stoichiometry to calculate the degree of homeostasis across trophic levels (Sterner & Elser 2002; Frost *et al.* 2005b; Persson *et al.* 2010) and threshold elemental ratios (Frost *et al.* 2006) to provide more detailed understanding why stoichiometry alters allometric scaling due to organismal demands (Reiners 1986; Elser *et al.* 1996; Sterner & Elser 2002). Overall, our approach provides a conceptual step towards synthesizing metabolic theory and ecological stoichiometry (Brown *et al.* 2004; Woodward *et al.* 2005; Sinsabaugh *et al.* 2009; Kaspari 2012) thus enabling a deeper understanding of constraints on population densities.

4.6. Acknowledgements

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Chapter 5.

Litter elemental stoichiometry and biomass densities of forest soil invertebrates

David Ott, Christoph Digel, Bernhard Klarner, Mark Maraun, Melanie Pollierer, Björn C. Rall, Stefan Scheu, Gesine Seelig and Ulrich Brose.

5.1. Abstract

To maintain constant chemical composition, i.e. elemental homeostasis, organisms have to consume resources of sufficient quality to meet their own specific stoichiometric demand. Therefore, concentrations of elements indicate resource quality, and rare elements in the environment may act as limiting factors for individual organisms scaling up to constrain population densities. We investigated how the biomass densities of invertebrate populations of temperate forest soil communities depend on 1) the stoichiometry of the basal litter according to ecological stoichiometry concepts and 2) the population average body mass as predicted by metabolic theory. We used a large data set on biomass densities of 4959 populations across 48 forests in three regions of Germany. Following various ecological stoichiometry hypotheses, we tested for effects of the carbon-to-element ratios of 10 elements. Additionally, we included the abiotic litter characteristics habitat size (represented by litter depth), litter diversity and pH, as well as forest type as an indicator for human management. Across 12 species groups, we found that the biomass densities scaled significantly with population-averaged body masses thus supporting metabolic theory. Additionally, 10 of these allometric scaling relationships exhibited interactions with stoichiometric and abiotic co-variables. The four most frequent co-variables were 1) forest type, 2) the carbon-to-phosphorus ratio (C:P), 3) the carbon-to-sodium ratio (C:Na), and the carbon-to-nitrogen ratio (C:N). Hence, our analyses support the sodium shortage hypothesis for microbi-detritivores, the structural elements hypothesis for some predator groups (concerning N), and the secondary productivity hypothesis (concerning P) across all trophic groups in our data. In contrast,

the ecosystem size hypothesis was only supported for some meso- and macrofauna detritivores. Our study is thus providing a comprehensive analysis how the elemental stoichiometry of the litter as the basal resource constrain population densities across multiple trophic levels of soil communities.

5.2. Introduction

The analogy of the "poor man´s tropical rainforest" illustrates that (forest) soils are colonized by a high number of species (Swift *et al.* 1979; Schaefer 1991; Giller 1996) connected by trophic relationships composing highly complex food webs (Scheu & Falca 2000; Scheu & Setälä 2002; Digel *et al.* 2014). Surprisingly, this high diversity and complexity of soil communities is supported by basal litter resources of poor nutritional quality (indicated by the elemental stoichiometry), which limits population and community biomasses (Scheu & Schaefer 1998; Maraun *et al.* 2001). Pioneering studies related the quality of litter resources to population densities in grassland ecosystems (Mulder, Van Wijnen & Van Wezel 2005; Mulder *et al.* 2011, 2013; Mulder & Elser 2009) and in tropical forests (Kaspari & Yanoviak 2009; Kaspari *et al.* 2009). However, comprehensive studies investigating constraints on population densities across trophic levels of forest soil animal communities are scarce (Moe *et al.* 2005).

Generally, two ecological theories predict variations in densities across populations, depending on either population-averaged body masses (metabolic theory, Brown et al. 2004, 2012, hereafter allometric scaling) or imbalances between elemental ratios of consumers and their resources (ecological stoichiometry, Sterner and Elser 2002). Extending recent approaches (Hillebrand *et al.* 2009; Mulder & Elser 2009; Mulder *et al.* 2011, 2013; Kaspari 2012), we introduced a concept that integrates allometric scaling of population densities with effects of litter elemental stoichiometry (Ott *et al.* 2014b). This conceptual approach demonstrated that this integration is necessary for providing an unbiased test of stoichiometric and allometric predictions. Here, we extend this approach by 1) specifically testing various hypotheses of ecological stoichiometry (as described below), 2) detailing the analyses for 12 species groups of the soil communities studied, and 3) including abiotic parameters such as pH, litter depth and forest type that can significantly affect invertebrate biomass density and the structure of soil communities (Mulder & Elser 2009; Klarner *et al.* 2014). Thus, the novelty of our study lies in the

combination of recent conceptual developments (Mulder *et al.* 2011, 2013; Kaspari 2012; Ott *et al.* 2014b)with large-scale analyses of abiotic and stoichiometric effects on biomass distributions across trophic levels of soil communities (Kaspari & Yanoviak 2009; Mulder & Elser 2009; Kaspari *et al.* 2009).

The body tissues of organisms are composed of approximately 22 chemical elements (Sterner & Elser 2002; Kaspari 2012). According to Liebig's law of the minimum, the limited availability of any of these elements can constrain growth. More recent hypotheses were based on specific mechanisms: The growth rate hypothesis focuses on the cellular allocation of ratios between carbon, nitrogen and phosphorous (C:N:P) covering demands of growing cells for P-rich ribosomal RNA (Elser *et al.* 2000b; Sterner & Elser 2002). Moreover, experimental evidence underlined that microbial biomass P was positively correlated with available P (Joergensen *et al.* 1995), microbial growth increased with the C:P ratio (Griffiths, Spilles & Bonkowski 2012) and P fertilization significantly increased litter decomposition rates (Kaspari & Yanoviak 2008). Consequently, Kaspari and Yanoviak (2009) coined the Secondary Productivity Hypothesis postulating that microbial biomass increases along gradients of available P, which should increase the abundance of microbi-detritivores (Kaspari & Yanoviak 2009). Thus, this hypothesis predicts that the availability of P in the litter should indirectly affect population densities of microbi-detritivores via the microbial channel. The structural element hypothesis is based on the importance of essential elements for building body skeletons and other structures (Kaspari & Yanoviak 2009). More specifically, it stresses the importance of calcium (Ca) for calcareous exoskeletons (e.g., isopods and diplopods) and nitrogen (N) for the silk of webs (spiders) (Kaspari & Yanoviak 2009). The Sodium Shortage Hypothesis focuses on the discrepancy between the little sodium (Na) supplied by plant litter resources and the higher demand of their animal consumers that arises due to the fact that plants use potassium (K) to maintain membrane gradients whereas animals use Na for this purpose (Kaspari et al. 2009). Consequently, animal biomasses should be limited by the Na-poor plant litter (Kaspari *et al.* 2009). While these mutually not exclusive hypotheses predict effects of specific elements, the concept of elemental stoichiometry generally also holds that low (limitation) and high (toxicity) contents of any of the 22 essential elements can potentially affect biomass production of animals (Sterner & Elser 2002; Frost *et al.* 2005b; Kaspari 2012).

In addition to these stoichiometry based hypotheses, the ecosystem size hypothesis predicts that with increasing habitat size more species and consequently more trophic

levels are sustained (Post 2002; Brose *et al.* 2004) On forest floors the available habitat size can be represented by the thickness of the litter layer. Moreover, in addition to this size-per-se effect, micro-habitat heterogeneity can also affect ecological communities (Tews *et al.* 2004). In forest floor communities, leaf species richness contributes to the variety of micro-habitats in the litter layer. Hence, the density of predatory species should increase with litter depth and diversity, and in consequence microbi-detritivores should dominate in forests with shallow and less diverse litter layers (Kaspari & Yanoviak 2009). Furthermore, we included two additional co-variables in our analysis possibly affecting population densities: the pH and the different forest types of our sampling sites. The pH is a general predictor of communities and processes in the soil (Schaefer & Schauermann 1990; Mulder *et al.* 2005; Mulder & Elser 2009). The forest types express the dominant tree species and the harvesting practice thus, representing a gradient of human land use. Here, we follow recent research (Ehnes *et al.* 2014) and aim to disentangle in which groups of soil animals the differences in the management intensity of forest types mediate changes in population densities.

We investigated how biomass densities of invertebrates in a large dataset of forest soil communities (Ehnes *et al.* 2014) depend on the elemental stoichiometry (i.e., the carbon-to-element ratios) of the basal resource (i.e. the litter) or habitat characteristics (forest type, litter depth and pH). Accounting for the scaling of biomasses with population-averaged body masses (body-size spectra sensu Mulder and Elser 2009, Mulder et al. 2011, 2013) enabled us to pool population densities across populations varying in the body size of individuals. Following the 1) structural elements hypothesis we predicted that groups of organisms depend on single elements (or corresponding element ratios), i.e. especially Ca and N for soil invertebrates. We tested the 2) sodium shortage hypothesis predicting limitation of animal biomasses by Na. According to the 3) secondary productivity hypothesis the densities of animals should be limited by P. Furthermore, we examined the 4) ecosystem size hypothesis by relating soil fauna biomass to the litter depth (representing habitat size) and litter diversity (indicating habitat heterogeneity). Moreover, the influence of 5) human management (Fischer *et al.* 2010) was tested by examining variations in biomass densities of the soil fauna with forest types. By integrating biomass density–body mass scaling relationships our study provides a unified analysis of which habitat parameters drive biomass densities of forest soil animal communities.

5.3. Methods

Study site

Data were collected from forest plots in three regions of Germany forming part of an integrative research platform (<www.biodiversity-exploraties.de>) described in more detail in Fischer *et al*.(2010): 1) The UNESCO Biosphere Reserve Swabian Alb (462–858 m a.s.l., 700–1000 mm annual mean precipitation and 6–7°C mean temperature) in the southwest of Germany, 2) the National Park Hainich in the Hainich-Dun region (285–550 m a.s.l., 500–800 mm and 6.5–8°C) in central Germany and 3) the UNESCO Biosphere Reserve Schorfheide-Chorin (3–140 m a.s.l, 500– 600 mm and 8–8.5°C) in the northeast of Germany. Parent rock is limestone with soils rich in clay in these two regions. Parent rock in the Schorfheide is glacial till covered with sandy soils (Fischer *et al.* 2010). The study sites included forest types varying in their management intensity (i.e., gradient of rotation time of cutting or harvesting events). These types ranged from unmanaged (i.e., no management since at least 60 years with an approximate age of 120 years) to old and young managed beech *Fagus sylvatica* forests (approximate age of 70 and 30 years, respectively) to intensively managed coniferous forests. The latter were represented by spruce *Picea abies* in the Swabian Alb and the Hainich-Dun, and by Scots pine *Pinus sylvestris* in the Schorfheide. For each of the combinations of four forest types with three regions, four plots were chosen leading to a total of 48 sampling sites. All samplings were taken from randomly chosen locations in a representative defined area (GPS fix point coordinates) of 25 m² per sampling site.

Sampling of animals

We sampled soil cores of a diameter of 5 cm (for mesofauna) and 20 cm (for macrofauna) and extracted animals by heat. In addition, we applied mustard solution for collecting earthworms and large mobile animals (including Gastropoda) were collected by sieving of leaf litter. Samples for extracting soil animals and earthworms were taken in spring 2008 and those for mobile litter animals in spring 2011. Invertebrates were determined to species level and individual body masses (mg) were measured or estimated with mass-length regressions (Ehnes *et al.* 2014). Some species occurred with multiple life stages or distinct size classes, and we treated these trophically distinct sub-populations as

independent populations in the subsequent analyses. We calculated abundances (no. ind m^{-2}), population average body masses (mg) and corresponding biomasses (mg m^{-2}) for each population on each plot independently. More details of sampling methods, species determination and mass-length regressions are provided by (Klarner *et al.* 2014; Ehnes *et al.* 2014). Since all sampling methods differed in the size of the sample area covered, we converted all measurements into the units of abundance per square meter, which allowed pooling population densities for each site across sampling methods. In a final step, the abundances were averaged across sampling dates.

The highly resolved dataset included 5312 populations of 730 entries of macro- and mesofauna species (or higher taxonomic resolution, e.g. family level) across the 48 plots (872 trophic species after differentiating size classes). We excluded herbivorous species that did not depend on litter resources from the analyses. Thus, in total 4959 populations of 690 species (817 trophic species after differentiating size classes) remained for the analyses. Analyses were conducted with Arachnida (including Araneae, Pseudoscorpiones and Opiliones; 763 populations, hereafter arachnids), Chilopoda (378 populations, hereafter centipedes), Isopoda (127 populations, hereafter woodlice), Diplopoda (164 populations, hereafter millipedes), Lumbricidae (169 populations, hereafter earthworms), Collembola (690 populations, hereafter springtails), Oribatida (972 populations, hereafter oribatid mites), Mesostigmata (738 populations, hereafter mesostigmatic mites). Coleoptera were divided into predators (mainly Carabidae and Staphylinidae; 607 populations, hereafter predatory beetles) and non-predatory feeding types (77 populations, hereafter non-predatory beetles). Gastropoda were divided into slugs (35 populations) and snails (153 populations). We excluded Symphyla, Prostigmata, Dermaptera and Diplura as they were rare.

Litter parameters

From each of the 48 forest sites, four randomly chosen samples of the litter layer (representing all layers of the O-horizon) were taken in spring 2011 from different sampling locations (spaced approx. 2 m) in the defined area according to the sampling procedure of animals. Leaf litter and organic layer material were collected from inside a metal frame (0.25 m^2) and sieved (1 cm mesh-size) to exclude woody material. We subsequently refer to this mixture of litter with the organic horizon by simply litter or litter layer. The litter samples were dried at 60°C until no further weight loss and ground

to fine powder with a ball mill. Prior to the elemental analysis the powder from the four samples per plot was merged into one mixed sample to ensure homogeneity (i.e. the data represent the average conditions of the sample area). Subsequently, total carbon and nitrogen were analyzed by an automated CHNSO analyzer from an amount of five milligram powder material per sample. For the analysis of eleven other elements (i.e. phosphorus (P), calcium (Ca), sodium (Na), potassium (K), manganese (Mn), magnesium (Mg), iron (Fe), aluminium (Al), sulphur (S), copper (Cu) and zinc (Zn)) 50 mg of each sample was digested by adding 2 ml of 65% nitric acid (HNO3) in teflon containers and pressure digested at 185°C for 9. Samples were filtered and rinsed quantitatively with double distilled H2O into 50 ml volumetric flasks and analyzed by inductively coupled plasma optical emission spectroscopy (ICP-OES). Litter pH (O-horizon) was measured by adding 10 ml 0.01 M CaCl2 solution to 1 g litter. Soil pH (A-horizon) was measured in the same way but using 2 g of soil and 20 ml of CaCl2 solution. Since values were highly correlated (e.g. a low pH in the litter was reflected by a low pH in the soil; Pearson´s product-moment correlation coefficient, Pr = 0.74 [data not shown], hereafter "Pr") we averaged both and used one representative value for pH per sample area. Litter diversity was measured as species richness of leaves from needle and deciduous trees in the litter determined on the four subplots (inside of the metal frame) and averaged across subsamples per plot. Litter depth was measured on the edges that were cut by the metal frame into the A horizon; it included the combined thickness of the leaf litter (OL horizon) and the humus layer (OF and OH horizons).

We excluded the elements copper (Cu) and zinc (Zn) from further analysis, because the measured values of samples were in the range of the standard deviation of blank controls (blinds) between ICP-OES runs and thus close to the detection threshold of the machine. For statistical analyses, we used Carbon-to-element ratios for the remaining 10 elements (based on milligram per gram dry weight) as well as pH, litter depth and litter diversity (supporting information figure 5.S1).

Statistical analysis

We analyzed the dependence of population biomasses on 1) the population-averaged body masses of the species (i.e., allometric scaling of densities), 2) independent additive co-variable effects of land use (indicated by forest type), the litter stoichiometry (i.e. the relative abundance of elements indicated by the carbon-to-element ratios) and litter

characteristics (i.e. litter depth and diversity and the pH) on the densities and 3) interactions between body masses and each of the co-variables. Please note that we defined explanatory variables other than body mass as co-variables. Data were analyzed using the statistical program R ver. 3.0.2. (R Development Core Team 2013). All continuous variables were $\log_{10}$ transformed to meet assumptions of normality and homoscedasticity. Further, the co-variables were normalized to a mean of zero and a variance of unity. We tested co-variables for collinearity (function "cor.test"). Co-variables with a Pr larger than 0.75, or a variance inflation factor (VIF) larger than 5 are highly correlated and need further consideration before testing their predictive power (Zuur *et al.* 2007, 2009). In our data, pH and the C:Ca ratio were strongly negatively correlated (Pr = -0.78, table 5.S1 in supporting information). Also the C:Fe and C:Al ratios correlated strongly positively (Pr = 0.83) and yielded high VIF (8.3 for C:Fe and 6.4 for C:Al, table 5.S1 in supporting information). The C:Mg ratio yielded a VIF of 7.3 (table 5.S1 in supporting information). Since the C:Fe and C:Al ratio did fail to fulfill both of our selection criteria, we tested their effects independent of each other in alternative model sequences combined with the other explanatory co-variables and chose the better fitting model (selected via Akaike's information criterion, AIC). Thus, we applied 15 explanatory co-variables (one categorical and 14 continuous) independent of each other to the biomass – body mass scaling relationships of animal groups per model.

We used linear mixed effects models (function "lme", Pinheiro *et al.* 2012) with the landscape blocks (i.e., the "exploratories") set as a random factor. This random intercept structure was selected by AIC comparing different random structures with restricted maximum likelihood (method = REML), with all fixed effects included (Zuur *et al.* 2009 p. 20). For the fixed effects, we applied four different model types: as starting points we created 1) a null model which includes only the biomass–mass scaling without any other co-variables and 2) a full model including all independent co-variables together with their two-way interaction terms with body mass. Subsequently, we independently applied the automated algorithm "stepAIC" (mode of stepwise search "both", Venables and Ripley 2002) to both models leading to two additional models – 3) an increase model (step function applied to the null model) and 4) a decrease model (step function applied to the full model). The "stepAIC" function deletes or adds explanatory co-variables one by one in order to obtain the most parsimonious model by using Akaike's information criterion (AIC). Since a restricted maximum likelihood is not defined for the "step" function, we

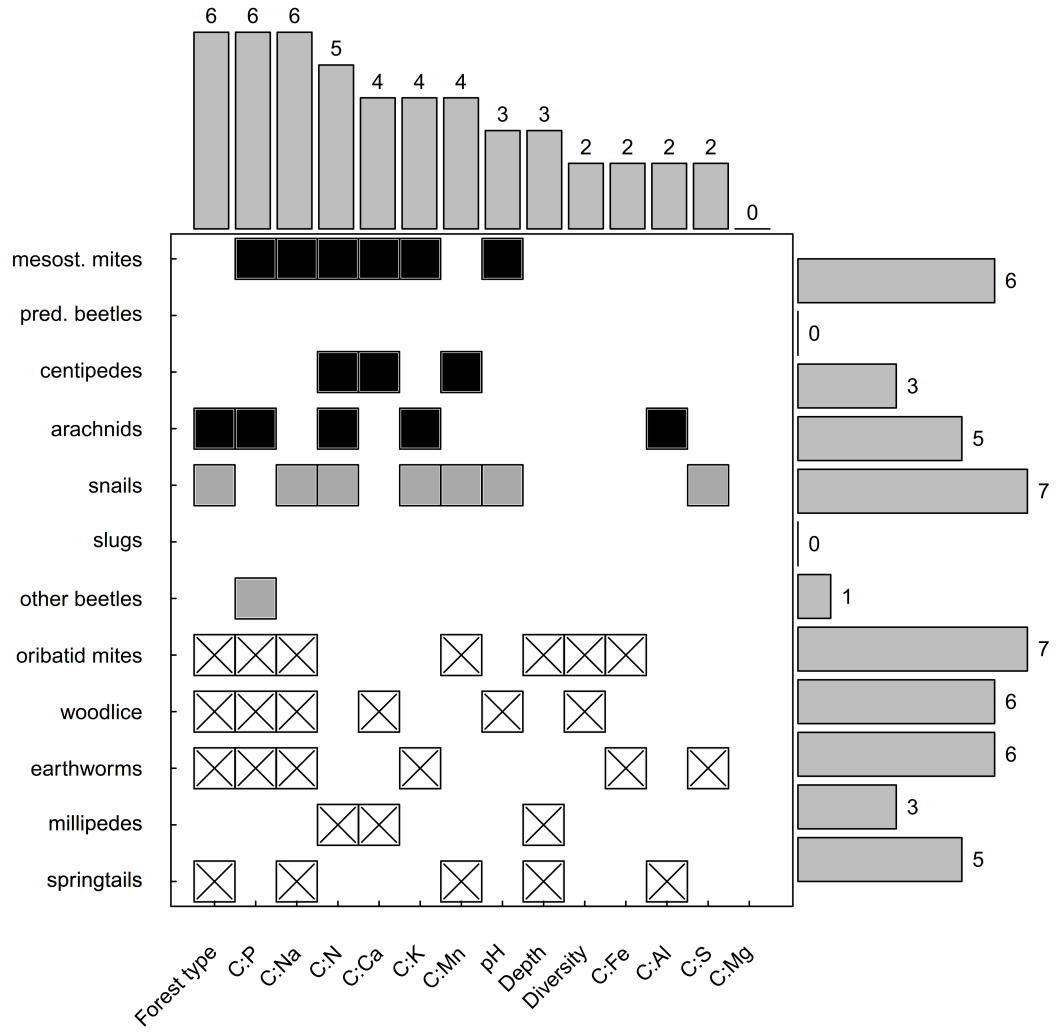

Figure 5.1: Frequency of stoichiometric co-variables in models explaining biomass densities of soil animal groups. The occurrence of explanatory co-variables in the most parsimonious models predicting biomass–mass scaling for predators (black squares), omnivores (grey squares) and microbi-detritivores (white squares with crosses) is shown. Litter depth and diversity is indicated by depth and diversity on the x-axis. Beetles were separated into predatory (pred.) and non-predatory (other) feeding types. Mesostigmatic mites are indicated (mesost. mites). Vertical grey bars on the top of the plot indicate the total frequency for each co-variable in the plot (histogram according to columns), whereas the horizontal grey bars on the right side denote the sum of co-variables occurring per animal group (histogram according to rows). More details in supporting information table 5.S2.

ran the linear mixed effect models with unrestricted maximum likelihood (method = ML). We judged models to be most parsimonious if all other models showed a $\Delta AIC > 2$ (Burnham & Anderson 2004). If $\Delta AIC < 2$ among models in this procedure, we chose models with the lowest AIC. After model selection, we applied the restricted maximum likelihood (method = REML) with the most parsimonious models in order to obtain correctly estimated model coefficients (Zuur *et al.* 2009).

5.4. Results

We applied independent models to the 12 species groups of the forest soil ecosystems studied (figure 5.1). All variables included in models according to the AIC selection procedure are of equal importance for the model selection. Thus, we did not base our conclusions on the significance of individual variables. Instead, we decided to keep all variables included in the models (see supporting information table 5.S2 for details of coefficients of the models). Each of these models included the scaling of biomass densities with population- average body masses that were documented in a prior study (Ehnes et al. 2014). The most parsimonious models for ten out of 12 groups included at least two fixed co-variables expressing stoichiometric parameters and plot characteristics (figure 5.1, supporting information table 5.S2). Thus, the simple allometric null model of the biomass–body mass scaling independent of other parameters was rejected in the majority of cases based on AIC comparisons. The co-variable interactions with the biomass–body mass scaling caused the relationships to be shallower and steeper than assumed at average levels of the stoichiometric contents, pH, litter depth or diversity (figure 5.2, 5.3, supporting information table 5.S2) which implies variable effects on small and large-bodied species. We illustrated this variation showing the extremes of the variable ranges by comparing the highest C:X ratios or lowest contents of abiotic parameters in our data (blue lines in figure 5.2 and 5.3) and the lowest C:X ratios or highest contents of abiotic parameters (red lines in figure 5.2 and 5.3) to the average scaling relations (orange lines in figure 2 and 3). We interpreted effects of the forest type in the same way as for the other co-variables. Thus, the highest management intensity (i.e. coniferous forests: brown lines in figure 5.2 and 5.3) is compared with all intensities levels down to the lowest intensity (i.e. unmanaged beech forest: dark green lines in figure 5.2 and 5.3).

While we found highly variable effects of the various environmental parameters tested that were often specific to the species group (figure 5.2, 5.3), the frequency and dominance of these effects showed some regularities (figure 5.1). Across all 12 different groups, oribatid mites and snails depended on most plot and litter characteristics, because results demonstrated the importance of seven parameters (figure 5.1, supporting information table 5.S2). Compared to other groups, earthworms depended second most on parameters of the litter (figure 5.1, supporting information table 5.S2). In contrast, predatory beetles and slugs did not depend on co-variables and non-predatory beetles

depended only on one parameter (figure 5.1, supporting information table 5.S2). Our results demonstrate that the C:Na and the C:P ratio together with forest type were most frequent in interactions with allometric scaling of the forest soil communities (figure 5.1). The C:Na ratio affected the densities of the mesofauna groups orbatid mites (figure 5.2a3), springtails (figure 5.2b2), mesostigmatic mites (figure 5.2c3) and the macrofauna groups snails (figure 5.3a3), earthworms (figure 5.3b3) and woodlice (figure 5.3c3). Interestingly, none of the predatory groups of the macrofauna depended on the C:Na ratio (figure 5.1), whereas the other most important co-variables, the C:P ratio and the forest type, were included as predictors in the model for arachnids (figure 5.1). Thus, the latter two co-variables affected densities of the groups across size classes (i.e. meso- and macrofauna) and feeding types (i.e. predators or detritivores) (figure 5.1, supporting information table 5.S2). The C:P ratio was included in models of oribatid mites (figure 5.2a2), mesostigmatic mites (figure 5.2c2), arachnids (figure 5.2d2), earthworms (figure 5.3b2), woodlice (figure 5.3c2) and non-predatory beetles (figure 5.3e1). Forest type affected oribatid mites (figure 5.2a1), springtails (figure 5.2b1), arachnids (figure 5.2d1), snails (figure 5.3a1), earthworms (figure 5.3b1) and woodlice (figure 5.3c1). The C:N ratio was among the second most frequently occurring co-variables (figure 5.1, supporting information table 5.S2). The C:N ratio was included in models for the predator groups mesostigmatic mites (figure 5.2c4), arachnids (figure 5.2d4) and centipedes (figure 5.2f2) as well as for snails (figure 5.3a2) and millipedes (figure 5.3d2). The C:Ca ratio (an important stoichiometric variable regarding to our hypotheses), the C:K and the C:Mn ratios composed the group of the third most frequently occurring co-variables (figure 5.1, supporting information table 5.S2). The C:Ca dependency of the allometric scaling relationship occurred for the predatory groups mesostigmatic mites and centipedes (figure 5.2c5 and 5.2f3 respectively) and the decomposer groups woodlice (figure 5.3c4) and millipedes (figure 5.3d3). Litter depth and diversity, key co-variables associated to the ecosystem size hypothesis, ranked with moderate to minor frequency amongst predictor co-variables (figure 5.1). Litter depth was included in models explaining population densities of oribatid mites, springtails and millipedes (figure 5.2a5, 5.2b4 and 5.3d1, respectively, supporting information table 5.S2). Litter diversity was included in models for oribatid mites (figure 5.2a6) and woodlice (figure 5.3c6). Further, pH was included in the models for mesostigmatic mites, snails and woodlice (figure 5.2c1, 5.3a5 and 5.3c5, respectively, supporting information table 5.S2) and thus achieved an intermediate frequency in the ranking of explanatory co-variables (figure 5.1).

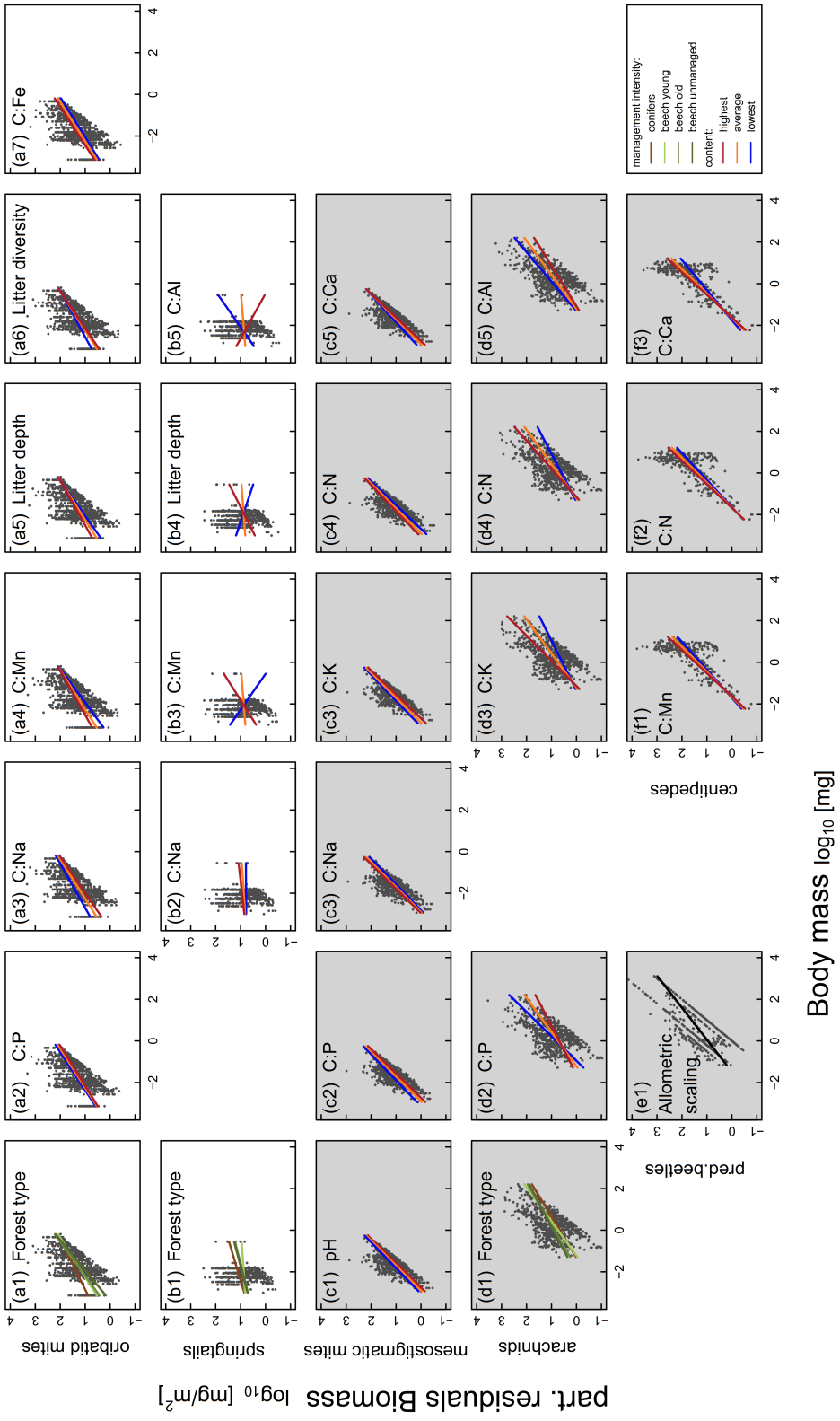
part. residuals Biomass log10 [mg/m2]
oribatid mites
springtails
mesostigmatic mites
arachnids
centipedes
pred.beetles
(a1) Forest type
(a2) C:P
(a3) C:Na
(a4) C:Mn
(a5) Litter depth
(a6) Litter diversity
(a7) C:Fe
(b1) Forest type
(b2) C:Na
(b3) C:Mn
(b4) Litter depth
(b5) C:Al
(c1) pH
(c2) C:P
(c3) C:Na
(c3) C:K
(c4) C:N
(c5) C:Ca
(d1) Forest type
(d2) C:P
(d3) C:K
(d4) C:N
(d5) C:Al
(e1) Allometric scaling
(f1) C:Mn
(f2) C:N
(f3) C:Ca
management intensity:
conifers
beech young
beech old
beech unmanaged
content:
highest
average
lowest
Body mass log10 [mg]

Figure 5.2 (page 90): Effects on population densities of microbi-detritivorous mesofauna and predatory mesofauna and macrofauna. Points indicate partial residuals of biomass depending on the population average body masses in interaction with the selected effect of a single co-variable after accounting for all the other explanatory co-variables included in the group specific models. These partial residuals plots include the model intercepts. Mesofauna groups shown are: oribatid mites (a1–7), springtails (b1–5) and mesostigmatic mites (c1–5). Macrofauna groups shown are: arachnids (d1–5), predatory beetles (e1) and centipedes in (f1–3). Panels with a background color in white represent results for microbi-detritivores and in grey for predators. Regressions are based on allometric scaling varying either with forest type or with co-variables derived from the litter. These were either abiotic characteristics like litter species richness (Litter diversity), thickness of the litter layer (Litter depth), pH or litter quality expressed in the ratios total carbon-to-element (C:X). Forest types are indicated varying in their management intensity (i.e. gradient of rotation time of cutting events): coniferous forests (brown line, highest intensity), young (light green line, 30 year rotation) and old (green line, 70 year rotation) managed beech or unmanaged beech forests (dark green line, lowest intensity). Orange lines represent allometric scaling with average contents of the continuous parameters or elemental ratios. These scaling relationships can vary from depletion (blue lines, i.e. the lowest parameter values of abiotic characteristics or highest C:X ratios) to enrichment (red lines, i.e. the highest parameter values or lowest C:X ratios). The biomass-mass scaling relationship of predatory beetles did not depend on any of the co-variables (e1). The regression (black line) is based on full data and not on partial residuals. Note, that arachnids included Araneae, Pseudoscorpiones and Opiliones. The predatory beetles were dominated by Carabidae and Staphylinidae. Regression estimates are given in supporting information table 5.S2.

Amongst the co-variables that ranked with low frequency across groups, we highlight the occurrence of the C:Fe ratio as predictor affecting the allometric scaling relationships of earthworms (figure 5.3b4). The C:Mg ratio did not occur in a single model predicting population densities, indicating that the C:Mg ratio may be relatively unimportant in our analyses (figure 5.1).

5.5. Discussion

We investigated a large dataset comprising the biomasses of forest soil invertebrates across 48 communities (Ehnes *et al.* 2014) and found systematic scaling relationships of population biomass densities with population-averaged body masses thus supporting metabolic theory. These scaling relationships were strongly modified by effects of litter stoichiometry, depth and diversity, forest type and pH on the densities of groups of the soil meso- and macrofauna across trophic levels. Our analyses revealed that the simple allometric null model relating population densities only to body masses can be improved substantially by including stoichiometric co-variables. These co-variables yielded variations in the biomass–body mass scaling (i.e. the size spectrum, Mulder *et al.* 2013) leading to modified allometric exponents (Ott *et al.* 2014b). Specifically, our analyses support the structural elements hypothesis for some predator groups (concerning N,

included as C:N) and for microbi-detritivores (concerning Ca, included as C:Ca) as well as the sodium shortage hypothesis for microbi-detritivores and Mesostigmata. Furthermore, the secondary productivity hypothesis (concerning P, included as C:P) was supported across all trophic groups of the food webs. In contrast, we found only limited support for the ecosystem size hypothesis. Moreover, we also found a general effect of the forest type. Thus our study revealed which parameters of the elemental litter stoichiometry constrain animal biomass densities in soil communities.

Structural elements hypothesis

The structural elements hypothesis for soil invertebrates focuses on Ca, as a component for the exoskeleton hardening, and N that is necessary for silk production (Kaspari & Yanoviak 2009). Both elements occurred in five (C:N) and four (C:Ca) of the 12 explanatory models of the groups in our study, indicating their relative higher importance than less frequent variables. Both of the macrofauna groups with calcareous exoskeletons (i.e. woodlice and millipedes; Kaspari and Yanoviak 2009) included the C:Ca ratio in the most parsimonious model. These results are consistent with Kaspari and Yanoviak (2009) demonstrating that the abundance of isopods increased with Ca content of the litter. One important distinction between our and previous studies is that we accounted for the strong scaling relationships between biomass densities and population-average body masses (Ehnes *et al.* 2014), which allows pooling biomasses of populations differing in body size. Ignoring allometric scaling relationships of biomasses (as used in our study) or abundances (as used by Mulder and colleagues: Mulder and Elser 2009, Mulder *et al.* 2011, 2013) can lead to erroneous conclusions concerning effects of stoichiometric co-variables (Ott *et al.* 2014b). Interestingly, our results are consistent with previous findings obtained without allometric scaling (Kaspari & Yanoviak 2009). Surprisingly, we found that mesostigmatic mites were also affected by the C:Ca ratio in the litter. Further, in contrast to our expectations, C:Ca did not impose effects on oribatid mites with Ca-based exoskeletons (Norton & Behan-Pelletier 1991) and snails with their calcareous shells. Presumably, these groups are well adapted to cope with the limited supply of Ca in the basal resource of the food web, which prevented limitation of their biomass production. Overall, however, our results indicate a possible high importance of Ca for the soil animal communities.

The second element in focus of the structural element hypothesis, N, is particularly important for species groups with silk production such as spiders and pseudoscorpions (Kaspari & Yanoviak 2009), which were pooled with Opiliones in the group arachnids in our analyses. For arachnids, the C:N ratio was one of the explanatory co-variables in the final models, which is consistent with a prior study of tropical forest ecosystems (Kaspari & Yanoviak 2008). Additionally, the C:N ratio also remained in the final models for mesostigmatic mites and centipedes. This finding may find its explanation in the limitation of mesostigmatic mites by the body tissue N concentration of their microbi-detritivorous prey that is controlled by the litter stoichiometry. Similar bottom-up cascades were found for other predator - prey interactions (Fagan *et al.* 2002; Fagan & Denno 2004; Martinson *et al.* 2008). Overall, our results suggest that N availability may be important for predatory groups such as arachnids, mesostigmatic mites and centipedes and detritivorous groups such as millipedes and snails. This highlights the importance of C:N across trophic levels of the soil food webs. In summary, our results support the predictions by the structural elements hypothesis that elements such as Ca and N, which are essential for the structural components of the body tissues, can limit the biomass densities of animal populations.

Sodium shortage hypothesis

C:Na occurred in models of six of the 12 groups analyzed, and it was together with forest type and C:P the most frequent independent co-variable in our analyses. Interestingly, the final model predicting allometric scaling of predatory mesostigmatic mites included C:Na, whereas the final models for all other predatory macrofauna groups did not include C:Na. This suggests that the bottleneck of Na supply in soil food webs occurs at the litter–microbi-detritivore interface and does not propagate to higher trophic levels, which is in line with the sodium shortage hypothesis. In contrast, in experiments in tropical rainforests not only decomposer but also predator abundance increased with Na fertilization (Kaspari *et al.* 2009). These findings suggest a bottom-up limitation of soil communities by sodium availability. In general, our results point to a strong Na importance for the allometric scaling relationships across several groups, which emphasizes the common demand in animals for Na to maintain membrane gradients. Thus, our results provide, in general, support for the Sodium Shortage Hypothesis proclaimed by Kaspari *et al.* (2009).

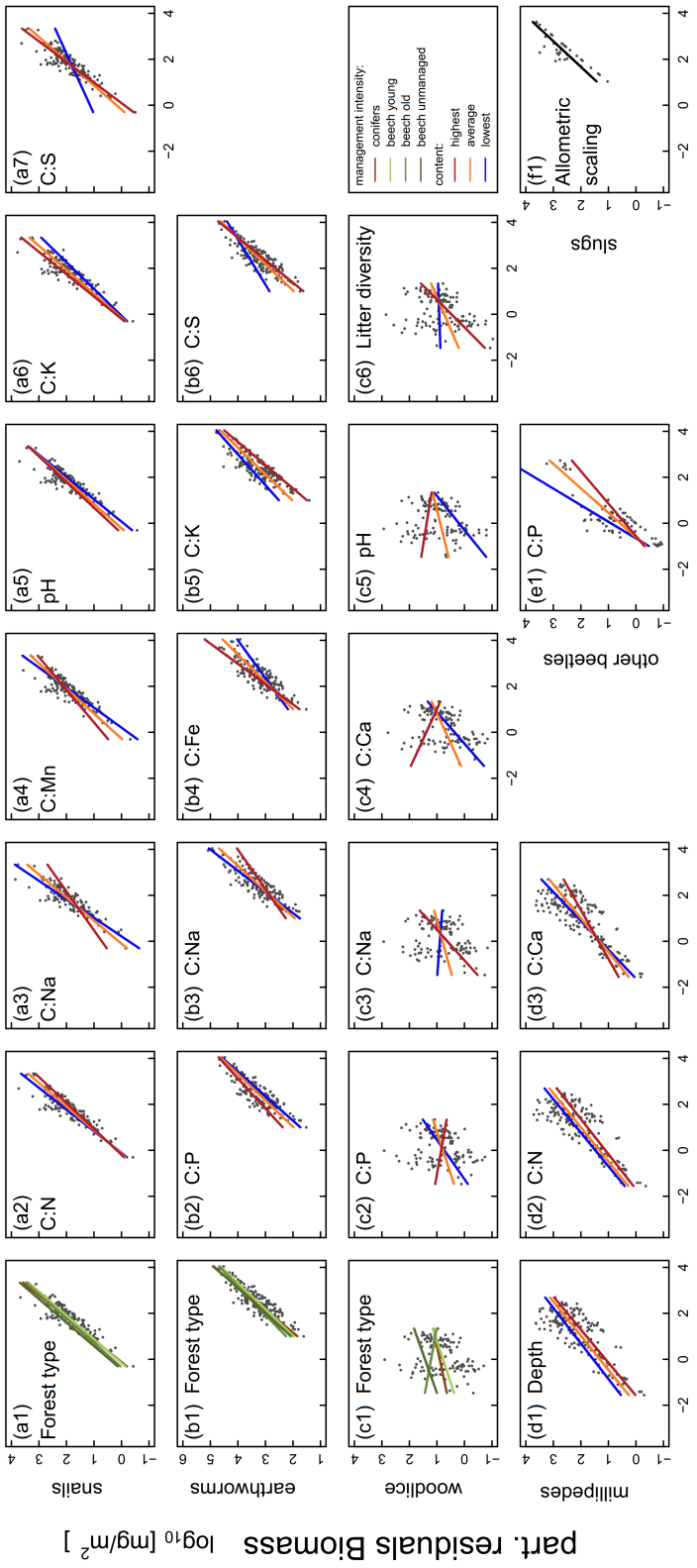
part. residuals Biomass log10 [mg/m2]
Body mass log10 [mg]
snails
earthworms
woodlice
millipedes
other beetles
slugs
(a1) Forest type
(a2) C:N
(a3) C:Na
(a4) C:Mn
(a5) pH
(a6) C:K
(a7) C:S
(b1) Forest type
(b2) C:P
(b3) C:Na
(b4) C:Fe
(b5) C:K
(b6) C:S
(c1) Forest type
(c2) C:P
(c3) C:Na
(c4) C:Ca
(c5) pH
(c6) Litter diversity
(d1) Depth
(d2) C:N
(d3) C:Ca
(e1) C:P
(f1) Allometric scaling
management intensity:
conifers
beech young
beech old
beech unmanaged
content:
highest
average
lowest

Figure 5.3 (page 96): Effects on population densities of detritivorous macrofauna groups. Points indicate partial residuals of biomass depending on the population average body masses in interaction with the selected effect of a single co-variable after accounting for all the other explanatory co-variables included in the group specific models. These partial residuals plots include the model intercepts. Results are shown for: snails (a1–7), earthworms (b1–6), woodlice (c1–6), millipedes (d1–d3) and for non-predatory (other) beetles (e1). Effects on densities of slugs are illustrated in panel (f1). Panels with a background color in white resemble results for microbi-detritivores and in grey for predators. Regressions are based on allometric scaling varying either with forest type or with co-variables derived from the litter. These were either abiotic characteristics like litter species richness (Litter diversity), thickness of the litter layer (Litter depth), pH or litter quality expressed in the ratios total carbon-to- element (C:X). Forest types are indicated varying in their management intensity (i.e. gradient of rotation time of cutting events): coniferous forests (brown line, highest intensity), young (light green line, 30 year rotation) and old (green line, 70 year rotation) managed beech or unmanaged beech forests (dark green line, lowest intensity). Orange lines represent allometric scaling with average contents of the continuous parameters or elemental ratios. These scaling relationships can vary from depletion (blue lines, i.e. the lowest values of abiotic characteristics or highest C:X ratios) to enrichment (red lines, i.e. the highest parameter values or lowest C:X ratios). The biomass-mass scaling relationship of slugs did not depend on any of the co-variables (f1). The regression (black line) is based on full data and not on partial residuals. Regression estimates are given in supporting information table 5.S2.

Secondary Productivity Hypothesis

This hypothesis focuses on P, whose availability in the litter should directly increase microbial biomass and consequently influence microbi-detritivore densities (Kaspari & Yanoviak 2009). Indeed, the C:P ratio was among the three most common co-variables correlating with soil population densities in our study, including effects on the predatory meso- and macrofauna (mesostigmatic mites and arachnids), the detritivorous macrofauna (earthworms and woodlice), and the microbi-detritivorous mesofauna (oribatid mites). Our results thus point to a strong dependency of species of all trophic groups on P. Hence, our results support the secondary productivity hypothesis that soil organisms are limited by P, especially when considering that microbial communities seem to be constrained by C:N:P ratios (Joergensen *et al.* 1995; Griffiths *et al.* 2012). The hypothesis in its strict sense only applies to populations of microbi-detritivores assuming that their densities follow the biomass production of microorganisms (Kaspari & Yanoviak 2008). In our study, however, the C:P ratio was also included in the final models of predatory groups such as arachnids and mesostigmatic mites. This supports the more general growth rate hypothesis explaining P limitation by the demands of organism for ribosomal RNA and protein biosynthesis (Sterner & Elser 2002). Overall, our results support recent conclusions that P is not only limiting in aquatic but also in terrestrial ecosystems (Elser *et al.* 2000a, 2007).

Ecosystem Size Hypothesis

According to the Ecosystem Size Hypothesis, a deeper and more complex litter structure should provide more refuges and offer habitat to more species (Post 2002; Brose *et al.* 2004). We tested whether 1) litter depth indicating the total volume of the habitat for our 1-m^2 samples and 2) litter diversity as a surrogate variable for habitat heterogeneity affect biomass densities. Interestingly, we found that litter depth as well as litter diversity rarely occurred in the models: both co-variables had no effect on the population densities of predatory macrofauna groups, and only the densities of some microbi-detritivores were correlated with litter depth (i.e. oribatid mites, springtails and millipedes) or litter diversity (i.e. woodlice and oribatid mites). This pattern is in line with a recent study demonstrating the density of oribatid mites to be correlated with the mass of the litter layer (Erdmann, Scheu & Maraun 2012). Interestingly, for the two microbi-detritivorous mesofauna groups higher litter depths resulted in increased population biomasses of small species (blue lines in figure 5.2a5 and 5.2b4) and decreased biomasses of large species (red lines in figure 5.2a5 and 5.2b4). This suggests that in particular small microbi-detritivorous species are sensitive to reduced litter, which may be caused by the increased top-down predation pressure in simple litter habitats (Kalinkat *et al.* 2013a). Overall, our results do not support conclusions that litter depth yields higher abundances of predatory groups (Kaspari & Yanoviak 2009). Instead, our findings suggest that ecosystem size affects mesofauna and macrofauna detritivores, possibly due to limited access to root-derived resources (Klarner *et al.* 2014), whereas for macrofauna predators the thickness of the litter layer is of minor importance. Potentially, large predatory species may integrate across larger spatial scales than the one square meter plots investigated in our study, which might explain the lack of habitat size as determinant for their densities. Similarly, this may also explain the absence of effects of the local stoichiometry on predatory beetles. However, other mobile predatory groups such as arachnids depended on several stoichiometric variables, which suggests that integration across larger spatial scales does not generally explain the presence or absence of local stoichiometry effects on the densities of large and mobile organisms.

Forest type

Forest type was among the most important co-variables (six of 12 cases) in the explanatory models of this study. For instance, biomass densities of woodlice and

arachnids differed markedly between forest types. In particular, populations of small bodied species among these groups exhibited lower biomasses in coniferous forests than in beech forests. In contrast, oribatid mites and springtails generally reached higher biomass densities in coniferous forest than in beech forests, which may be due to the thicker litter depths in coniferous forest compared to beech forest (Erdmann *et al.* 2012). The effect of the main tree species, i.e. beech or conifers, potentially drives the differences across forest types (Ferlian & Scheu 2013; Klarner *et al.* 2014). Surprisingly, snails and earthworms exhibited only marginal differences in their biomass densities between the forest types, whereas prior studies suggested strong differences between forest types (Scheu & Falca 2000), which may be due to different responses in earthworm ecological groups (Scheu & Falca 2000; Eisenhauer 2010). In contrast to prior studies, we included ten stoichiometric and three environmental variables in our models (including pH) in addition to the forest type. Instead of being a surrogate of stoichiometric variables, forest type is thus a compound indicator of management intensity, the frequency of disturbances, and the time since the last complete cutting. Overall, our results indicate that – irrespective of variation in stoichiometric and abiotic conditions – forest management is an important factor affecting the biomass densities of soil animals.

Litter pH

Differences in the pH of the soil can play an important role in forming soil communities (Schaefer & Schauermann 1990; Mulder *et al.* 2005; Mulder & Elser 2009). While effects on microorganisms are opposite to each other for fungal biomass (i.e. increase at low pH) and bacterial biomass (i.e. increase at high pH, Rousk *et al.* 2009), a universal inhibition of growth related response variables was found at pH below a threshold of 4.5 (Rousk *et al.* 2009). In our study, pH influenced only the biomass densities of snails, woodlice and mesostigmatic mites, whereas the expected effect on earthworms could not be confirmed. Across most arthropod groups, pH was not kept in the most parsimonious statistical models. This is consistent with a recent study on litter decomposition across biomes: Instead of pH, water saturation capacity, Mg and condensed tannins were the main litter traits driving litter decomposition (Makkonen *et al.* 2012). Overall, our results do not support the hypothesis that pH is the directly dominating factor determining the density of soil animal populations, but it could indirectly drive soil chemical processes contributing to the bioavailability of elements. Beside the direct effects of acidity or

alkalinity, pH exhibits complex indirect effects on the soil communities due to interactions with precipitation, soil particle distribution, the redox potential and the cation exchange capacity. These mechanisms contribute to the elements' availability. For instance, acidic soils rich in Fe and Al oxides control the availability of phosphate for soil organisms. Future studies should keep on including the effect of pH in combination with stoichiometric co-variables since allometric scaling relationships are interrelated with pH (Mulder & Elser 2009; Mulder *et al.* 2011).

Caveats

We based our study on several assumptions. First, we did not analyze the different structural fractions of C separately in our models. Instead, we used the corresponding total carbon-to-element ratios to characterize the elemental stoichiometry (Sterner & Elser 2002). Generally, the C:P and the C:N ratio are crucial for decomposition processes at the food-web base (Joergensen *et al.* 1995; Kaspari & Yanoviak 2008; Griffiths *et al.* 2012). While total carbon availability or lignin concentrations showed no significant direct effect on decomposition rates (Enríquez *et al.* 1993a), a recent approach demonstrated how different structural carbon compounds control litter decomposition (Adair *et al.* 2008). Consequently, carbon quality is an important driver of litter decomposition, because structural carbon compounds such as lignin and cellulose affect the palatability for decomposers and decomposition rates (Anderson *et al.* 2004; Adair *et al.* 2008; Hättenschwiler & Jørgensen 2010). However, differences in carbon quality are also reflected in carbon-to-element ratios: the higher the C:N ratio the higher is the amount of structural components (Anderson *et al.* 2004; McGroddy *et al.* 2004). In this vein, we have accounted somewhat for varying litter quality by the carbon-to-element ratios, which represents a stoichiometric perspective that intrinsically includes differences in fiber contents of low palatability.

Second, our study focused on litter as the basal resource of the decomposer system, whereas roots and root-derived carbon as the alternative basal resource of soil animal communities (Ruf, Kuzyakov & Lopatovskaya 2006; Pollierer *et al.* 2007) were ignored. However, stable isotope analyses of the same communities as in our study (Klarner *et al.* 2014) indicate that litter is the predominant resource of the animal community, which is increasingly decoupled from the root compartment with increasing thickness of the litter layer.

Third, the litter horizons that we sampled integrate across a gradient of different litter decay levels of the same material starting from the fresh and coarse material on top and to the fragmented material in more progressed decay states of deeper litter layers. Hence, the material we analyzed represents a resource in different decay states. While it is certainly true that not all decomposers feed on all decay levels of the material, we had no a-priori information which species groups feed predominantly on which decay levels and thus assumed that species generally feed on the continuous resource gradient. We caution, however that future studies should disentangle the stoichiometry of different layers of the O-horizon to analyze more specific effects on layer-specific species groups.

Fourth, we based our analyses on leaf samples that were taken in spring, whereas the stoichiometric quality of the leaf material may vary throughout the year as decomposers may initially predominantly feed on the most nutritious material. This may lead to a discrepancy between the litter material found on the forest floor and the subset of it that is used by the decomposing animal community for building up their biomasses. Due to logistical constraints imposed by working on many different field sites we have limited our litter sampling to early spring, which allows analyzing the material at the beginning of the season. More detailed analyses of element fluxes would require replicated sampling and analyses of litter and animal tissues throughout the year. The present study thus preferred generality across many sites over accurate flux predictions at individual sites. Hence, the predictions made by our across-site comparison require thorough testing by time-series analyses at individual sites in future studies. The carbon-to-element ratios used in our study normalize the absolute element contents, which allows such comparisons in time and between studies when the total amount of litter material fluctuates.

Fifth, among the elements we intended to study, we excluded Cu and Zn because of methodological reasons However, we recommend including these elements in future studies as we expect them to be limiting for population densities when they occur in low bioavailable amounts (e.g. oxygen transport affected by scarce copper for building hemocyanin), whereas they should be toxic when occurring in higher amounts.

Sixth, our study comprised animals of the meso- and macrofauna, whereas microfauna species were not included in our data. However, these animal groups can also exhibit pronounced responses to the basal resource stoichiometry (Mulder *et al.* 2005, 2011, 2013; Mulder & Elser 2009).

Seventh, we did not measure the stoichiometric contents in body tissue of the animal groups. Thus, we included only half of the data necessary to calculate consumer-resource imbalances that are important for the maintenance of homeostasis (Sterner & Elser 2002; Frost *et al.* 2005b). While assessing the stoichiometry of animal tissues would thus be highly desirable, they were impossible in our study of 48 field communities with 4959 populations. As our study thus focused on the broad-scale patterns in the biomass scaling relationships across macro- and mesofauna species groups, future studies should detail our results and test predictions by including measurements of litter and animal stoichiometry for some representative groups at fewer field sites.

Conclusions

We found systematic variations of allometric scaling relationships with litter stoichiometry and forest type. Our results documented the importance of several stoichiometric hypotheses: 1) the structural elements hypothesis (concerning N and Ca), 2) the sodium shortage hypothesis for microbi-detritivores, and 3) the secondary productivity hypothesis (concerning P) across all trophic groups of the food webs. In contrast, the ecosystem size hypothesis found only partial and more limited support for some meso- and macrofauna (microbi-) detritivores. The constraints found by single elements like P, Na, Ca, N or Mn studied as C:X ratios on the population densities are according to the predictions of Liebig's law of the minimum for ecological stoichiometry (Kaspari 2012). Moreover, our approach revealed the importance of multiple elements for the majority of the species groups thereby coping with potential co-limitation by more than one element (Sperfeld, Martin-Creuzburg & Wacker 2012). Overall, the study provided a comprehensive analysis of meso- and macrofauna how multiple aspects of elemental stoichiometry of the basal resource of the decomposer system interactively constrain population densities across multiple trophic levels of soil animal communities.

5.6. Acknowledgements

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Chapter 6.

Land use, decomposer community composition and leaf species interactively control litter decomposition.

David Ott, Esra H. Sohlstroem and Ulrich Brose

6.1. Abstract

It is crucially important to understand the underlying mechanisms maintaining the productivity of forest ecosystems, because worlds´ forests provide a variety of resources and services that are valuable to humans. Litter decomposition is the ecosystem function that regulates the quality and the accessibility of nutrients in the soil, which has a feedback to the system´s productivity. The decomposition process is controlled by environmental conditions, both biotoc and abiotic. Silvicultural management can lead to changes in these conditions, which subsequently may alter the decomposition process and ultimately the systems´productivity. Here, we investigated several of the factors affecting litter decomposition: 1) varying litter quality in different leaf species, 2) microorganisms in the absence and presence of meso - and macrofauna, 3) land use via forest management intensity, 4) exclusion of living roots by trenching and 5) species richness of the soil communities. To address these research goals we conducted a litter bag study in different forests varying in management by humans. We manipulated the meshsize of the litterbags (5 mm and 45µm) and the species of the leaf litter (either Norway maple, *Acer platanoides* L., or European beech, *Fagus sylvatica* L.). We found significant differences in litter decomposition between levels of the main effects mesh size and leaf litter species. Additionally, we found significant interactions between the leaf species type, the presence of meso- and macrofauna, and land use on the final litter mass. In contrast, neither species richness of the community nor the exclusion of living roots affected litter decomposition. Our results showed that the microorganisms alone and acting in concert with the larger decomposers preferred maple litter over beech litter, indicating that maple litter was of higher resource quality than beech litter. This result is consistent with their elemental

stoichiometry. Moreover, litter decomposition was higher when meso- and macrofauna had access to the leaf litter, suggesting facilitative interactions between meso- and macrofauna and the microbial community. Finally, we found a gradient from highest decomposition rates in the most intensively managed coniferous forests to lowest decomposition rates in the unmanaged beech forests. Our study thus provides striking insights into how major components of decomposition processes interact with each other managed ecosystems.

6.1. Introduction

Litter decomposition

Numerous resources and services that are of high value for mankind such as the provision of wood and timber, non-timber products, clean water and air, wildlife and preservation of biodiversity are provided by forest ecosystems (Fox 2000; Hooper *et al.* 2005; Balvanera *et al.* 2006). Hence, it is a major goal to understand ecosystem processes (such as nutrient cycling) in order to sustain the productivity and resilience of ecosystems that we depend on (Swift *et al.* 1979; Wolters 2000; Hooper *et al.* 2005; Balvanera *et al.* 2006). It has been acknowledged that soil organic matter plays a vital role in the maintenance of soil quality (Swift *et al.* 1979; Wolters 2000). In particular, the key factor that affetcs many soil functions and thus is of crucial relevance for the productivity of an ecosystem is the availability of nutrients (Swift *et al.* 1979; Wolters 2000). Fox (Fox 2000) summarized that soil quality can be defined as the capacity of the soil to support tree and plant growth. This originates from, e.g. the availability of organic matter, texture and mineralogy, all of which are soil properties (Carter *et al.* 1997; Fox 2000). The essential process for the transfer of nutrients and energy in ecosystems is litter decomposition (Swift *et al.* 1979; Irmler 2000). Litter decomposition fundamentally "*serves to reduce dead*" plant or animal "*residues to carbon dioxide and soil organic matter and to release nutrient elements for entry into soil food webs and*" eventually for the consumption "*by plants*" (Coleman 2004). Swift (Swift *et al*. 1979) described that the main organic inputs into the soil system come from organic materials washed out from other systems, leachate from plant cover and root exudates, animal corpses and faeces, and perhaps most importantly the direct return of nutrients from plants as litter fall.

However, belowground plant residues are a mixture of dead roots and a multitude of liquid compounds exuded by roots (Scheu & Setälä 2002). There is evidence that the input of belowground carbon by the root system is consumed by the majority of soil invertebrates in addition to the leaf litter input (Ruf *et al.* 2006; Pollierer *et al.* 2007). How these liquid root exudates affect litter decomposition by the decomposer community, however, remains unexplored.

Factors affecting the decomposition process

Climate and tree canopy characteristics are of major importance amongst the abiotic factors controlling litter decomposition, because they influence temperature, hydrology and the chemical composition of precipitation (Coûteaux *et al.* 1995; Aerts 1997; Hättenschwiler *et al.* 2005). Moreover, physical and chemical properties, specifically the contents of secondary metabolites (such as phenolic compounds like tannins, lignin, and the lignin-to-nitrogen ratio) and elemental ratios (such as ratios of nitrogen and phosphorus to carbon), exert control over rates of litter decomposition (Coûteaux *et al.* 1995; Aerts 1997; Hättenschwiler *et al.* 2005; Ågren *et al.* 2013). Microorganisms are accounted to the biotic factors that control litter decomposition, because they perform crucial roles in biogeochemical cycling and mediate the mineralization and immobilization of organic compounds (van der Heijden, Bardgett & van Straalen 2008). In addition, "*soil invertebrates are considered to play an important role in the process of litter decomposition*" (Coûteaux *et al.* 1995; Aerts 1997; Hättenschwiler *et al.* 2005; Bokhorst & Wardle 2013). Classically, the fauna of the soil community is differentiated into three size classes: the microfauna (< 0.2 mm), the mesofauna (0.2 mm - 2.0 mm) and the macrofauna (> 2 mm) (Swift *et al.* 1979; Wolters 2000). These three classes carry out different roles in mediating nutrient cycling and soil structure. Organisms of the microfauna regulate bacterial and fungal populations and alter the nutrient turnover, whereas the mesofauna additionally fragment plant residues. The macrofauna is able to modify the environment by its mechanical activity (Wolters 2000). The fragmentation and redistribution of organic material and the concurrent production of faeces facilitate microbial community activity (Wolters 2000; Scheu & Setälä 2002; Bokhorst & Wardle 2013). Recent studies have stressed the importance of macrofaunal species identity, abundance and activity for the mass loss of different leaf litter species (Hättenschwiler & Gasser 2005; Vos *et al.* 2011). Finally, land use such as forest management – which is

often not considered in decomposition studies - influences the soil and associated biota in various ways. Forest management practices like harvesting and site preparation result in soil displacement, compaction, organic matter loss, changes in microclimate, or acidification (Burger & Kelting 1999; Marshall 2000; Grigal 2000). Moreover, temperature and moisture conditions become more extreme through clear-cutting of forest sites (Marshall 2000). The anthropogenic nitrogen input by use of fertilizers is assumed to affect decomposition by suppression of the ligninolytic enzymes of microorganisms (Jandl *et al.* 2007). Modification "*in quality and quantity of litter, alteration of root exudates, leaching of some plant nutrients, and changes in the microclimate"* are the consequence (Prescott 1997; Marshall 2000). However, the addition of organic matter, improved drainage, and the use of fertilizers may improve soil conditions (Burger & Kelting 1999) and thus enhance decomposition. In sum, forest management affects microbial activity and species composition in the soil and thus the soil productivity.

Study overview and questions

In this study, we used "*litterbags containing a*" defined "*mass of leaf litter placed on the forest floor*" to measure litter mass loss by decomposition (Coleman 2004). Litterbags are a major technique to examine the breakdown of litter (Swift *et al.* 1979; Bokhorst & Wardle 2013). This technique has been shown to be useful in analyzing differences between various factors such as leaf species and habitat or forest types (Coleman 2004). We investigated 1) effects of litter quality on decomposition using litter (varying in elemental contents and thus stoichiometry) from two common deciduous tree species - Norway maple and European beech. If soil detritivores preferentially discriminate in their feeding between the two leaf species, the final litter masses will differ between the two leaf species. Further, different mesh sizes allowed exclusion of specific animal size classes. This enabled us to 2) disentangle effects between soil decomposer groups on litter decomposition. More specifically, by varying mesh size of litterbags, we compared communities with soil macro- and mesofauna present to communities with only microorganisms where the larger fauna were excluded. Our study was replicated across forest types varying in main tree species and management practice, enabling us to 3) examine effects of different land-use intensities on decomposition. In all forest types and plots, our litterbags were embedded in a trenching installation. This allowed us to 4) discern root exclusion effects on decomposition. Finally, we included data from previous

studies on soil communities of our study plots. We thus investigated 5) how macro- and mesofauna species richness contributed to the leaf litter mass loss.

6.1. Methods

Study sites

The decomposition experiment was conducted on forest plots in two different regions in Germany: in the Schorfheide-Chorin UNESCO Biosphere Reserve in North-Eastern Germany (52° 57′ 0′′ N, 13° 37′ 0′′ E) and in the Hainich National Park (51° 5′ 48′′ N, 10° 23′ 27′′ E) and the surrounding area Hainich-Dün in central Germany (Fischer *et al.* 2010). These regions form part of an integrative research platform (www.biodiversity-exploraties.de Fischer *et al.* 2010). Schorfheide-Chorin (or simply Schorfheide) is situated in a geologically young glacial landscape (3-140 m a.s.l) with regional annual mean characteristics of 500-600 mm precipitation and 8-8.5 °C temperature. Hainich-Dün on the other hand is situated on calcareous bedrock (285-550 m a.s.l.), with a mean annual precipitation of 500-800 mm and 6.5-8 °C temperature (Fischer *et al.* 2010). In both regions 16 forest plots were chosen along a gradient of management intensity, characterized by a gradient of rotation time of cutting or harvesting events, yielding 32 plots in total. This gradient spanned over four different forest types: three beech (Fagus sylvatica L.) forest types including unmanaged beech (old grown stands, hereafter beech unmanaged), old beech and young managed beech (approximate age of 70 and 30 years, hereafter beech old and beech young, respectively), and intensively managed coniferous forests (hereafter conifer) (Fischer *et al.* 2010). The latter were represented by spruce (*Picea abies* L.) in the Hainich-Dün, and by Scots Pine (*Pinus sylvestris* L.) in the Schorfheide (Fischer *et al.* 2010).

Experimental design

Litterbags with two different mesh sizes were used to study the effect of animal presence and absence: the micro-mesh (45 µm) prevented animals from entering the litterbags and allowed litter decomposition by microorganisms only. The macro-mesh (5 mm) allowed all meso- and macrofauna up to a body diameter of 5 mm to access the litterbag and thus

litter decomposition could be carried out by the full decomposer community. For each mesh size, litterbags were filled with five gram dried leaf litter material of two single leaf species representing four different combinations. The leaf species used were maple and beech (see below). These litterbags were embedded in each treatment on each plot. The treatment refers to a root exclusion experiment (i.e., trenching) that was installed on each plot in fall 2011. The subplots of the trenching experiment (treatments: trenched and untrenched control) measured 1.20 m^2. For the trenching experiment, roots were cut 50 cm deep down into the soil around the trenching plots and plastic boards were embedded as a barrier to prevent roots growing in again. Aboveground was a protrusion of 5 cm of the boards. To achieve equal climatic conditions in the untrenched control, the subplot was framed with a 5 cm high plastic board. Aboveground vegetation in the trenched subplots was clipped periodically during the growing seasons. Additionally, soil water content was controlled by periodically taking small soil cores (diameter 5cm, depth 10cm). Soil cores were measured with a precision scale before and after drying (12h at 180°C). The difference between wet and dry weight equals the amount of water content. Differences in soil water contents of trenched plots compared to untrenched controls were calculated in liter for the whole plot. The calculated amount of water was applied to equal soil water contents of treatments and maintain relatively constant water contents. The combination of the plots (32), the treatment (± trenching), the two leaf species and the two mesh sizes summed up to an amount of 256 litterbags. The litterbags were placed in the plots in February 2012 and were collected in May 2013. Due to loss or damage, only 254 litterbags were used in this study.

Leaf litter

Litter samples of beech and Norway maple (*Acer platanoides* L., hereafter maple) were collected in Hainich National Park in autumn 2010. After sampling, the litter was air dried, sorted into species and stored under room conditions until further usage. Randomly chosen samples (six leaves of each species) were dried at 60°C until no further weight was lost and ground to fine powder with a ball mill (Retsch Mixer Mill MM200, Haan, Germany). Prior to the elemental analysis the powder from the three leaves of each species was merged yielding two mixed samples (i.e., the data represent the average conditions of these leaves). Elemental analyses were conducted from the Albrecht-von-Haller Institute for Plant Sciences, Göttingen. Total carbon (C) and nitrogen (N) were

analyzed by an automated CHNSO analyzer (ElementarVario EL III, Elementar Analysensysteme GmbH, Hanau, GE) from an amount of five milligrams powder material per sample. For the analysis of eleven other elements [i.e., phosphorus (P), calcium (Ca), sodium (Na), potassium (K), manganese (Mn), magnesium (Mg), iron (Fe), aluminium (Al), sulphur (S), copper (Cu) and zinc (Zn)] 50 mg of each sample was digested by adding 2 ml of 65% nitric acid (HNO_3) in teflon containers and pressure digested at 185°C for 9 h (6-AM autoclave system, Loftfields Analytical Solutions GbR, Neu Eichenberg, GE). Samples were filtered and rinsed quantitatively with double distilled H_2O into 50 ml volumetric flasks and analyzed by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) (Optima 5300 DV, PerkinElmer Inc., Wellesley, MA, USA). From these measurements we obtained equal litter quality between maple and beech considering either single elements (figure 6.S1) or carbon-to-element ratios (figure 6.S2). Further conducted chemical measurements were analyses of contents of phenols, total tannins, lignin and cellulose.

After the collection of the litterbags in May 2013, they were air dried for several weeks before sorting and separation of original leaf material and leaf pieces from soil residues and foreign plant material took place. The cleaned litter samples were packed into paper bags to ensure no loss or mixture of samples. Paper bags containing sample material were than dried in a drying oven for three days at 60°C and weighed afterwards using precision scales with 0.1 mg accuracy. A random sample of 30 empty paper bags was weighed to gain an average paper bag mass. This average value was subtracted from all dry weight measurements to obtain the final sample dry masses.

Data analyses

We examined the dependence of decomposition (expressed as final litter masses, a continuous variable) on the explanatory variables forest type (categorical), mesh size (categorical), leaf species (categorical), trenching (i.e., the root exclusion treatment, a categorical variable) and species richness (continuous). Statistical analyses were performed using the statistical program R (version 3.1.0, R Core Team 2014). We inspected the statistical premises for a linear regression and analysis of variance with the Shapiro-Wilk test and Fligner test for the main effects against the residuals. The data were not normally distributed and heteroscedastic. To increase normality and homogeneity of variances, the litter data were $\log_{10}$ transformed for further analyses. Data of soil

invertebrate species occurring on the forest plots of the experiment were taken from a large dataset on soil communities (Klarner *et al.* 2014; Ott *et al.* 2014a; b; Ehnes *et al.* 2014). Different sampling methods were used in spring 2008 and 2011 to obtain a complete database on the soil animal community in the plots: soil sampling with soil corers, earthworm extraction using mustard solution and sieving of ground covering leaf litter material (Klarner *et al.* 2014; Ott *et al.* 2014a; b; Ehnes *et al.* 2014). For detailed description of the sampling methods, species identification and species data establishment see (Klarner *et al.* 2014; Ott *et al.* 2014a; b; Ehnes *et al.* 2014). We obtained total species richness by quantifying the total number of species per plot from individual entries on species or morphospecies level.

In a series of one-way analyses of variance (ANOVA) we examined the importance of the categorical explanatory main effects on leaf litter mass loss. However, these main effects were not independent from each other, as they were partially spatially autocorrelated and grouped in landscape blocks. Furthermore, because our explanatory variables were a combination of factorial and continuous variables, an analysis of covariance (ANCOVA) classically would have been the statistical approach of choice. We applied linear mixed effects models (function "lme", Pinheiro *et al.* 2012) to overcome issues with pseudo-replication and to take the landscape blocks into account. To do so, the landscape blocks and the spatial autocorrelation were set as random effects in a nested annotation from the highest to the lowest spatial order: region/forest type/plot/trenching. To identify which of the explanatory variables (fixed effects) explained the most variation in litter decomposition rates, we used a full model that included all explanatory variables and all interactions. Further we applied the subsequent procedure that we modified after successful application in previous studies (Ott *et al.* 2014a; b). In addition to the full model, we used a null model (i.e., intercept-only) model, which includes no explanatory variable. On these two models, we applied a modification of an automated step algorithm (function "stepAIC", Venables & Ripley 2002; mode of stepwise search "both", method = restricted maximum likelihood) in order to obtain the minimal adequate model by using a corrected Akaike´s Information Criterion (AICc [Burnham & Anderson 2004]). Thus, we obtained two additional models - an increase model (step function used on the null model) and a decrease model (step function used on the full model). Since a restricted maximum likelihood is not defined for the stepAIC function, we ran the linear mixed effect models with unrestricted maximum likelihood (method = ML). After model selection procedure, we applied the restricted maximum

likelihood method (method = REML) to the best model in order to obtain correctly estimated model coefficients (Zuur *et al.* 2009). AICc takes into account when sample sizes are small relative to the number of variables in the model, but converges to AIC at larger sample sizes (Burnham & Anderson 2004). We used the function "glht - general linear hypothesis test" (package "multcomp", Hothorn, Bretz & Westfall 2008) to apply the posthoc test "Tukey´s HSD (Honestly Significant Difference)" after linear mixed effects models.

6.2. Results

Analyses of variance of the main effects (one-way)

The rates of litter decomposition between mesh sizes were significantly different - the macro-mesh bags had a lower final litter mass (2.85 ± 0.97; mean and standard deviation in milligram dry weight) than the micro-mesh bags (3.24 ± 0.44 g; table 6.1, figure 6.1d). Thus, the average mass loss was 42.9 % in macro-mesh and 35.1 % in micro-mesh bags. Final litter mass was significantly different between the leaf litter species whereby maple had lower final litter masses (2.51 ± 0.73 g) than beech (3.59 ± 0.28 g; table 6.1, figure 6.1c). This was characterized by an average mass loss of 49.9 % in maple and of 28.1 % in beech. The root exclusion treatment revealed no significant effects on final litter masses between control (3.03 ± 0.74 g) and trenching units (3.06 ± 0.81 g; table 6.1, figure 6.1b), which yielded a litter mass loss of 39.3 % in the controls and 38.8 % in the trenching. Furthermore, we found no overall significant effects of forest types on litter decomposition (table 6.1, figure 6.1a). Nevertheless, final litter masses were lowest in conifer (2.93 ± 0.95 g) and higher in young beech (2.97 ± 0.76 g), old beech (3.08 ± 0.65 g), and in unmanaged beech (3.21 ± 0.70 g). These values yielded a mass loss of 41.3 % in coniferous forests, 40.6 % in young beech, 38.5 % in old beech and 35.9 % in unmanaged beech forests.

Table 6.1: Results of one-way ANOVAs testing separately the main predictors of the final leaf litter mass.

Predictor		DF*	SSq†	MSq‡	F-value	p-value	
Forest type		3	0.168	0.06	2.01	0.11	
	Residuals	250	6.971	0.03			
Trenching		1	0.001	<0.01	0.04	0.85	
	Residuals	252	7.138	0.03			
Mesh size		1	0.536	0.54	20.45	<0.001	***
	Residuals	252	6.603	0.03			
Leaf species		1	2.198	2.20	112.10	<0.001	***
	Residuals	252	4.941	0.02			

* Degrees of freedom, † Sum of squares, ‡ Mean squares. Significance codes: *** < 0.001, ** < 0.01, * < 0.05, . < 0.1.

Table 6.2: Results of model selection process of linear mixed effects models examining interactive effects of mesh size, leaf litter species, forest type, trenching and species richness on the final leaf litter mass. ΔAIC = 0 shows the models describing the results best; the higher the ΔAIC the greater is the deviation from the best model(s).

Model	DF*	AIC	ΔAIC
Null	6	-174.41	175.67
Increase	21	-350.08	0
Full	69	-301.68	48.40
Decrease	21	-350.08	0

Table 6.3: Results of F-statistic of the best linear mixed effects model including interactive effects of mesh size, leaf litter species and forest type on the final leaf litter mass.

Parameter	numDF*	denDF*	F-value	p-value
Intercept	1	178	2490.63	<.0001
Mesh size	1	178	43.60	<.0001
Leaf species	1	178	180.45	<.0001
Forest type	3	27	2.63	0.071
Mesh size x Leaf species	1	178	45.46	<.0001
Mesh size x Forest type	3	178	3.72	0.013
Leaf species x Forest type	3	178	4.80	0.003
Mesh size x Leaf species x Forest type	3	178	2.60	0.054

* numerator and denominator Degrees of freedom.

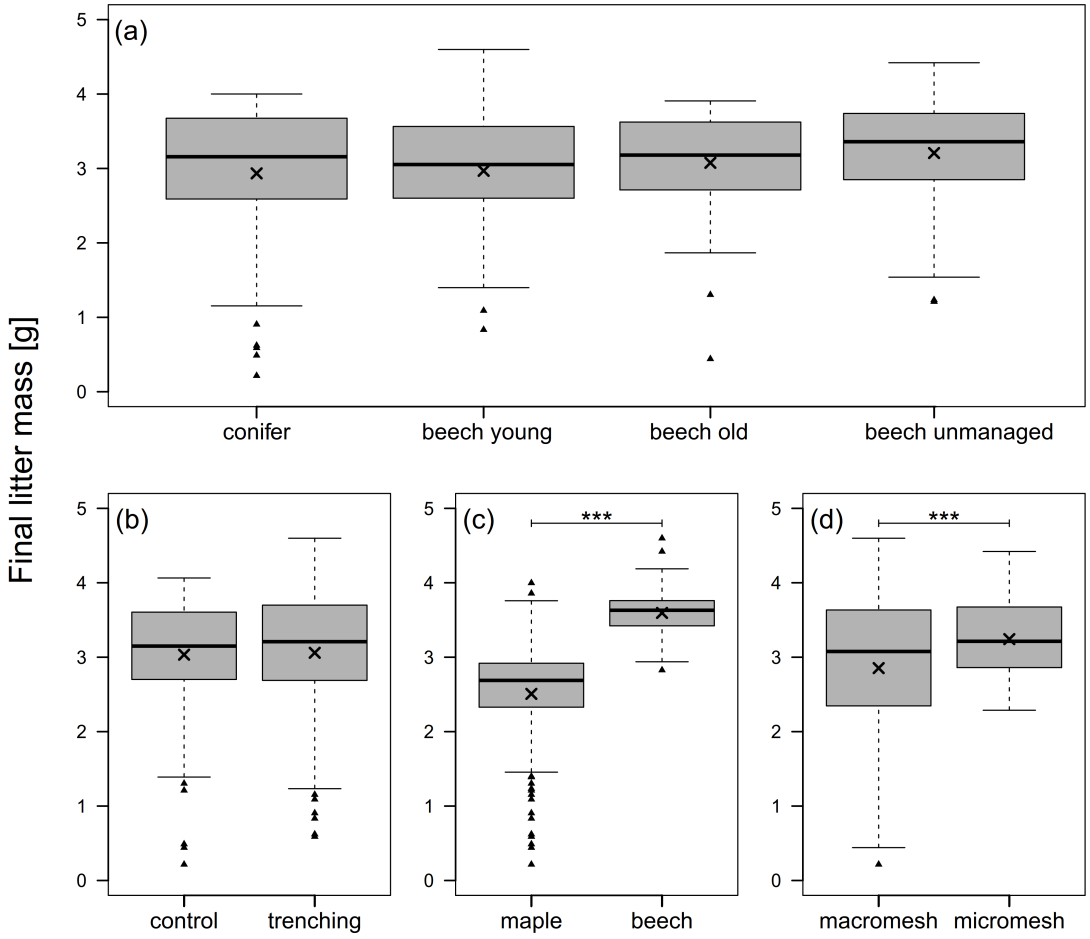

Figure 6.1: Differences across factor levels separately for each of the main effects on final litter mass (dry weight): a) forest types, b) trenching, c) leaf litter species and d) mesh size. Horizontal lines in the grey boxes indicate medians, crosses indicate arithmetic means and triangles indicate outliers. Stars (***) indicate significant differences between treatment means ($p < 0.05$; posthoc Tukey test). See table 6.1 for ANVOA results.

Linear mixed effects models on interacting predictors

In the model selection procedure, the increase and the decrease models performed best: both models obtained a delta AIC (ΔAIC) of zero (table 6.2). Thus, both models were indistinguishable from each other and in their final model structure included leaf species, forest type and mesh size as explanatory variables. Species richness and trenching were dropped as explanatory variables. This implicated that either one of the models could be used as the minimal adequate model describing effects on final litter mass correctly. The three-way interaction of all explanatory variables had no significant effect on litter decomposition (table 6.3, table 6.S1), whereas both leaf species and mesh size

independently and interactively affected litter decomposition, significantly. Forest type showed significant effects in the two-way interactions (table 6.3, table 6.S1). This translated into significant differences across factor levels (figure 6.2, table 6.S2) whereby macro-mesh bags containing maple litter in conifer differed significantly from all other treatments except for bags in beech young (figure 6.2, letters "a"). Macro-mesh bags containing maple litter in beech young, beech old and beech unmanaged were similar in litter mass loss (figure 6.2, letters "b") indicating no differences among these forest types. The macro-mesh bags of beech old yielded very similar litter mass loss to micro-mesh bags of conifer, beech young and beech old (figure 6.2, letters "c"). Regarding maple litter, all micro-mesh bags and macro-mesh bags in beech unmanaged yielded similar mass loss (figure 6.2, letters "d"). Both groupings point to equality in litter mass loss of the macro-mesh bags with all the maple micro-mesh bags from less intense managed forest types. All bags containing beech litter and micro-mesh bags containing maple litter exhibited similar levels of litter mass loss and thus were not significantly different from each other (figure 6.2, letters "e"). Taken together, these results suggest that when macro-mesh bags contained maple leaf litter, mass loss was greatest on intensively managed forest types.

6.3. Discussion

In this litterbag study, we investigated the combined effects of the decomposer community structure (examined by experimentally varying mesh sizes) and diversity, and root exclusion on the decomposition of the leaf litter of Norway maple and European beech across a gradient of managed forest types. We found that decomposition was significantly different between the two types of leaf litter (final lower litter masses in litterbags containing maple) and mesh size (final lower litter masses in litterbags with macro-mesh) when we considered only main effects. Furthermore, we revealed significant interactions of leaf litter species, mesh size and forest type (representing human management) on litter decomposition. Final litter masses were lowest in litterbags containing maple litter where macro- and mesofauna were present (i.e., macro-mesh bags) and in forests with high management intensity (conifer and young beech forests). However, we found no effect of root exclusion or species richness on the decomposition of litter.

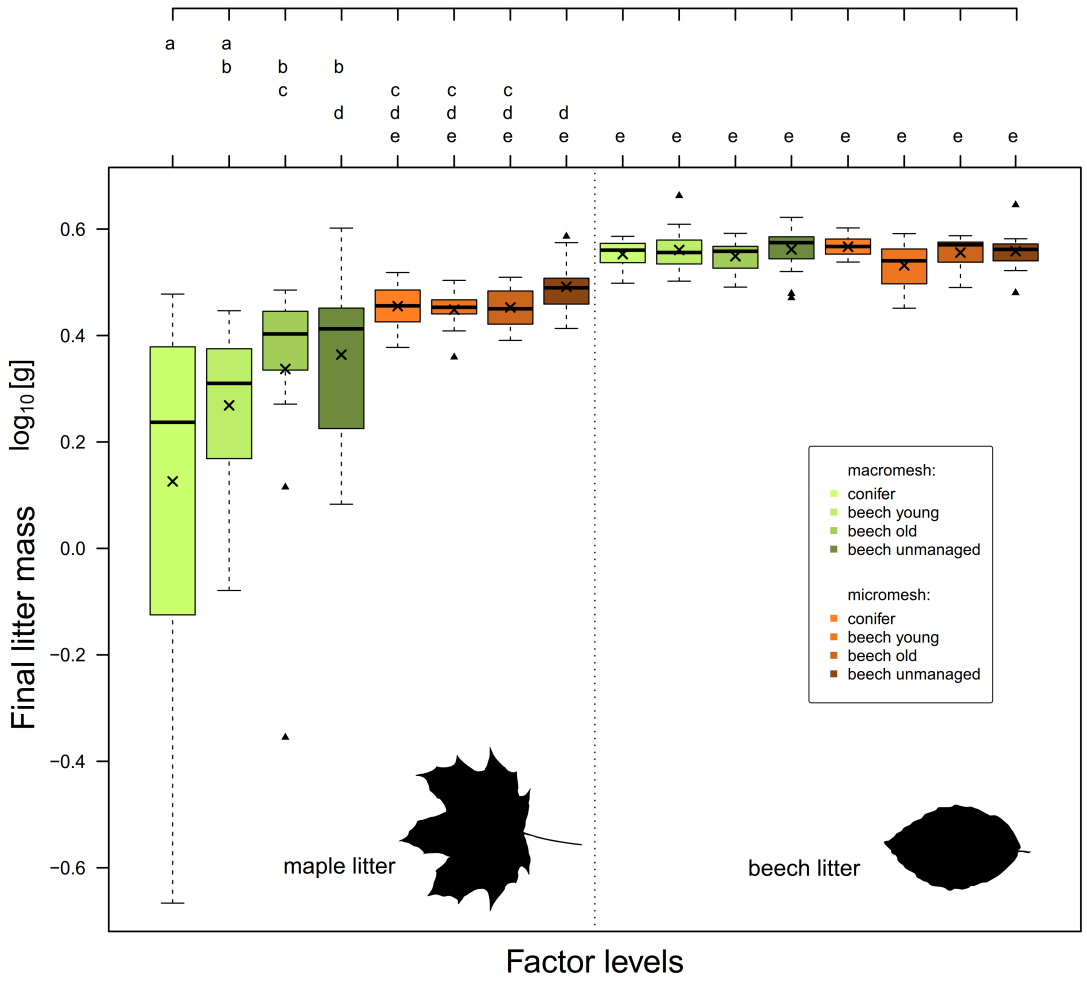

Figure 6.2: Differences across factor levels of interacting main effects on final litter mass (log_{10} dry weight): the left half of the plot corresponds to treatments with maple as the leaf litter species, whereas the right half corresponds to treatments with beech. Colors indicate mesh sizes: green colors indicate the macro-mesh and brown colors indicate the micro-mesh. The different forest types are symbolized by the gradients of these colors with respect of the management intensity ranging from light green and light brown (conifer, most intense management) to dark green and dark brown (unmanaged stands with beech as the main tree species). Horizontal lines in the boxes indicate medians, crosses indicate arithmetic means and triangles indicate outliers. Letters above each box outside of the figure correspond to posthoc Tukey test after linear mixed effects model, supporting information table 6.S2. Same letters indicate no significant difference, whereas different letters indicate significant differences among treatment means ($p < 0.05$). See tables 6.3 and supporting information table 6.S1 for results.

Effects of litter quality on decomposition

The soil community preferred leaf litter of maple in all cases over leaf litter of beech (figures 6.1 & 6.2; tables 6.1 & 6.3). We account this finding of food preference of the detritivorous soil fauna to result from the higher resource quality of maple litter compared to beech litter. Previous studies already reported beech litter to slowly decompose (Swift

et al. 1979; Hättenschwiler & Gasser 2005; Hobbie *et al.* 2006) The resource quality and thus the leaf litter palatability is derived by the chemical composition and the physical property of the leave, both of which are determined by contents such as the C:N ratio, phenolic acids and lignin (Cornelissen 1996; Aerts 1997; Hättenschwiler & Gasser 2005; Ågren *et al.* 2013). Moreover, other elements such as calcium play an important role in the decomposition process: the abundance of earthworms increases with litter calcium, which has a feedback to increased litter decomposition (Hobbie *et al.* 2006). Both leaf litter species in our study initially had equal amounts of carbon, nitrogen and calcium and the corresponding ratios of these elements. Accordingly, decomposers should show no preference for one of the leaf litter species, resulting in equal mass losses of leaf litter. Recent studies highlight the importance of sodium for decomposers (Kaspari & Yanoviak 2009; Kaspari *et al.* 2009; Clay *et al.* 2014). The Norway maple in our study initially had a lower carbon-to-sodium ratio than beech (figure 6.S2) which points to a possible preference of decomposers for maple. While we are lacking clear support for certain stoichiometric ratios determining decomposition in our study, we were able to determine that leaf litter identity, i.e. maple, in part explained the differences in final litter masses.

Litter decomposition in the pre- & absence of soil macro- & mesofauna

After 14 months at the end of our experiment, mass loss in litterbags with 5 mm mesh size (i.e. the macro-mesh) had significant lower final litter masses than litterbags with micro-mesh (45 µm) that prevented macro-and mesofauna from entering the bags (figure 6.1 & 6.2; tables 6.1 & 6.3). Thus, litter decomposition was enhanced in macro-mesh litterbags and there was an indication for a strong effect of the presence of larger soil invertebrates on litter decomposition. The contribution of the microorganisms to the litter decomposition process was 35.1 % loss of the initial litter mass.In contrast, the activity of the soil community including macro- and mesofauna in addition to microorganisms increased decomposition about 7.8 % to a mass loss of 42.9 %. Thus, the presence of soil fauna with a body diameter larger than 45 µm facilitated decomposition of about 22.2% of the activity of microorganisms. The biochemical degradation of organic litter is done by microorganisms of the soil community and the larger soil fauna is important for pre-conditioning the litter and facilitating microbial action (Coleman 2004). This facilitation is due to enhanced accessibility of nutrients by the fragmentation and shredding of leaves into small pieces with larger surface area and a stimulation of bacterial growth by the

production of faeces (Wolters 2000; Scheu & Setälä 2002). However, the soil fauna exhibits a direct interaction via selective grazing on the microbial community (Faber & Verhoef 1991; Wolters 2000), which is part of a classical debate (Cummins 1974). Moreover, the contribution of the soil fauna is not an experimental artefact of the litterbag study system (Bokhorst & Wardle 2013). Taken together, our results showed that the presence of soil invertebrates enhanced litter decomposition, thus support the conclusions of prior studies (Setälä & Huhta 1990; Makkonen *et al.* 2012; Handa *et al.* 2014).

Effects of land use intensity across forest types on litter decomposition

We found a clear pattern along the land-use gradient, in which the litter mass loss increased with increasing management intensity (figure 6.1 & 6.2; tables 6.1 & 6.3). These results suggest that land use like harvesting in forests enhances decomposition, thus supporting the finding of previous studies and (Marshall 2000; Jandl *et al.* 2007). One mechanism explaining this is higher microbial activity due to increased soil temperature and soil moisture after clear cutting subsequently leads toan enhanced decomposition process (Prescott 1997; Marshall 2000). More generally, some forest management practices result in heavily altered soil conditions that affect soil organisms (Burger & Kelting 1999; Marshall 2000; Grigal 2000). Impacts on species composition in the soil, and thus on the soil productivity, seem to be very likely under these circumstances. Nevertheless, other forest management practices may improve soil condition (Burger & Kelting 1999) and thus enhance decomposition. Moreover, anthropogenic nitrogen input might promote decomposition of fresh litter but suppress decomposition of old litter (Jandl *et al.* 2007). Finally, Prescott (1997) found higher decomposition rates in unmanaged forests, which is contrary to the results of this study. This might reflect the overall complex effects of high land-use intensity on litter decomposition, as discussed above in relation to other studies. However, it should be considered that the gradient of management intensity along the forest types might be masked by differences in the main tree species. Specifically, in our study the most intensively used forests were coniferous forest and the three types with lower land use intensities were forests mainly formed by deciduous trees (beech). The possible land-use effects thus could be biased by the contrast of main tree species, i.e. the differences in the forest type instead. Since there were no significant differences among the beech forests in any mesh size category, the higher decomposition rates in the coniferous forests might

result from the poor resource quality provided by the environment of coniferous trees compared to the embedded leaf litter species of the deciduous trees. In particular, high lignin and low nitrogen content and the thick waxy cuticle (Dickinson & Pugh 1974) of coniferous litter make it a resource with low palatability. Therefore, it is very likely that if deciduous leaf litter is placed in coniferous forest stands it is decomposed first. The highest mass loss of maple litter and relatively high mass losses of beech litter in coniferous forests compared to the beech forests suggested such a preference of deciduous leaf litter to coniferous leaf litter by the soil food-web. However, needle litter in coniferous forest forms thick layers and lowers the soil pH, which results in communities dominated by acidophilic fungi and mesofauna (Dickinson & Pugh 1974; Klarner *et al.* 2014). Species of the macrofauna with a high demand of soil bases, including most earthworms, are absent or present in low densities in coniferous forests (Dickinson & Pugh 1974; Klarner *et al.* 2014). Nevertheless, the high quality maple litter had highest mass loss when larger soil fauna had access to the litter, irrespective of the forest type. In summary, we obtained no clear evidence wether forest management instensity or simply differences in forest composition were more important for the fast litter mass loss in the coniferous stands.

Litter decomposition under the aspect of root exclusion

Important resources other than leaf litter the soil community relies on are considered to be exudates and litter of roots (Ruf *et al.* 2006; Pollierer *et al.* 2007). Studies with root chambers have demonstrated that living roots can have positive effects on microbial biomass and additionally enhance the accessibility of soil carbon, which can lead to enhanced decomposition in maize (Helal & Sauerbeck 1986) and rye (Cheng & Coleman 1990). Trenching removes carbon sources such as root exudates (Bond-Lamberty *et al.* 2011), thus decreasing the availability of carbon as well as microbial carbon and nitrogen (Kuzyakov 2006). As such, we expected negative effects of our trenching experimental treatment, yielding decreased litter decomposition. However, the exclusion of living roots showed no effect on litter decomposition in our study (figure 6.1 & 6.2; tables 6.1 & 6.3). It should be noted that there are several methodological issues with the trenching method (Hanson *et al.* 2000; Kuzyakov 2006; Bond-Lamberty *et al.* 2011), none of which we can completely exclude. We assume the weak effect of trenching on decomposition resulted

from root residues in the trenched areas. Prior to the onset of the experiment, root residues cannot be removed from the trenched area and, thus, may compensate for the missing carbon input from the root exudates as a resource for the soil organisms. Effects of missing carbon input from belowground sources may emerge when the root residues are removed through consumption by the soil community. However, this would presumably occur on a longer time scale than that seen in our study.

Does species richness affect litter decomposition?

Our results indicate that there is no general relationship between the total species richness and the decomposition process (figure 6.1 & 6.2; tables 6.1 & 6.3). Moreover, the lowest mean species richness was 105 species in conifer forest compared to the highest mean species richness of 117 species in an intensively managed beech forest (beech young) and to on average 107 species in old and unmanaged beech. This contradicts expectations of a positive relationship between species richness and litter decomposition, because low decomposition rates occurred in the beech forests where species richness was higher than in conifers. Among the species sampled, many important functional groups were present, including macro - and mesofauna detritivores and macro- and mesofauna predators. However, the species number per se does not reveal which of the functional groups dominates within the forests, as factors such as functional dissimilarity might drive ecosystem process rates (Heemsbergen *et al.* 2004). Furthermore, species identities, particularly of the macrofauna, influence the microbial composition and activity in the soil system and thus the decomposition rates (Hättenschwiler & Gasser 2005; Vos *et al.* 2011). For example, the importance of community composition of soil mesofauna has been reported for springtail species (Cragg and Bardgett, 2001). A possible explanation for the weak effect of species richness on litter decomposition could be the hypothesized generalized feeding behavior of decomposers (Andrén, Bengtsson & Clarholm 1995; Wolters 2001; Scheu & Setälä 2002). Members of a certain functional group are considered to provide equal contribution to soil processes. Therefore, high redundancy in the use of resources can be expected among soil animals (Andrén *et al.* 1995; Wolters 2001; Scheu & Setälä 2002). This redundancy would translate into a weak relationship between species richness and litter decomposition (Andrén *et al.* 1995; Wolters 2001; Scheu & Setälä 2002), because a relatively low number of species present would maintain all functions. Further investigations that include functional group richness or biomass

densities could improve current knowledge on how animal diversity affects ecosystem processes such as litter decomposition.

Conclusion

Litter decomposition is a crucial ecological function in (forest) ecosystems (Hooper *et al.* 2005; Balvanera *et al.* 2006) that is mediated by decomposer communities, which can be directly linked to nutrient cycling and feeds back to the productivity of forests (Swift *et al.* 1979; Wolters 2000; Scheu & Setälä 2002; Hättenschwiler *et al.* 2005). Here, we demonstrated that intensive forest management (conifer and young beech forests), the type of leaf litter (whether it is maple or beech) and the presence of meso- and macrofauna in addition to microbial decomposers affect litter decomposition. Interestingly, we found no effect of root exclusion or species richness on the decomposition of litter. Root exclusion experiments using trenching methods could have the potential to reveal the effect of reduced carbon input from belowground sources on litter decomposition. Further studies including the relative abundance and biomass of functional groups (Heemsbergen *et al.* 2004) and the relative abundances of species (Hättenschwiler & Gasser 2005; Vos *et al.* 2011) could improve current knowledge on how complex and diverse decomposer communities affect ecosystem processes such as litter decomposition (Makkonen *et al.* 2012; Handa *et al.* 2014). Furthermore, parallel manipulations of horizontal (species richness within trophic levels) and vertical diversity (trophic level richness), including mixtures of different leaf litter (Gartner & Cardon 2004; Hättenschwiler & Gasser 2005), are key to revealing the complex patterns that are not only present in soil during decomposition (Duffy *et al.* 2007; Srivastava *et al.* 2009b; Gessner *et al.* 2010). We believe that addressing these factors acting in concert is a very challenging, but very promising and necessary task for future studies.

6.4. Acknowledgements

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Part III

General discussion

Chapter 7.

Synopsis

7.1. Intro

The metabolic theory of ecology (or simply metabolic theory[2]) and the theory of ecological stoichiometry (or simply ecological stoichiometry) are important theories that explore and describe various patterns determining species interactions, density of populations, complex food webs and entire ecosystems (Lotka 1925; Sterner & Elser 2002; Brown *et al.* 2004, 2012; Kaspari 2012). However, both theories underlie some limitations and an integrative approach will substantially increase their predictive power and help to overcome the respective limitations (Allen & Gillooly 2009). Models of metabolic theory include "components that are related to the supply and function of essential elements" (Kaspari 2012). Thus, metabolic theory, in principle, is capable to cope with stoichiometric constrains on metabolic rates (Brown *et al.* 2004). Surprisingly, a combined perspective has rarely been addressed (but see Allen & Gillooly 2009 for an exception).

In the research chapters presented in this thesis, I studied the interplay of important variables considered in metabolic theory and ecological stoichiometry, i.e. decomposer body masses and the stoichiometry of leaf-litter resources, respectively. I disentangled how this interplay affected interactions at the level of individual feeding and how this scaled up from communities to whole food webs. The systematic variation of woodlice body masses and the integration of environmental temperature and litter stoichiometry in a functional response represents a novel step in the research field of species interactions (Chapter 2). I demonstrated that *per capita* consumption rates of a terrestrial woodlice species depended on woodlice body mass, temperature and varied with litter quality. This

[2] The metabolic theory of ecology is often referred to as the metabolic theory, even though other theories are abbreviated differently (theory of ecological stoichiometry, becomes ecological stoichiometry) and a similar abbreviation ("Metabolic Ecology", Sibly et al. (2012)) would also be possible. For clarity and convenience of the reader, I will use the notation metabolic theory throughout my thesis.

highlights already the importance of an interplay between those predictors. In Chapter 3, I accounted for this interdependency of factors in a microcosm study. I innovatively combined two promising experimental designs and investigated how diversity effects on decomposition are influenced by body mass and resource stoichiometry. I revealed that mechanisms of allometry, stoichiometry and diversity are interwoven and affected the communities´ performance in achieving the ecosystem function of decomposition.

Consequently, after I found these relationships across trophic levels (Chapter 3), I increased the complexity of the target communities to entire soil food webs (Chapters 4 and 5). Using a dataset of forest soil communities that consisted of several trophic levels, taxonomic and functional groups, I first developed a novel conceptional framework to predict population densities from a combination of allometric and stoichiometric variables (Chapter 4). I found that the scaling of biomass densities with population-averaged body masses was not independent of litter quality (i.e., scaled interactively).

Applying this framework, I revealed that the scaling of biomass with population-averaged body mass in the phylogenetic sub-groups of the same dataset depended on either litter stoichiometry or habitat metrics or both (Chapter 5). Overall, this framework successfully elucidated how population densities across multiple trophic levels of soil communities are constrained by the elemental stoichiometry of the leaf litter. In Chapter 6, I addressed the effects of body mass and litter quality in a litterbag study across differently managed forest types. I revealed enhanced litter-mass loss in the presence of larger decomposers and on the high quality litter, which corroborates all of my previous findings.

Summarizing, I studied in experiments in the laboratory and field, as well as with analytical work on population densities under the umbrella of an integrative framework: the interplay of allometric and stoichiometric variables, which are major components of the metabolic theory and the ecological stoichiometry.

7.2. Discussion

A mechanistic tool that had so far not been used to quantify decomposer consumption is the framework of the consumer-resource functional response (Holling 1959; Brose 2010; Rall *et al.* 2012). I applied this concept to the feeding of a terrestrial woodlice species on leaf litter in a laboratory experiment (Chapter 2). In contrast to other approaches that

quantified decomposer feeding (Hättenschwiler & Bretscher 2001; Hedde *et al.* 2007), the functional response framework intrinsically relates *per capita* consumer feeding strength to resource density (Holling 1959; Brose 2010). Moreover, the two mechanisms behind the functional response concept, attack rates and handling times, depend on body mass and temperature (Yodzis & Innes 1992; Brown *et al.* 2004; Brose 2010; Englund *et al.* 2011; Rall *et al.* 2012). This general scaling makes the decomposer consumption, as derived by the functional response, directly comparable to those traditionally measured in predator-prey systems (Vucic-Pestic *et al.* 2010b; Lang *et al.* 2011; Rall *et al.* 2011, 2012a; Kalinkat *et al.* 2013b). My results that attack rates and handling times scaled with body masses and temperature are consistent with metabolic theory (Yodzis & Innes 1992; Gillooly *et al.* 2001; Brown *et al.* 2004; Rall *et al.* 2012). Furthermore, these scaling relationships depended on litter quality as revealed by differences in the attack rates of small and large woodlice. First, these differences suggested compensatory feeding of large woodlice and avoidance behavior of small woodlice. Second, the demand for an increased consumption may be explained by the higher metabolism of woodlice at higher temperatures. I was able to compare woodlice handling times to metabolic rates via budgets of activation energies (Brown *et al.* 2004; Rall *et al.* 2010; Ehnes *et al.* 2011). I found that woodlice consumption rates "*should increase more strongly with warming than their metabolism*" (Ott *et al.* 2012), which is in contrast to studies in which predators failed to cover their warming induced increase in metabolic demands (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011; Ehnes *et al.* 2011). I concluded that if my finding generalizes, "*this may lead to increased population growth of decomposers*" owing to accelerated feeding and reduced top-down pressure by predators (Ott *et al.* 2012). Altogether, these results (Chapter 2) illustrate that effects "*of consumer body mass, temperature and resource stoichiometry*" on consumption rates "*are not independent of each other*", and interactively affect rates of litter consumption (Ott *et al.* 2012).

In Chapter 3, I investigated how this interdependency of factors affected decomposition, along gradients of horizontal and vertical diversity in a mesocosm experiment under controlled laboratory conditions. Following the allometric design by Schneider *et al.* (Schneider *et al.* 2012; Schneider & Brose 2013), I calculated species abundances (i.e. the numeric density of individuals of each species in the microcosms) in dependence of allometric scaling (Damuth 1981; Peters 1983; Meehan 2006a; Ehnes *et al.* 2014). This design, in combination with the differing stoichiometry of the leaf litter, yielded constraints on the invertebrate community on all trophic levels. Moreover, the

combination of the allometrically constraint community with the random partitions design (Bell *et al.* 2009) allowed to discriminate between diversity effects in and across trophic levels on ecosystem functioning: Total diversity (i.e., combined decomposer and predator richness) affected decomposition along the predicted quality gradient of resources (ranked by C:N and C:P ratios). However, this effects was driven by of horizontal diversity (i.e., the manipulated richness of the decomposer level). Whereas, vertical diversity (i.e., predator richness, which was full-factorially manipulated), exerted intra-guild (on other predators) and extra-guild (on decomposers) predation and a release of interspecific competition among decomposers. All these findings in my study highlight the great potential of such a combined application of the aforementioned designs to explain biodiversity on ecosystem functioning relationships and thus should be considered in future research.

These outstanding insights into the coupled mechanisms of horizontal and vertical diversity that drive decomposition of litter of different quality (Chapter 3), led to investigations of a comprehensive dataset of complex soil food webs in forests (Chapters 4, 5 and 6). A previous study (Ehnes *et al.* 2014), demonstrated that the ecological state variables in this dataset, abundance and biomass, follow the power-law scaling relationships with body mass as predicted by metabolic theory (Gillooly *et al.* 2001; Brown *et al.* 2004). However, across phylogenetic and functional groups substantial variation in the scaling relationships was found (Ehnes *et al.* 2014). Here, I tested if population densities additionally depend on litter stoichiometry according to ecological stoichiometry. Thus, I integrated allometric and stoichiometric variables in one multiple regression approach (Chapter 4). Strikingly, this model that integrated the biomass - body mass scaling relationship with stoichiometric variables was superior to the model that accounted for the body mass scaling alone. I found that the scaling of biomass densities with population-averaged body masses interactively scaled with litter stoichiometry (i.e., carbon-to-element ratios, such as C:N and C:P). Moreover, when I accounted for the substructure of phylogenetic or functional groups in the dataset in addition to the original models, I found again that the integrated allometric-stoichiometric type of model was most adequate in describing the data. This highlights the robustness of the model framework and the potential to include additional predictors to the allometric scaling. For instance the perspective of a compound variable of ratios between multiple co-limiting nutrients (Sperfeld *et al.* 2012), or ratios other than to the base of total carbon (such as lignin:X, which is considered in litter decomposition (Hladyz *et al.* 2009)). Thus, this

integrative model offers a broad applicability of my approach to other research that aims to predict combined effects of allometry and stoichiometry.

Subsequently (Chapter 5), I applied this model framework to the phylogenetic groups of the same dataset separately. For the majority of the phylogenetic groups (i.e., ten out of the twelve tested groups) I found that the scaling of biomass with population-averaged body mass depended on either litter stoichiometry or habitat metrics (such as forest type, pH value or litter depth) or both. I found forest type, the carbon-to-phosphorus ratio (C:P), the carbon-to-sodium ratio (C:Na), and the carbon-to-nitrogen ratio (C:N) to be the most frequent among the predictors that I tested for their influence on the allometric scaling relationship. This result is consistent with Chapters 3 and 4, and underpins the high importance of these carbon-to-element ratios as stoichiometric variables in determining species interactions and relationships within phylogenetic groups and trophic levels. Studies in tropical forests (Kaspari & Yanoviak 2009) and temperate grasslands (Mulder & Elser 2009; Mulder *et al.* 2011), reported similar significance of these elements (i.e. carbon, nitrogen, phosphorus and sodium) in predicting abundances. However, "*one important distinction between mine and these previous studies*" (namely Kaspari & Yanoviak 2009; Mulder & Elser 2009; Mulder *et al.* 2011) "*is that I accounted for the scaling relationships between biomass densities and population-average body masses, which allows pooling biomasses of populations differing in body mass*" (Ott *et al.* 2014a). Generally, our results follow the traditional focus on C:N:P ratios in ecological stoichiometry (Elser *et al.* 1996; Sterner & Elser 2002) and their importance for decomposition processes and nutrient turnover (Enríquez, Duarte & Sand-Jensen 1993b). However, since additional elements may be of equal importance (Sterner & Elser 2002; Kaspari 2012). I followed this more general perspective of elemental stoichiometry, i.e. all biological relevant elements can be limiting in some way, e.g. for rates or processes, and included ten elements in my analyses. This is different to Chapters 2 and 3, where I discriminated litter quality only by C:N and C:P ratios. In Chapter 4 I found that e.g. calcium and potassium interacted with the allometric scaling of population densities. Both elements were already considered being important for decomposition processes decades ago and also more recently (Swift *et al.* 1979; Kaspari *et al.* 2008). Interestingly, in Chapter 5 the elements calcium and potassium occurred in high frequency in the best models, but were of lesser importance than expected from the outcome of Chapter 4. Instead, forest type and sodium were amongst the most frequent variables interacting with the allometric scaling of population densities, pointing to a possible context dependency

in regard to the taxonomic resolution. Overall, my concept of an integration of allometry and stoichiometry provides an important development towards unifying metabolic theory and ecological stoichiometry.

In Chapter 6, I found significant interacting effects of litter quality (as indicated by stoichiometric differences of leaf species), the decomposers body mass (manipulated with different mesh sizes) and forest type on litter decomposition. The litter-mass loss was increased on high-quality litter, with macro-meshes (i.e., the meso- and macrofauna had access to the litter in addition to the microorganisms) and in the most intensively managed coniferous forests. Thus, in accordance to previous studies (Wall *et al.* 2008; Makkonen *et al.* 2012; Handa *et al.* 2014), I found enhanced decomposition rates when larger decomposers had access to the leaf litter. In contrast to my expectations from other studies (Srivastava *et al.* 2009a; Gessner *et al.* 2010) and results from Chapter 3, I found no effect of species richness on litter-mass loss. Instead, the higher decomposition rates can be explained by the facilitation between the larger soil fauna and the microorganisms. This was likely to have led to an increased nutritional quality of the litter for the microorganisms after gut passage of the macrofauna (Maraun & Scheu 1996; Hedde *et al.* 2007). Furthermore, this implies that horizontal and vertical diversity effects (Chapter 3) span across the full decomposer community. Moreover, the constraints of resource stoichiometry on population densities apply to decomposers (Chapters 4 and 5) as to microorganisms (Mooshammer *et al.* 2011, 2014). In summary, I revealed that major components of decomposition processes, i.e. resource quality, decomposer body mass and decomposer diversity, interact with each other. These results corroborate my findings of all previous chapters. Ultimately, I found evidence of the interplay of allometric and stoichiometric variables in predicting consumption rates on the individual level (Chapter 2), in determining trophic and non-trophic diversity effects on the community level (Chapter 3), for the prediction of biomasses densities on the population level (Chapter 4 and Chapter 5) and affecting rates of litter decomposition (the ecosystem functioning) on the ecosystem level. Thus, my results strongly advocate an integration of predictor variables of metabolic theory (i.e., body mass and temperature) and ecological stoichiometry (i.e., the availability and the ratios of elements) for studying species interactions which scale up from individuals to food webs.

7.3. Outlook

In this thesis, I present several novel approaches. These innovative designs of the laboratory experiments will stimulate future research and offer a promising way to quantify decomposer consumption. Furthermore, future studies on multi-trophic diversity effects might want to consider the combination of the random-partitions design (Bell *et al.* 2009) with an allometric design (Schneider *et al.* 2012; Schneider & Brose 2013). I developed a concept for an integrative ecological perspective combining metabolic theory and ecological stoichiometry. While this is still by no means a "unifying theory of everything" (Woodward *et al.* 2005), this work is a novel contribution to, and a groundbreaking step towards an overarching framework in community and population ecology. The multiple regression framework is flexible enough to include various other predictor variables. To make this approach even more powerful, several onsets for future research are imaginable.

First, the functional response as a baseline measure to investigate the individual decomposer-leaf litter interaction should be applied to more species and taxa than studied here. Moreover, determining decomposer functional responses on litter mixtures is necessary to enable parallel measurements of feeding preferences (Kalinkat *et al.* 2011). This solid background of empirically derived parameter coefficients will tremendously benefit theoretical approaches that examine population dynamics in whole food webs. Second, manipulations of broader gradients of horizontal and vertical diversity, including microorganisms in combination with larger invertebrates, would aid our understanding of biodiversity effects on multiple ecosystem functions (Wagg *et al.* 2014). Third, the effects of stoichiometry on metabolic rates should be examined. Jeyasingh (Jeyasingh 2007) set the scene for experimental approaches that examine possible changes in metabolism due to a stoichiometric consumer-resource mismatch, i.e. the food quality varies from balanced (matches consumer body stoichiometry) to imbalanced (mismatch). Moreover, recent developments (Gillooly *et al.* 2002, 2005; Allen & Gillooly 2009) used the concept of invariance in the subunits of an organism (see introduction, alternatively summarized in Kaspari 2012). These approaches used phosphorus concentrations in RNA and ATP to estimate whole-organism pools, and predicted zooplankton growth rates (Gillooly *et al.* 2002, 2005; Allen & Gillooly 2009). While these concepts are impressive at first sight, they rely on knowledge of e.g. tissue density of subunits and nutrient concentrations in these (Kaspari 2012) - which seems a complex challenge given the fact of approx. 22

biologically relevant elements (Sterner & Elser 2002; Kaspari 2012). Definitely, this offers work packages to microbiology and genetics. Fourth, the importance of resource elemental contents in comparison to macro-nutrient availability (proteins, lipids and carbohydrates) for consumers remains debated (Anderson *et al.* 2004; Raubenheimer, Simpson & Mayntz 2009) and needs further consideration for a unified perspective. Fifth, most of the research chapters in this thesis were conducted in relatively short time spans or used data from a certain season. To investigate the influence of stoichiometry on phylogeny and evolution, one need to consider microorganism with short generation times and high mutation rates in combination with e.g. the experimental design presented in this thesis. Sixth and finally, the approaches in this thesis used resource stoichiometry without measurements of consumer stoichiometry, thus resting on the assumption of a general mismatch of consumer and resource stoichiometry that constraints the feeding interactions. Knowledge of stoichiometric contents of both consumers and their resources will shed more light on why biomass densities of populations scale with (a) particular element(s) or carbon-to-element ratio(s).

While all these points seem to be appealing, some of these require profound methodological considerations to be addressed in empirical or theoretical work. In this thesis, I provide promising novel experimental solutions for measurements of interaction strengths via quantification of decomposer consumption rates (Chapter 2) and for disentangling horizontal and vertical diversity effects (Chapter 3). Moreover, the way I implemented and integrated allometric and stoichiometric variables into one model framework to predict population biomass densities (Chapter 4 and 5) has much potential and flexibility for a broad application. All in all, my results strongly emphasize that a combination of metabolic theory and ecological stoichiometry builds ground to stimulate future research.

Part IV

Appendix

References

Abbas, M., Klein, A.-M., Ebeling, A., Oelmann, Y., Ptacnik, R., Weisser, W.W. & Hillebrand, H. (2014) Plant diversity effects on pollinating and herbivorous insects can be linked to plant stoichiometry. *Basic and Applied Ecology*, **15**, 169–178.

Aber, J.D., Melillo, J.M. & McClaugherty, C.A. (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Canadian Journal of Botany*, **68**, 2201–2208.

Achler, M. (2013) Effects of decomposer diversity on decomposition: Horizontal and vertical diversity drive ecosystem functioning. Master Thesis, University of Göttingen, Göttingen.

Adair, E.C., Parton, W.J., Del Grosso, S.J., Silver, W.L., Harmon, M.E., Hall, S.A., Burke, I.C. & Hart, S.C. (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Global Change Biology*, **14**, 2636–2660.

Aerts, R. (1997) Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship. *Oikos*, **79**, 439.

Aerts, R. (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, **94**, 713–724.

Ågren, G.I., Hyvönen, R., Berglund, S.L. & Hobbie, S.E. (2013) Estimating the critical N:C from litter decomposition data and its relation to soil organic matter stoichiometry. *Soil Biology and Biochemistry*, **67**, 312–318.

Allen, A.P. & Gillooly, J.F. (2009) Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecology Letters*, **12**, 369–384.

Anderson, T.R., Boersma, M. & Raubenheimer, D. (2004) Stoichiometry: linking elements to biochemicals. *Ecology*, **85**, 1193–1202.

Andrén, O., Bengtsson, J. & Clarholm, M. (1995) Biodiversity and species redundancy among litter decomposers. *The Significance and Regulation of Soil Biodiversity* Developments in Plant and Soil Sciences. (eds H.P. Collins, G.P. Robertson & M.J. Klug), pp. 141–151. Springer Netherlands.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Bastian, M., Pearson, R.G. & Boyero, L. (2008) Effects of diversity loss on ecosystem function across trophic levels and ecosystems: A test in a detritus-based tropical food web. *Austral Ecology*, **33**, 301–306.

Bell, T., Lilley, A.K., Hector, A., Schmid, B., King, L. & Newman, J.A. (2009) A linear model method for biodiversity-ecosystem functioning experiments. *The American Naturalist*, **174**, 836–849.

Bell, T., Newman, J.A., Silverman, B.W., Turner, S.L. & Lilley, A.K. (2005) The contribution of species richness and composition to bacterial services. *Nature*, **436**, 1157–1160.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., Anta, R.C., Couteaux, M., Escudero, A., Gallardo, A., Kratz, W., Madeira, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V., Muñoz, F., Piussi, P., Remacle, J. & Santo, A.V. (1993) Litter mass loss rates in pine forests of Europe and Eastern United States: some

relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.

Berg, B., Johansson, M.-B., Ekbohm, G., McClaugherty, C., Rutigliano, F. & Santo, A.V.D. (1996) Maximum decomposition limits of forest litter types: a synthesis. *Canadian Journal of Botany*, **74**, 659–672.

Bergmann, K. (1847) *Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*.Göttinger Studien, Vandenhoek & Ruprecht, 1848, Göttingen.

Berlow, E.L., Navarrete, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999) Quantifying variation in the strenghts of species interactions. *Ecology*, **80**, 2206–2224.

Berlow, E.L., Neutel, A., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585–598.

Bertram, S.M., Bowen, M., Kyle, M. & Schade, J.D. (2008) Extensive Natural Intraspecific Variation in Stoichiometric (C:N:P) Composition in Two Terrestrial Insect Species. *Journal of Insect Science*, **8**, 7pp.

Binzer, A., Guill, C., Brose, U. & Rall, B.C. (2012) The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2935–2944.

Boersma, M., Aberle, N., Hantzsche, F.M., Schoo, K.L., Wiltshire, K.H. & Malzahn, A.M. (2008) Nutritional Limitation Travels up the Food Chain. *International Review of Hydrobiology*, **93**, 479–488.

Bokhorst, S. & Wardle, D.A. (2013) Microclimate within litter bags of different mesh size: Implications for the "arthropod effect" on litter decomposition. *Soil Biology and Biochemistry*, **58**, 147–152.

Bolker, B.M. (2008) *Ecological Models and Data in R*. Princeton University Press, Princeton.

Bond-Lamberty, B., Bronson, D., Bladyka, E. & Gower, S.T. (2011) A comparison of trenched plot techniques for partitioning soil respiration. *Soil Biology and Biochemistry*, **43**, 2108–2114.

Boyero, L., Cardinale, B.J., Bastian, M. & Pearson, R.G. (2014) Biotic vs. Abiotic Control of Decomposition: A Comparison of the Effects of Simulated Extinctions and Changes in Temperature. *PLoS ONE*, **9**, e87426.

Brose, U. (2010) Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, **24**, 28–34.

Brose, U., Dunne, J.A., Montoya, J.M., Petchey, O.L., Schneider, F.D. & Jacob, U. (2012) Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2903–2912.

Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. (2008) Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology*, **77**, 1072–1078.

Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. (2004) Unified spatial scaling of species and their trophic interactions. *Nature*, **428**, 167–171.

Brose, U. & Scheu, S. (2014) Into darkness: unravelling the structure of soil food webs. *Oikos*, **123**, 1153-1156.

Brown, J.H. & Gillooly, J.F. (2003) Ecological food webs: High-quality data facilitate theoretical unification. *Proceedings of the National Academy of Sciences*, **100**, 1467–1468.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Brown, J.H. & Sibly, R.M. (2012) The Metabolic Theory of Ecology and Its Central Equation. *Metabolic Ecology* (eds R.M. Sibly, J.H. Brown & A.

Kodric-Brown), pp. 21–33. Wiley-Blackwell, Chichester.

Brown, J.H., Sibly, R.M. & Kodric-Brown, A. (2012) Introduction: Metabolism as the Basis for a Theoretical Unification of Ecology. *Metabolic Ecology* (eds R.M. Sibly, J.H. Brown & A. Kodric-Brown), pp. 1–6. Wiley-Blackwell, Chichester.

Bruno, J.F. & Cardinale, B.J. (2008) Cascading effects of predator richness. *Frontiers in Ecology and the Environment*, **6**, 539–546.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, **18**, 119–125.

Burger, J.A. & Kelting, D.L. (1999) Using soil quality indicators to assess forest stand management. *Forest Ecology and Management*, **122**, 155–166.

Burnham, K.P. & Anderson, D.R. (2004) Multimodel Inference. *Sociological Methods & Research*, **33**, 261–304.

Byrnes, J.E. & Stachowicz, J.J. (2009) The consequences of consumer diversity loss: different answers from different experimental designs. *Ecology*, **90**, 2879–2888.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, **415**, 426–429.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.

Carter, M.R., Gregorich, E.G., Anderson, D.W., Doran, J.W., Janzen, H.H. & Pierce, F.J. (1997) Chapter 1 Concepts of soil quality and their significance. *Developments in Soil Science* Soil Quality for Crop Production and Ecosystem Health. (ed E.G. Gregorich and M.R. Carter), pp. 1–19. Elsevier.

Cebrian, J. (1999) Patterns in the Fate of Production in Plant Communities. *The American Naturalist*, **154**, 449–468.

Cebrian, J. & Lartigue, J. (2004) Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs*, **74**, 237–259.

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

Cheng, W. & Coleman, D.C. (1990) Effect of living roots on soil organic matter decomposition. *Soil Biology and Biochemistry*, **22**, 781–787.

Chen, B. & Wise, D.H. (1999) Bottom-Up Limitation of Predaceous Arthropods in a Detritus-Based Terrestrial Food Web. *Ecology*, **80**, 761.

Clay, N.A., Yanoviak, S.P. & Kaspari, M. (2014) Short-term sodium inputs attract microbi-detritivores and their predators. *Soil Biology and Biochemistry*, **75**, 248–253.

Cohen, J.E., Jonsson, T. & Carpenter, S.R. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences*, **100**, 1781–1786.

Coleman, D.C. (2004) *Fundamentals of Soil Ecology, Second Edition*, 2 edition. Academic Press, Amsterdam ; Boston.

Cornelissen, J.H.C. (1996) An Experimental Comparison of Leaf Decomposition Rates in a Wide Range of Temperate Plant Species and Types. *The Journal of Ecology*, **84**, 573.

Coûteaux, M.-M., Bottner, P. & Berg, B. (1995) Litter decomposition, climate and liter quality. *Trends in Ecology & Evolution*, **10**, 63–66.

Cummins, K.W. (1974) Structure and Function of Stream Ecosystems. *BioScience*, **24**, 631–641.

Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.

David, J. & Gillon, D. (2009) Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. *Global Change Biology*, **15**, 156–165.

David, J. & Handa, I.T. (2010) The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biological Reviews*, **85**, 881–895.

Dell, T., Pawar, S. & Savage, V.M. (2011) Systematic Variation in the Temperature Dependence of Physiological and Ecological Traits. *Proceedings of the National Academy of Sciences*, **108**, 10591–10596.

Dickinson, C.H. & Pugh, G.J.F. (1974) *Biology of Plant Litter Decomposition*. Elsevier.

Digel, C., Curtsdotter, A., Riede, J., Klarner, B. & Brose, U. (2014) Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos*, **123**, 1157-1172.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, **10**, 522–538.

Ehnes, R.B. (2014) *Allometry - Relations to Energy and Abundance*. Doctoral Thesis, University of Darmstadt, Darmstadt.

Ehnes, R.B., Pollierer, M.M., Erdmann, G., Klarner, B., Eitzinger, B., Digel, C., Ott, D., Maraun, M., Scheu, S. & Brose, U. (2014) Lack of energetic equivalence in forest soil invertebrates. *Ecology*, **95**, 527–537.

Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters*, **14**, 993–1000.

Eisenhauer, N. (2010) The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, **53**, 343–352.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**, 1135–1142.

Elser, J.J., Dobberfuhl, D.R., MacKay, N.A. & Schampel, J.H. (1996) Organism Size, Life History, and N:P Stoichiometry. *BioScience*, **46**, 674–684.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000a) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M. & Weider, L.W. (2000b) Biological stoichiometry from genes to ecosystems. *Ecology Letters*, **3**, 540–550.

Elser, J.J. & Urabe, J. (1999) The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology*, **80**, 735–751.

Elser, J.J., Watts, T., Bitler, B. & Markow, T.A. (2006) Ontogenetic coupling of growth rate with RNA and P contents in five species of Drosophila. *Functional Ecology*, **20**, 846–856.

Elton, C.S. (1927) *Animal Ecology, by Charles Elton; with an Introduction by Julian S. Huxley.* Macmillan Co., New York,.

Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011) Temperature dependence of the functional response. *Ecology Letters*, **14**, 914–921.

Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D. & Gillooly, J.F. (2003) Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–642.

Enríquez, S., Duarte, C.M. & Sand-Jensen, K. (1993a) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, **94**, 457–471.

Enríquez, S., Duarte, C.M. & Sand-Jensen, K. (1993b) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, **94**, 457–471.

Erdmann, G., Scheu, S. & Maraun, M. (2012) Regional factors rather than forest type drive the community structure of soil living oribatid mites (Acari, Oribatida). *Experimental & Applied Acarology*, **57**, 157–169.

Faber, J.H. & Verhoef, H.A. (1991) Functional differences between closely-related soil arthropods with respect to decomposition processes in the presence or absence of pine tree roots. *Soil Biology and Biochemistry*, **23**, 15–23.

Fagan, W.F. & Denno, R.F. (2004) Stoichiometry of actual vs. potential predator–prey interactions: insights into nitrogen limitation for arthropod predators. *Ecology Letters*, **7**, 876–883.

Fagan, W.F., Siemann, E., Mitter, C., Denno, R.F., Huberty, A.F., Woods, H.A. & Elser, J.J. (2002) Nitrogen in Insects: Implications for Trophic Complexity and Species Diversification. *The American Naturalist*, **160**, 784–802.

Ferlian, O. & Scheu, S. (2013) Shifts in trophic interactions with forest type in soil generalist predators as indicated by complementary analyses of fatty acids and stable isotopes. *Oikos*, **123**, 182-1191.

Finke, M.D. (2007) Estimate of chitin in raw whole insects. *Zoo biology*, **26**, 105–115.

Finke, D.L. & Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature*, **429**, 407–410.

Finke, D.L. & Denno, R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, **8**, 1299–1306.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D. & Weisser, W.W. (2010) Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, **11**, 473–485.

Fox, T.R. (2000) Sustained productivity in intensively managed forest plantations. *Forest Ecology and Management*, **138**, 187–202.

Frost, P.C., Benstead, J.P., Cross, W.F., Hillebrand, H., Larson, J.H., Xenopoulos, M.A. & Yoshida, T. (2006) Threshold elemental ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters*, **9**, 774–779.

Frost, P.C., Cross, W.F. & Benstead, J.P. (2005a) Ecological stoichiometry in freshwater benthic ecosystems: an introduction. *Freshwater Biology*, **50**, 1781–1785.

Frost, P.C., Evans-White, M.A., Finkel, Z.V., Jensen, T.C. & Matzek, V. (2005b) Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos*, **109**, 18–28.

Gartner, T.B. & Cardon, Z.G. (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos*, **104**, 230–246.

Gaston, K.J. & Spicer, J.I. (2003) *Biodiversity: An Introduction*, 2nd Edition edition. Wiley-Blackwell, Malden, USA, Oxford, UK, Victoria, AUS.

Van Geffen, K.G., Berg, M.P. & Aerts, R. (2011) Potential macro-detritivore range expansion into the subarctic stimulates litter decomposition: a new positive feedback mechanism to climate change? *Oecologia*, **167**, 1163–1175.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H. & Hättenschwiler, S. (2010) Diversity meets decomposition. *Trends in Ecology & Evolution*, **25**, 372–380.

Giller, P.S. (1996) The diversity of soil communities, the "poor man"s tropical rainforest'. *Biodiversity & Conservation*, **5**, 135–168.

Gillooly, J.F., Allen, A.P., Brown, J.H., Elser, J.J., Rio, C.M. del, Savage, V.M., West, G.B., Woodruff, W.H. & Woods, H.A. (2005) The metabolic basis of whole-organism RNA and phosphorus content. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 11923–11927.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of Size and Temperature on Metabolic Rate. *Science*, **293**, 2248–2251.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. & Brown, J.H. (2002) Effects of size and temperature on developmental time. *Nature*, **417**, 70–73.

Glazier, D.S. (2005) Beyond the "3/4-power law": variation in the intra-and interspecific scaling of metabolic rate in animals. *Biological Reviews*, **80**, 611–662.

Glazier, D.S. (2014) Is metabolic rate a universal "pacemaker" for biological processes? *Biological Reviews*, **90**, 377-407.

González, A.L., Fariña, J.M., Kay, A.D., Pinto, R. & Marquet, P.A. (2011) Exploring patterns and mechanisms of interspecific and intraspecific variation in body elemental composition of desert consumers. *Oikos*, **120**, 1247–1255.

Griffiths, B.S., Spilles, A. & Bonkowski, M. (2012) C:N:P stoichiometry and nutrient limitation of the soil microbial biomass in a grazed grassland site under experimental P limitation or excess. *Ecological Processes*, **1**, 6.

Grigal, D.F. (2000) Effects of extensive forest management on soil productivity. *Forest Ecology and Management*, **138**, 167–185.

Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu, S., Schmid, B., van Ruijven, J., Vos, V.C.A. & Hättenschwiler, S. (2014) Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, **509**, 218–221.

Hanson, P.J., Edwards, N.T., Garten, C.T. & Andrews, J.A. (2000) Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry*, **48**, 115–146.

Hassall, M., Edwards, D.P., Carmenta, R., Derhé, M.A. & Moss, A. (2010) Predicting the effect of climate change on aggregation behaviour in four species of terrestrial isopods. *Behaviour*, **147**, 151–164.

Hättenschwiler, S. & Bretscher, D. (2001) Isopod effects on decomposition of litter produced under elevated CO2, N deposition and different soil types. *Global Change Biology*, **7**, 565–579.

Hättenschwiler, S., Coq, S., Barantal, S. & Handa, I.T. (2011) Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *The New Phytologist*, **189**, 950–965.

Hättenschwiler, S. & Gasser, P. (2005) Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 1519 –1524.

Hättenschwiler, S. & Jørgensen, H.B. (2010) Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology*, **98**, 754–763.

Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 191–218.

Hechinger, R.F., Lafferty, K.D., Dobson, A.P., Brown, J.H. & Kuris, A.M. (2011) A Common Scaling Rule for Abundance, Energetics, and Production of Parasitic and Free-Living Species. *Science (New York, N.Y.)*, **333**, 445–448.

Hedde, M., Bureau, F., Akpa-Vinceslas, M., Aubert, M. & Decaëns, T. (2007) Beech leaf degradation in laboratory experiments: Effects of eight detritivorous invertebrate species. *Applied Soil Ecology*, **35**, 291–301.

Heemsbergen, D.A., Berg, M.P., Loreau, M., van Hal, J.R., Faber, J.H. & Verhoef, H.A. (2004) Biodiversity Effects on Soil Processes Explained by Interspecific Functional Dissimilarity. *Science*, **306**, 1019–1020.

Van der Heijden, M.G.A., Bardgett, R.D. & van Straalen, N.M. (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, **11**, 296–310.

Helal, H.M. & Sauerbeck, D. (1986) Effect of plant roots on carbon metabolism of soil microbial biomass. *Journal of Plant Nutrition and Soil Science*, **149**, 181–188.

Hendriksen, N.B. (1990) Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils*, **10**, 17–21.

Hillebrand, H., Borer, E.T., Bracken, M.E.S., Cardinale, B.J., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner, D.S., Stanley Harpole, W., Ngai, J.T., Sandin, S., Seabloom, E.W., Shurin, J.B., Smith, J.E. & Smith, M.D. (2009) Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. *Ecology Letters*, **12**, 516–527.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences*, **104**, 10904–10909.

Hladyz, S., Gessner, M.O., Giller, P.S., Pozo, J. & Woodward, G. (2009) Resource quality and stoichiometric constraints on stream ecosystem functioning. *Freshwater Biology*, **54**, 957–970.

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C. & Karolewski, P. (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology*, **87**, 2288–2297.

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effetcs of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous Inference in General Parametric Models. *Biometrical Journal*, **50**, 346–363.

IPCC (2007) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, **446**, Geneva, Switzerland.

Irmler, U. (2000) Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two

deciduous forests. *Pedobiologia*, **44**, 105–118.

Isaac, N.J.B. & Carbone, C. (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters*, **13**, 728–735.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C. & Thomas, F.M. (2009) Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biology and Biochemistry*, **41**, 2122–2130.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K. & Byrne, K.A. (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma*, **137**, 253–268.

Jeyasingh, P.D. (2007) Plasticity in metabolic allometry: the role of dietary stoichiometry. *Ecology Letters*, **10**, 282–289.

Joergensen, R.G., Kübler, H., Meyer, B. & Wolters, V. (1995) Microbial biomass phosphorus in soils of beech (*Fagus sylvatica* L.) forests. *Biology and Fertility of Soils*, **19**, 215–219.

Jonsson, M. & Malmqvist, B. (2003) Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia*, **134**, 554–559.

Kalinkat, G., Brose, U. & Rall, B.C. (2013a) Habitat structure alters top-down control in litter communities. *Oecologia*, **172**, 877–887.

Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U. (2011) The allometry of prey preferences. *PLoS ONE*, **6**, e25937.

Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013b) Body masses, functional responses and predator–prey stability. *Ecology Letters*, **16**, 1126–1134.

Kaspari, M. (2004) Using the Metabolic Theory of Ecology to predict global patterns of abundance. *Ecology*, **85**, 1800–1802.

Kaspari, M. (2012) Stoichiometry. *Metabolic Ecology* (eds R.M. Sibly, J.H. Brown & A. Kodric-Brown), pp. 34–47. Wiley-Blackwell, Chichester.

Kaspari, M., Garcia, M.N., Harms, K.E., Santana, M., Wright, S.J. & Yavitt, J.B. (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters*, **11**, 35–43.

Kaspari, M. & Yanoviak, S.P. (2008) Biogeography of litter depth in tropical forests: evaluating the phosphorus growth rate hypothesis. *Functional Ecology*, **22**, 919–923.

Kaspari, M. & Yanoviak, S.P. (2009) Biogeochemistry and the structure of tropical brown food webs. *Ecology*, **90**, 3342–3351.

Kaspari, M., Yanoviak, S.P., Dudley, R., Yuan, M. & Clay, N.A. (2009) Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences*.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C. & Brose, U. (2012) More than a meal… integrating non-feeding interactions into food webs. *Ecology Letters*, **15**, 291–300.

Klarner, B. (2014) *Changes in Trophic Structure of Decomposer Communities with Land Use in Central European Temperate Forests*. Doctoral thesis, Georg-August University Göttingen, Göttingen, Germany.

Klarner, B., Ehnes, R.B., Erdmann, G., Eitzinger, B., Pollierer, M.M., Maraun, M. & Scheu, S. (2014) Trophic shift of soil animal species with forest type as indicated by stable isotope analysis. *Oikos*, **123**, 1173-1181.

Kleiber, M. (1932) Body size and Metabolism. *Hilgardia*, **6**, 315–332.

Kleiber, M. (1947) Body Size and Metabolic rate. *Physiological Reviews*, **27**, 511–541.

Kuzyakov, Y. (2006) Sources of CO2 efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry*, **38**, 425–448.

Lang, B., Rall, B.C. & Brose, U. (2011) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, **81**, 516–23.

Lang, B., Rall, B.C., Scheu, S. & Brose, U. (2014) Effects of environmental warming and drought on a size-structured soil community. *Oikos*, **123,** 1224-1233.

Liebig, J. von. (1855) *Principles of Agricultural Chemistry with Special Reference to the Late Researches Made in England*. Walton & Maberly, London, UK.

Loreau, M. (2001) Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 303 –309.

Loreau, M. (2010) Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 49–60.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science (New York, N.Y.)*, **294**, 804–808.

Lotka, A.J. (1925) *Elements of Physical Biology*. Williams & Wilkins Company, Baltimore.

Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M. & Aerts, R. (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology letters*, **15**, 1033–1041.

Malzahn, A.M., Aberle, N., Clemmesen, C. & Boersma, M. (2007) Nutrient limitation of primary producers affects planktivorous fish condition. *Limnology and Oceanography*, **52**, 2062–2071.

Maraun, M., Alphei, J., Beste, P., Bonkowski, M., Buryn, R., Migge, S., Peter, M., Schaefer, M. & Scheu, S. (2001) Indirect effects of carbon and nutrient amendments on the soil meso- and microfauna of a beechwood. *Biology and Fertility of Soils*, **34**, 222–229.

Maraun, M. & Scheu, S. (1996) Changes in microbial biomass, respiration and nutrient status of beech (Fagus sylvatica) leaf litter processed by millipedes (Glomeris marginata). *Oecologia*, **107**, 131–140.

Marshall, V.G. (2000) Impacts of forest harvesting on biological processes in northern forest soils. *Forest Ecology and Management*, **133**, 43–60.

Martinson, H.M., Schneider, K., Gilbert, J., Hines, J.E., Hambäck, P.A. & Fagan, W.F. (2008) Detritivory: stoichiometry of a neglected trophic level. *Ecological Research*, **23**, 487–491.

McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004) Scaling of C: N: P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology*, **85**, 2390–2401.

McKie, B.G., Woodward, G., Hladyz, S., Nistorescu, M., Preda, E., Popescu, C., Giller, P.S. & Malmqvist, B. (2008) Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. *The Journal of Animal Ecology*, **77**, 495–504.

Meehan, T.D. (2006a) Energy use and animal adbundance in litter and soil communities. *Ecology*, **87**, 1650–1658.

Meehan, T.D. (2006b) Mass and temperature dependence of metabolic rate in litter and soil invertebrates. *Physiological*

and biochemical zoology: PBZ, **79**, 878–884.

Moe, S.J., Stelzer, R.S., Forman, M.R., Harpole, W.S., Daufresne, T. & Yoshida, T. (2005) Recent advances in ecological stoichiometry: insights for population and community ecology. *Oikos*, **109**, 29–39.

Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. & Wall, D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584–600.

Moorhead, D.L., Westerfield, M.M. & Zak, J.C. (1998) Plants retard litter decay in a nutrient-limited soil: a case of exploitative competition? *Oecologia*, **113**, 530–536.

Mooshammer, M., Wanek, W., Schnecker, J., Wild, B., Leitner, S., Hofhansl, F., Blöchl, A., Hämmerle, I., Frank, A.H., Fuchslueger, L., Keiblinger, K.M., Zechmeister-Boltenstern, S. & Richter, A. (2011) Stoichiometric controls of nitrogen and phosphorus cycling in decomposing beech leaf litter. *Ecology*, **93**, 770–782.

Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S. & Richter, A.A. (2014) Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources. *Terrestrial Microbiology*, **5**, 22.

Mulder, C., Ahrestani, F.S., Bahn, M., Bohan, D.A., Bonkowski, M., Griffiths, B.S., Guicharnaud, R.A., Kattge, J., Krogh, P.H., Lavorel, S., Lewis, O.T., Mancinelli, G., Naeem, S., Peñuelas, J., Poorter, H., Reich, P.B., Rossi, L., Rusch, G.M., Sardans, J. & Wright, I.J. (2013) Connecting the Green and Brown Worlds. *Advances in Ecological Research*, **49**, 69–175.

Mulder, C. & Elser, J.J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology*, **15**, 2730–2738.

Mulder, C., Vonk, J.A., Den Hollander, H.A., Hendriks, A.J. & Breure, A.M. (2011) How allometric scaling relates to soil abiotics. *Oikos*, **120**, 529–536.

Mulder, C., Van Wijnen, H.J. & Van Wezel, A.P. (2005) Numerical abundance and biodiversity of below-ground taxocenes along a pH gradient across the Netherlands. *Journal of Biogeography*, **32**, 1775–1790.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–737.

Naeem, S. & Wright, J.P. (2003) Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567–579.

Nichols, J.D. & MacKenzie, D.I. (2004) Abundance estimation and Conservation Biology. *Animal Biodiversity and Conservation*, **27**, 437–439.

Nielsen, U.N., Ayres, E., Wall, D.H. & Bardgett, R.D. (2011) Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity–function relationships. *European Journal of Soil Science*, **62**, 105–116.

Noon, B.R., Bailey, L.L., Sisk, T.D. & McKelvey, K.S. (2012) Efficient species-level monitoring at the landscape scale. *Conservation biology: the journal of the Society for Conservation Biology*, **26**, 432–441.

Norton, R.A. & Behan-Pelletier, V.M. (1991) Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari: Oribatida). *Canadian Journal of Zoology*, **69**, 1504–1511.

De Oliveira, T., Hättenschwiler, S. & Tanya Handa, I. (2010) Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. *Functional Ecology*, **24**, 937–946.

Ott, D., Digel, C., Klarner, B., Maraun, M., Pollierer, M.M., Rall, B.C., Scheu, S., Seelig, G. & Brose, U. (2014a) Litter elemental stoichiometry and biomass densities of forest soil invertebrates. *Oikos*, **123**, 1212-1223.

Ott, D., Digel, C., Rall, B.C., Maraun, M., Scheu, S. & Brose, U. (2014b) Unifying elemental stoichiometry and metabolic theory in predicting species abundances. *Ecology Letters*, **17**, 1247-1256.

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J. & Brose, U. (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, **89**, 134–144.

Ott, D., Rall, B.C. & Brose, U. (2012) Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. *Philosophical Transactions of the Royal Society B*, **367**, 3025–3032.

Paine, R.T. (1980) Food Webs: Linkage, Interaction Strength and Community Infrastructure. *The Journal of Animal Ecology*, **49**, 666.

Passy, S.I. (2012) A hierarchical theory of macroecology. *Ecology letters*, **15**, 923–934.

Persson, J., Fink, P., Goto, A., Hood, J.M., Jonas, J. & Kato, S. (2010) To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. *Oikos*, **119**, 741–751.

Petchey, O.L. & Dunne, J.A. (2012) Predator-Prey Relations and Food Webs. *Metabolic Ecology: A Scaling Approach*, 2nd ed (eds R.M. Sibly, J.H. Brown & A. Kodric-Brown), p. 392. Wiley-Blackwell, Chichester.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2012) *Nlme: Linear and Nonlinear Mixed Effects Models*.

Pollierer, M.M., Langel, R., Körner, C., Maraun, M. & Scheu, S. (2007) The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology letters*, **10**, 729–736.

Post, D.M. (2002) The long and short of food-chain length. *Trends in Ecology & Evolution*, **17**, 269–277.

Prescott, C.E. (1997) Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. *Forest Ecology and Management*, **95**, 253–260.

Price, C.A., Weitz, J.S., Savage, V.M., Stegen, J., Clarke, A., Coomes, D.A., Dodds, P.S., Etienne, R.S., Kerkhoff, A.J., McCulloh, K., Niklas, K.J., Olff, H. & Swenson, N.G. (2012) Testing the metabolic theory of ecology. *Ecology Letters*, **15**, 1465–1474.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O. & Petchey, O.L. (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **367**, 2923–2934.

Rall, B.C., Guill, C. & Brose, U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, **117**, 202–213.

Rall, B.C., Kalinkat, G., Ott, D., Vucic-Pestic, O. & Brose, U. (2011) Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, **120**, 483–492.

Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M. & Brose, U. (2010) Temperature, predator–prey interaction strength and population stability. *Global Change Biology*, **16**, 2145–2157.

Raubenheimer, D., Simpson, S.J. & Mayntz, D. (2009) Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology*, **23**, 4–16.

R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*. R Foundation For Statistical Computing, Vienna, Austria.

R Development Core Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation For Statistical Computing, Vienna, Austria.

R Development Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation For Statistical Computing, Vienna, Austria.

Redfield, A.C. (1958) The biological control of chemical factors in the environment. *American Scientist*, **46**, 205–221.

Reiners, W.A. (1986) Complementary models for ecosystems. *The American Naturalist*, **127**, 59–73.

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514.

Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, **11**, 1216–1228.

Riede, J.O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C.R. & Jonsson, T. (2011) Stepping in Elton´s footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, **14**, 169–178.

Rogers, D. (1972) Random Search and Insect Population Models. *Journal of Animal Ecology*, **41**, 369–383.

Rousk, J., Brookes, P.C. & Bååth, E. (2009) Contrasting Soil pH Effects on Fungal and Bacterial Growth Suggest Functional Redundancy in Carbon Mineralization. *Applied and Environmental Microbiology*, **75**, 1589–1596.

Rubner, M. (1883) Ueber den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Zeitschrift für Biologie, Z. Biol.*, **19**, 535–562.

Ruf, A., Kuzyakov, Y. & Lopatovskaya, O. (2006) Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labelling and ^{13}C natural abundance. *Soil Biology and Biochemistry*, **38**, 2390–2400.

Salamon, J.-A., Alphei, J., Ruf, A., Schaefer, M., Scheu, S., Schneider, K., Sührig, A. & Maraun, M. (2006) Transitory dynamic effects in the soil invertebrate community in a temperate deciduous forest: Effects of resource quality. *Soil Biology and Biochemistry*, **38**, 209–221.

Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J. & Brown, J.H. (2004) The predominance of quarter-power scaling in biology. *Functional Ecology*, **18**, 257–282.

Schaefer, M. (1991) The animal community: diversity and resources. *Röhrig, E., Ulrich, B. (eds), Temperate deciduous forests.* Ecosystems of the world. pp. 51–120. Elsevier, Amsterdam.

Schaefer, M. & Schauermann, J. (1990) The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia*, **34**, 299–314.

Scheu, S. (2002) The soil food web: structure and perspectives. *European Journal of Soil Biology*, **38**, 11–20.

Scheu, S. & Falca, M. (2000) The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia*, **123**, 285–296.

Scheu, S. & Schaefer, M. (1998) Bottom-up control of the soil macrofauna communitiy in a beechwood on limestone: manipulation of food resources. *Ecology*, **79**, 1573–1585.

Scheu, S. & Setälä, H. (2002) Multitrophic interactions in decomposer food webs. *Tscharntke, B., Hawkins, B.A. (eds), Multitrophic Level Interactions* pp.

223–264. Cambridge University Press, Cambridge.

Schmitz, O.J. (2003) Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters*, **6**, 156–163.

Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, **78**, 1388–1399.

Schneider, F.D. & Brose, U. (2013) Beyond diversity: how nested predator effects control ecosystem functions. *The Journal of Animal Ecology*, **82**, 64–71.

Schneider, F.D., Scheu, S. & Brose, U. (2012) Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters*, **15**, 436–443.

Schuler, M.S., Cooper, B.S., Storm, J.J., Sears, M.W. & Angilletta, M.J. (2011) Isopods Failed to Acclimate Their Thermal Sensitivity of Locomotor Performance during Predictable or Stochastic Cooling. *PLoS ONE*, **6**, e20905.

Seastedt, T.R. (1984) The Role of Microarthropods in Decomposition and Mineralization Processes. *Annual Review of Entomology*, **29**, 25–46.

Setälä, H. & Huhta, V. (1990) Evaluation of the soil fauna impact on decomposition in a simulated coniferous forest soil. *Biology and Fertility of Soils*, **10**, 163–169.

Sinsabaugh, R.L., Hill, B.H. & Follstad Shah, J.J. (2009) Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. *Nature*, **462**, 795–798.

Sohlström, E.H. (2013) Effect of land use and animal diversity on the decomposition of two common leaf species. Bachelor Thesis, University of Göttingen, Göttingen.

Sperfeld, E., Martin-Creuzburg, D. & Wacker, A. (2012) Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. *Ecology Letters*, **15**, 142–150.

Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M. & Wright, J.P. (2009a) Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology*, **90**, 1073–1083.

Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M. & Wright, J.P. (2009b) Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology*, **90**, 1073–1083.

Steel, C.G.H. (1993) Storage and translocation of integumentary calcium during the moult cycle of the terrestrial isopod Oniscus asellus (L.). *Canadian Journal of Zoology*, **71**, 4–10.

Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.

Swift, M.J. & Anderson, J.M. (1994) Biodiversity and Ecosystem Function in Agricultural Systems. *Biodiversity and Ecosystem Function* Springer Study Edition. (eds P.D.E.-D. Schulze & P.D.H.A. Mooney), pp. 15–41. Springer-Verlag, Berlin, Heidelberg, New York.

Swift, M.J., Andrén, O., Brussaard, L., Briones, M., Coûteaux, M.-M., Ekschmitt, K., Kjoller, A., Loiseau, P. & Smith, P. (1998) Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies. *Global Change Biology*, **4**, 729–743.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Sci. University of California Press, Berkely, Los Angeles.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C. & Lehman, C. (2004) Does Metabolic Theory apply to Community Ecology? It´s a matter of scale. *Ecology*, **85**, 1797–1799.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vasseur, D.A. & McCann, K.S. (2005) A Mechanistic Approach for Modeling Temperature-Dependent Consumer-Resource Dynamics. *The American Naturalist*, **166**, 184–198.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th ed. Springer New York, New York.

Vitousek, P.M. & Hooper, D.U. (1994) Biological Diversity and Terrestrial Ecosystem Biogeochemistry. *Biodiversity and Ecosystem Function* Springer Study Edition. (eds P.D.E.-D. Schulze & P.D.H.A. Mooney), pp. 3–14. Springer Berlin Heidelberg.

Vos, V.C.A., van Ruijven, J., Berg, M.P., Peeters, E.T.H.M. & Berendse, F. (2011) Macro-detritivore identity drives leaf litter diversity effects. *Oikos*, **120**, 1092–1098.

Vucic-Pestic, O., Birkhofer, K., Rall, B.C., Scheu, S. & Brose, U. (2010a) Habitat structure and prey aggregation determine the functional response in a soil predator–prey interaction. *Pedobiologia*, **53**, 307–312.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology*, **17**, 1301–1310.

Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010b) Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology*, **79**, 249–256.

Wagg, C., Bender, S.F., Widmer, F. & van der Heijden, M.G.A. (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 5266–5270.

Wall, D.H., Bardgett, R.D. & Kelly, E. (2010) Biodiversity in the dark. *Nature Geoscience*, **3**, 297–298.

Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.D.E., Dangerfield, M.J., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z., Ayuke, F.O., Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S., Henschel, J.R., Johnson, D.L., Jones, T.H., Kovarova, M., Kranabetter, J.M., Kutny, L., Lin, K.-C., Maryati, M., Masse, D., Pokarzhevskii, A., Rahman, H., Sabara, M.G., Salamon, J.-A., Swift, M.J., Varela, A., Vasconcelos, H.L., White, D. & Zou, X. (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, **14**, 2661–2677.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Putten, W.H. van der & Wall, D.H. (2004) Ecological Linkages Between Aboveground and Belowground Biota. *Science*, **304**, 1629–1633.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A General Model for the Origin of Allometric Scaling Laws in Biology. *Science*, **276**, 122–126.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, **22**, 323–330.

Williams, R.J. & Martinez, N.D. (2004) Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B - Condensed Matter*, **38**, 297–303.

Wolters, V. (2000) Invertebrate control of soil organic matter stability. *Biology and Fertility of Soils*, **31**, 1–19.

Wolters, V. (2001) Biodiversity of soil animals and its function. *European Journal of Soil Biology*, **37**, 221–227.

Woodward, G. (2009) Biodiversity, ecosystem functioning and food webs in fresh waters: assembling the jigsaw puzzle. *Freshwater Biology*, **54**, 2171–2187.

Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., Cross, W.F., Friberg, N., Ings, C., Jacob, U., Jennings, S., Ledger, M.E., Milner, A.M., Montoya, J.M., O`Gorman, E., Olesen, J.M., Petchey, O.L., Pichler, D.E., Reuman, D.C., Thompson, M.S.A., van Veen, F.J.F. & Yvon-Durocher, G. (2010) Ecological Networks in a Changing Climate. *Ecological Networks* Advances in Ecological Research. pp. 72–122. Academic Press.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–409.

Wootton, J.T. & Emmerson, M. (2005) Measurement of Interaction Strength in Nature. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 419–444.

Yodzis, P. & Innes, S. (1992) Body Size and Consumer-Resource Dynamics. *The American Naturalist*, **139**, 1151–1175.

Zimmer, M. (2002) Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. *Biological Reviews*, **77**, 455–493.

Zimmer, M. (2004) Effects of temperature and precipitation on a flood plain isopod community: a field study. *European Journal of Soil Biology*, **40**, 139–146.

Zimmer, M., Pennings, S.C., Buck, T.L. & Carefoot, T.H. (2002) Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Functional Ecology*, **16**, 596–607.

Zuur, A.F., Ieno, E.N. & Smith, G.M. (2007) *Analysing Ecological Data*. Springer, New York; London.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Supporting information - Chapter 3

Table 3.S1: Leaf litter quality. Contents of carbon (C), nitrogen (N), phosphorus (P) are given in milligram per gram dry weight with standard deviations. Corresponding ratios are shown. Leaf species were classified to different qualities and denoted by a quality index (Q), where 1 (i.e. ash) indicates the best quality.

Leaf species	C		N		P		C:N		C:P		N:P		Q
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	
Ash	432.9	1.0	15.6	1.9	0.7	0.3	28.0	3.4	704.5	343.6	24.6	9.3	1
Lime	457.7	13.8	13.5	1.9	0.5	0.2	34.2	3.7	918.5	325.2	27.6	11.7	2
Maple	432.9	7.0	9.7	0.1	0.3	< 0.01	44.5	1.1	1400.6	35.7	31.5	< 0.01	3
Beech	463.8	5.4	9.9	0.1	0.4	0.2	47.1	0.2	1499.9	823.8	31.9	17.6	4

s.d. standard deviation

Table 3.S2: Experimental design: realized species composition in the microcosms. Presence or absence of a particular species is coded with zero or one, respectively. We used the first-letter abbreviation of the species latin-binomial names: Gm indicates the pill millipedes (*Glomeris marginata*), Tt indicates the small isopods (*Trichorhina tomentosa*), Sc indicates the springtails (*Sinella curviseta*), Oa indicates the large isopods (*Oniscus asellus*), Ls indicates the centipedes (*Lithobius ssp.*) and Hm indicates the predatory mites (*Hypoaspis miles*). Further abbreviations code the design changed after Bell *et al*. (2009): P = partition series, Q = partitioned species pool, M = unique species composition, R.d and R.p = Richness of decomposers and predators, respectively. Ctr indicate the no animal controls.

No.	P	M	Q	R.d	R.p	Gm	Tt	Sc	Oa	Ls	Hm	No.	P	M	Q	R.d	R.p	Gm	Tt	Sc	Oa	Ls	Hm
1	1	1	1	4	0	1	1	1	1	0	0	37	2	5	4	2	1	0	1	0	1	0	1
2	1	3	3	2	0	1	1	0	0	0	0	38	2	6	4	2	1	1	0	1	0	0	1
3	1	4	3	2	0	0	0	1	1	0	0	39	2	11	6	1	1	0	0	1	0	0	1
4	1	7	5	1	0	0	0	1	0	0	0	40	2	12	6	1	1	0	0	0	1	0	1
5	1	8	5	1	0	1	0	0	0	0	0	41	2	13	6	1	1	0	1	0	0	0	1
6	1	9	5	1	0	0	1	0	0	0	0	42	2	14	6	1	1	1	0	0	0	0	1
7	1	10	5	1	0	0	0	0	1	0	0	43	1	1	1	4	2	1	1	1	1	1	1
8	2	2	2	4	0	1	1	1	1	0	0	44	1	3	3	2	2	1	1	0	0	1	1
9	2	5	4	2	0	0	1	0	1	0	0	45	1	4	3	2	2	0	0	1	1	1	1
10	2	6	4	2	0	1	0	1	0	0	0	46	1	7	5	1	2	0	0	1	0	1	1
11	2	11	6	1	0	0	0	1	0	0	0	47	1	8	5	1	2	1	0	0	0	1	1
12	2	12	6	1	0	0	0	0	1	0	0	48	1	9	5	1	2	0	1	0	0	1	1
13	2	13	6	1	0	0	1	0	0	0	0	49	1	10	5	1	2	0	0	0	1	1	1
14	2	14	6	1	0	1	0	0	0	0	0	50	2	2	2	4	2	1	1	1	1	1	1
15	1	1	1	4	1	1	1	1	1	1	0	51	2	5	4	2	2	0	1	0	1	1	1
16	1	3	3	2	1	1	1	0	0	1	0	52	2	6	4	2	2	1	0	1	0	1	1
17	1	4	3	2	1	0	0	1	1	1	0	53	2	11	6	1	2	0	0	1	0	1	1
18	1	7	5	1	1	0	0	1	0	1	0	54	2	12	6	1	2	0	0	0	1	1	1
19	1	8	5	1	1	1	0	0	0	1	0	55	2	13	6	1	2	0	1	0	0	1	1
20	1	9	5	1	1	0	1	0	0	1	0	56	2	14	6	1	2	1	0	0	0	1	1
21	1	10	5	1	1	0	0	0	1	1	0	57	ctr	ctr	ctr	0	0	0	0	0	0	0	0
22	2	2	2	4	1	1	1	1	1	1	0	58	ctr	ctr	ctr	0	0	0	0	0	0	0	0
23	2	5	4	2	1	0	1	0	1	1	0	59	ctr	ctr	ctr	0	0	0	0	0	0	0	0
24	2	6	4	2	1	1	0	1	0	1	0	60	ctr	ctr	ctr	0	0	0	0	0	0	0	0
25	2	11	6	1	1	0	0	1	0	1	0	61	ctr	ctr	ctr	0	0	0	0	0	0	0	0
26	2	12	6	1	1	0	0	0	1	1	0	62	ctr	ctr	ctr	0	0	0	0	0	0	0	0
27	2	13	6	1	1	0	1	0	0	1	0	63	ctr	ctr	ctr	0	0	0	0	0	0	0	0
28	2	14	6	1	1	1	0	0	0	1	0	64	ctr	ctr	ctr	0	0	0	0	0	0	0	0
29	1	1	1	4	1	1	1	1	1	0	1	65	ctr	ctr	ctr	0	0	0	0	0	0	0	0
30	1	3	3	2	1	1	1	0	0	0	1	66	ctr	ctr	ctr	0	0	0	0	0	0	0	0
31	1	4	3	2	1	0	0	1	1	0	1	67	ctr	ctr	ctr	0	0	0	0	0	0	0	0
32	1	7	5	1	1	0	0	1	0	0	1	68	ctr	ctr	ctr	0	0	0	0	0	0	0	0
33	1	8	5	1	1	1	0	0	0	0	1	69	ctr	ctr	ctr	0	0	0	0	0	0	0	0
34	1	9	5	1	1	0	1	0	0	0	1	70	ctr	ctr	ctr	0	0	0	0	0	0	0	0
35	1	10	5	1	1	0	0	0	1	0	1	71	ctr	ctr	ctr	0	0	0	0	0	0	0	0
36	2	2	2	4	1	1	1	1	1	0	1	72	ctr	ctr	ctr	0	0	0	0	0	0	0	0

Table 3.S3: Non-linear richness effects on residuals of the linear model that tested identity effects on leaf litter mass loss (step 2). Decomposer richness was used as a factor.

		Residuals of the 2nd step				
Response	Predictor	DF*	SSq†	MSq‡	F-value	p-value
Beech	Decomposer richness	3	0.01	<0.01	0.27	0.843
	Residual error	64	0.47	0.01		
Maple	Decomposer richness	3	0.06	0.02	1.66	0.184
	Residual error	66	0.76	0.01		
Lime	Decomposer richness	3	0.02	0.01	1.43	0.242
	Residual error	67	0.34	0.01		
Ash	Decomposer richness	3	<0.01	<0.01	0.25	0.860
	Residual error	67	0.39	0.01		

* Degrees of freedom, † Sum of squares, ‡ Mean squares

Table 3.S4: Correlation of species richness and leaf litter mass loss. Richness is total richness, decomposers and predators indicates the richness of these groups. Leaf litter mass loss is indicated by litter species or as combined mass loss of all species (i.e., total). The upper and lower diagonal parts contain correlation coefficient estimates and corresponding p – values, respectively. Method was Pearson´s Product moment correlation.

	Richness	Decomposers	Predators	Total	Beech	Maple	Lime	Ash
Richness	*****	**0.895**	**0.726**	**0.535**	**0.346**	0.164	**0.347**	**0.43**
Decomposers	**<0.001**	*****	**0.342**	**0.532**	**0.308**	0.083	**0.407**	**0.45**
Predators	**<0.001**	**0.003**	*****	**0.307**	**0.254**	0.217	0.105	0.2
Total	**<0.001**	**<0.001**	**0.009**	*****	**0.313**	**0.534**	**0.637**	**0.82**
Beech	**0.003**	**0.008**	**0.031**	**0.007**	*****	-0.02	-0.06	0.11
Maple	0.169	0.488	0.067	**<0.001**	0.872	*****	0.206	0.18
Lime	**0.003**	**<0.001**	0.382	**<0.001**	0.623	0.082	*****	**0.36**
Ash	**<0.001**	**<0.001**	0.085	**<0.001**	0.358	0.121	**0.002**	*****

Table 3.S5: Outlier elimination. Overview of microcosms that were skipped from further analyses of the subsets of each leaf litter type. Community composition is indicated.

		Community composition						
Microcosm No.	Leaf species	Decomposers*				Predators*		Control
		pill millipedes	large isopods	small isopods	springtails	centipedes	pred. mites	
3	Beech	-	1	-	1	-	-	-
7	Beech	-	1	-	-	-	-	-
19	Maple	1	-	-	-	1	-	-
44	Beech	1	-	1	-	1	1	-
58	Ash	-	-	-	-	-	-	1
71	Beech	-	-	-	-	-	-	1
72	Maple	-	-	-	-	-	-	1
72	Lime	-	-	-	-	-	-	1

* springtails = *Sinella curviseta*, small isopods = *Trichorhina tomentosa*, large isopods = *Oniscus asellus*, pill millipedes = *Glomeris marginata*, centipedes = *Lithobius ssp.*, predatory mites = *Hypoaspis miles*. Cosm indicates a microcosm as the experimental unit.

Supporting information - Chapter 4

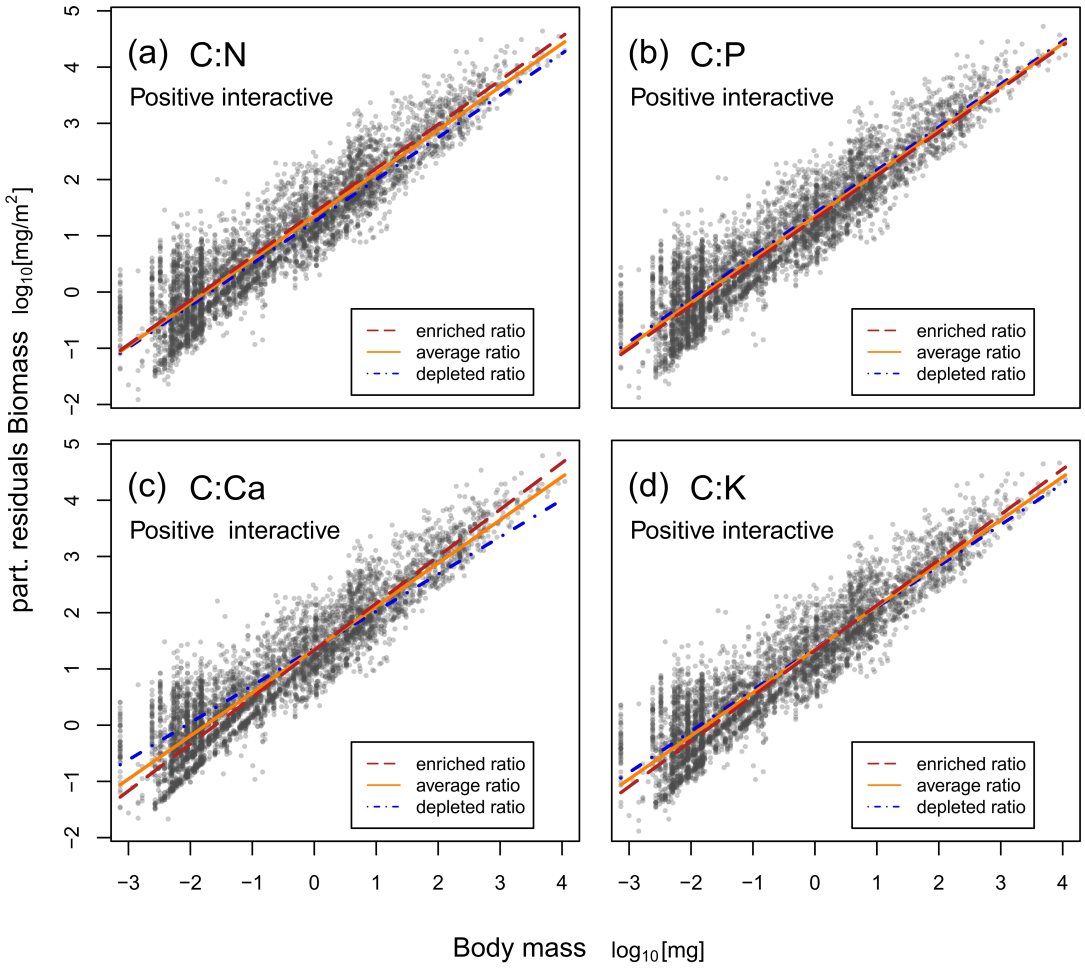

Figure 4.S1: Interactive effects of stoichiometry and body masses on population biomass densities with the altered random structure in comparison to the of the statistic model used in the manuscript. A nested random structure was applied (i.e. phylogenetic group is nested into sampling method which is nested into the factor region) in comparison to the simple random structure of the model in the manuscript (i.e., region as random factor). The spread in the residuals decreased. However, the interactive nature of the scaling relationships still holds in the more complex random model structure. Each panel shows the partial residuals of biomass densities depending on population average body masses and the scaling assuming average contents of the carbon-to-element ratios (average ratio, orange solid lines). Altered scaling relationships are shown with either the lowest (red dashed lines) or the highest (depleted ratio, blue dot-dashed lines) C:X ratios. Regressions are based on parameters according to Supp. Table 4.S2. Increasing intensity of grey points symbolizes differences in density of the data.

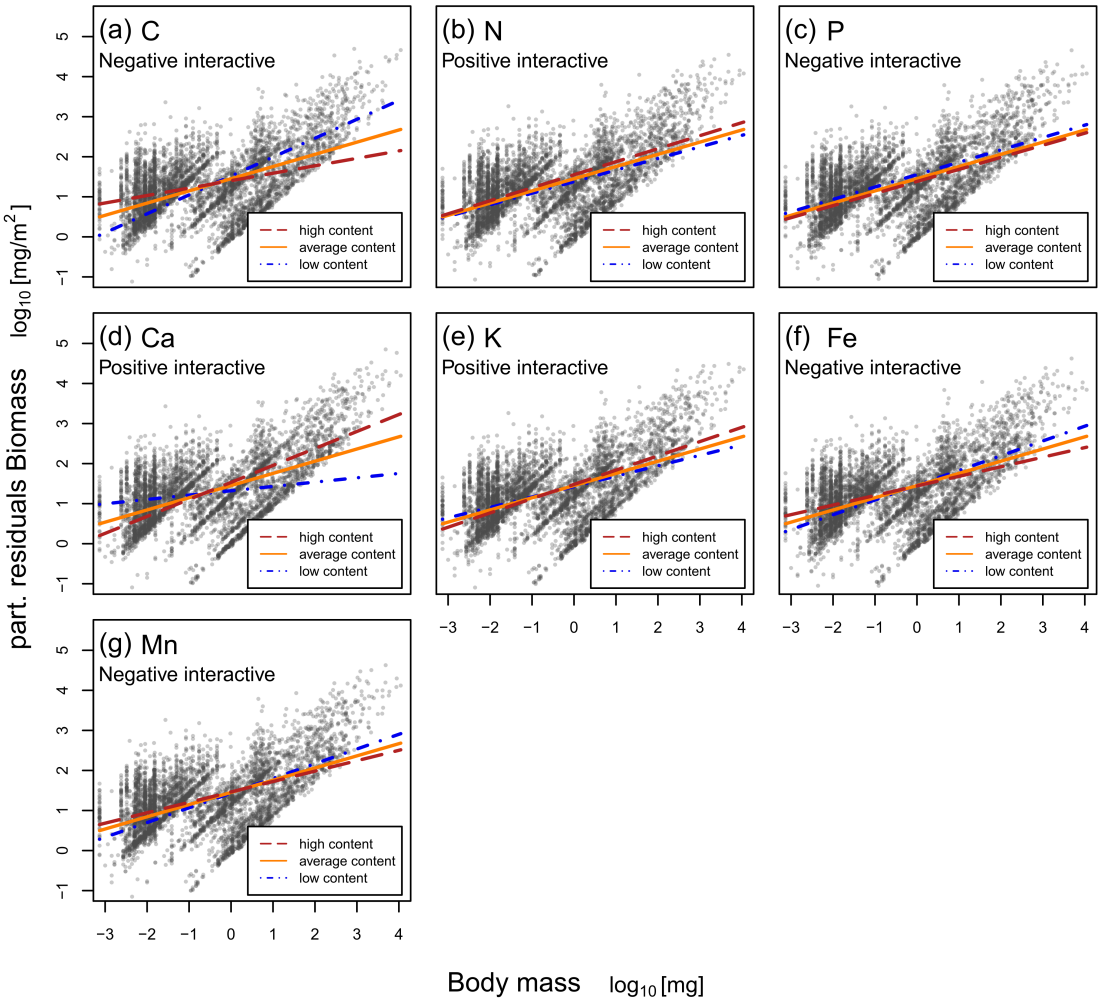

Figure 4.S2: Interactive effects of element availability and body masses on population biomass densities. Each panel shows the partial residuals of biomass densities depending on population average body masses and the scaling assuming average contents of each element (orange solid lines). Altered scaling relationships are shown with either the lowest. Altered scaling relationships are shown with either the highest (red dashed lines) or the lowest (blue dot-dashed lines) contents of an element. Regressions are based on parameters according to Supp. Table 4.S3. Increasing intensity of grey points symbolizes differences in density of the data.

Table 4.S1: Species list of the used dataset across all 48 forest sites.

species	phylogroup	family	feeding type	sampling	no
Abax ovalis	Coleoptera	Carabidae	predator	Sieve	859
Abax ovalis (juv)	Coleoptera	Carabidae	predator	Kempson	630
Abax parallelepipedus	Coleoptera	Carabidae	predator	Sieve	860
Abax parallelepipedus (juv)	Coleoptera	Carabidae	predator	Kempson	537
Abax parallelus (juv)	Coleoptera	Carabidae	predator	Kempson	86
Abax sp.	Coleoptera	Carabidae	predator	Sieve	881
Achipteria coleoptrata	Oribatida	Achipteriidae	detritivore	McFayden	295
Achipteria nitens	Oribatida	Achipteriidae	detritivore	McFayden	606
Acrotona crenata	Coleoptera	Stapylinidae	predator	Sieve	775
Acrotona sylvicola	Coleoptera	Stapylinidae	predator	Combination	132
Acrotrichis sp.	Coleoptera	Ptiliidae	detritivore	Kempson	126
Adoristes ovatus	Oribatida	Liacaridae	detritivore	McFayden	492
Adrastus sp. (juv)	Coleoptera	Elateridae	herbivore	Kempson	546
Aegopinella nitens	Pulmonata	Oxychilidae	detritivore	Sieve	809
Aegopinella nitens (juv)	Pulmonata	Oxychilidae	detritivore	Sieve	810
Aegopinella nitidula	Pulmonata	Oxychilidae	detritivore	Sieve	830
Aegopinella nitidula (juv)	Pulmonata	Oxychilidae	detritivore	Sieve	831
Aegopinella pura	Pulmonata	Oxychilidae	detritivore	Sieve	826
Aegopinella pura (juv)	Pulmonata	Oxychilidae	detritivore	Sieve	827
Agelenidae sp. (juv)	Araneae	Agelenidae	predator	Sieve	932
Agonum sexpunctatum (juv)	Coleoptera	Carabidae	predator	Kempson	538
Agonum sp. (juv)	Coleoptera	Carabidae	predator	Kempson	539
Agriotes acuminatus (juv)	Coleoptera	Elateridae	herbivore	Kempson	107
Agriotes aterrimus (juv)	Coleoptera	Elateridae	herbivore	Kempson	108
Agriotes sp.	Coleoptera	Elateridae	herbivore	Kempson	110
Agriotes sp. (juv)	Coleoptera	Elateridae	herbivore	Kempson	109
Agriotinae sp1 (juv)	Coleoptera	Elateridae	herbivore	Kempson	548
Agroeca cf brunnea (juv)	Araneae	Liocranidae	predator	Kempson	477
Aleochara sp.	Coleoptera	Stapylinidae	predator	Sieve	777
Aleocharinae sp1 (juv)	Coleoptera	Stapylinidae	predator	Kempson	130
Aleocharinae sp2	Coleoptera	Stapylinidae	predator	Combination	131
Allacma fusca	Collembola	Sminthuridae	detritivore	McFayden	1
Allaiulus nitidus (juv) {l}	Diplopoda	Julidae	detritivore	Kempson	752
Allaiulus nitidus (juv) {s}	Diplopoda	Julidae	detritivore	Kempson	382
Allaiulus nitidus {xl}	Diplopoda	Julidae	detritivore	Kempson	383
Allaiulus nitidus {xxl}	Diplopoda	Julidae	detritivore	Kempson	753
Allosuctobelba grandis	Oribatida	Suctobelbidae	predator	McFayden	296
Amara aenea	Coleoptera	Carabidae	predator	Sieve	886
Amaurobius fenestralis	Araneae	Amaurobiidae	predator	Sieve	990
Amaurobius sp. (juv)	Araneae	Amaurobiidae	predator	Combination	164
Amblyseius cf. nemorivagus	Mesostigmata	Phytoseinae	predator	McFayden	418
Amblyseius similifloridanus	Mesostigmata	Phytoseinae	predator	McFayden	198
Amerus polonicus	Oribatida	Ameridae	detritivore	McFayden	297
Anatis ocellata	Coleoptera	Coccinellidae	predator	Kempson	633
Anelasmocephalus cambridgei	Opiliones	Trogulidae	predator	Kempson	163
Anthicidae sp.	Coleoptera	Anthicidae	detritivore	Sieve	879
Anthicus flavipes	Coleoptera	Anthicidae	detritivore	Sieve	894
Anthicus floralis	Coleoptera	Anthicidae	detritivore	Sieve	883
Anthophagus caraboides	Coleoptera	Stapylinidae	predator	Sieve	778
Anyphaena accentuata (juv)	Araneae	Anyphaenidae	predator	Sieve	991
Apionidae sp.	Coleoptera	Apionidae	herbivore	Sieve	887
Aporectodea longa	Lumbricidae	Lumbricidae	detritivore	Mustard	575
Aporectodea longa (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	574
Aporrectodea caliginosa	Lumbricidae	Lumbricidae	detritivore	Mustard	271
Aporrectodea caliginosa (juv) {xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	272
Aporrectodea caliginosa (juv) {xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	740
Aporrectodea caliginosa (juv) {xxxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	741
Aporrectodea rosea	Lumbricidae	Lumbricidae	detritivore	Mustard	274
Aporrectodea rosea (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	275

Aporrectodea sp. (juv) {xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	277
Aporrectodea sp. (juv) {xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	742
Apostenus fuscus	Araneae	Liocranidae	predator	Sieve	958
Araneidae sp. (juv)	Araneae	Araneidae	predator	Sieve	959
Araniella cucurbitina	Araneae	Araneidae	predator	Sieve	971
Arctoseius magnanalis	Mesostigmata	Ascidae	predator	McFayden	199
Arianta arbustorum	Pulmonata	Helicidae	herbivore	Sieve	841
Arion ater	Pulmonata	Arionidae	detritivore	Sieve	828
Arion fuscus	Pulmonata	Arionidae	detritivore	Sieve	820
Arion intermedicus	Pulmonata	Arionidae	detritivore	Sieve	845
Arion silvaticus	Pulmonata	Arionidae	detritivore	Sieve	815
Arionidae sp.	Pulmonata	Arionidae	detritivore	Sieve	842
Armadillidium opacum	Isopoda	Armadillidae	detritivore	Kempson	639
Armadillidium sp.	Isopoda	Armadillidae	detritivore	Sieve	913
Arrhopalites pygmaeus	Collembola	Arrhopalitidae	detritivore	McFayden	2
Arrhophalites sp.	Collembola	Arrhopalitidae	detritivore	McFayden	676
Asca bicornis	Mesostigmata	Ascidae	predator	McFayden	646
Asthenargus paganus	Araneae	Linyphiidae	predator	Sieve	930
Atheta fungi	Coleoptera	Stapylinidae	predator	Kempson	133
Atheta myrmecobia	Coleoptera	Stapylinidae	predator	Kempson	134
Atheta sp.	Coleoptera	Stapylinidae	predator	Combination	135
Atheta sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	136
Athous haemorrhoidalis (juv)	Coleoptera	Elateridae	herbivore	Kempson	111
Athous sp. (juv)	Coleoptera	Elateridae	herbivore	Kempson	117
Athous subfuscus	Coleoptera	Elateridae	herbivore	Kempson	114
Athous subfuscus (juv) {l}	Coleoptera	Elateridae	herbivore	Kempson	720
Athous subfuscus (juv) {m}	Coleoptera	Elateridae	herbivore	Kempson	113
Athous vittatus (juv)	Coleoptera	Elateridae	herbivore	Kempson	115
Athous zebei (juv) {l}	Coleoptera	Elateridae	herbivore	Kempson	722
Athous zebei (juv) {m}	Coleoptera	Elateridae	herbivore	Kempson	721
Athous zebei (juv) {s}	Coleoptera	Elateridae	herbivore	Kempson	116
Atropacarus striculus	Oribatida	Phthiracaridae	detritivore	McFayden	298
Azeca goodalli	Pulmonata	Cochliopidae	detritivore	Sieve	843
Ballistura cf. hankoi	Collembola	Isotomidae	detritivore	McFayden	354
Ballus chalybeius	Araneae	Salticidae	predator	Kempson	165
Ballus chalybeius (juv)	Araneae	Salticidae	predator	Kempson	166
Bathyphantes gracilis	Araneae	Linyphiidae	predator	Sieve	938
Belba corynopus	Oribatida	Damaeidae	detritivore	McFayden	299
Berniniella bicarinata	Oribatida	Oppiidae	predator	McFayden	300
Berniniella conjuncta	Oribatida	Oppiidae	predator	McFayden	301
Berniniella dungeri	Oribatida	Oppiidae	predator	McFayden	607
Berniniella sigma	Oribatida	Oppiidae	predator	McFayden	493
Blaniulidae sp. (juv)	Diplopoda	Blaniulidae	detritivore	Kempson	481
Bolitochara sp.	Coleoptera	Stapylinidae	predator	Combination	551
Brachychthoniidae spp.	Oribatida	Brachychthoniidae	detritivore	McFayden	302
Brachyderinae sp.	Coleoptera	Curculionidae	herbivore	Sieve	871
Brachyiulus pusillus	Diplopoda	Julidae	detritivore	Kempson	491
Brachysomus sp.	Coleoptera	Curculionidae	herbivore	Sieve	864
Bryoporus sp.	Coleoptera	Stapylinidae	predator	Kempson	552
Buprestidae sp.	Coleoptera	Buprestidae	herbivore	Sieve	850
Byrrhidae sp.	Coleoptera	Byrrhidae	herbivore	Kempson	628
Bythinus acutangulus	Coleoptera	Pselaphidae	predator	Kempson	123
Calathus melanocephalus	Coleoptera	Carabidae	predator	Sieve	862
Callobius claustrarius	Araneae	Amaurobiidae	predator	Sieve	970
Campodea sp. {l}	Diplura	Campodeidae	predator	Kempson	749
Campodea sp. {m}	Diplura	Campodeidae	predator	Kempson	294
Cantharidae sp.	Coleoptera	Cantharidae	predator	Sieve	851
Cantharidae sp. (juv)	Coleoptera	Cantharidae	predator	Sieve	890
Carabidae sp.	Coleoptera	Carabidae	predator	Sieve	875
Carabidae sp. (juv)	Coleoptera	Carabidae	predator	Sieve	865
Carabidae sp1	Coleoptera	Carabidae	predator	Kempson	632
Carabodes coriaceus	Oribatida	Carabodidae	detritivore	McFayden	494

Carabodes femoralis	Oribatida	Carabodidae	detritivore	McFayden	495
Carabodes labyrinthicus	Oribatida	Carabodidae	detritivore	McFayden	304
Carabodes ornatus	Oribatida	Carabodidae	detritivore	McFayden	496
Carabodes subarcticus	Oribatida	Carabodidae	detritivore	McFayden	497
Carabus nemoralis	Coleoptera	Carabidae	predator	Sieve	901
Centomerus sylvaticus	Araneae	Linyphiidae	predator	Combination	167
Centromerus brevivulvatus	Araneae	Linyphiidae	predator	Kempson	582
Centromerus cavernarum	Araneae	Linyphiidae	predator	Kempson	583
Centromerus prudens	Araneae	Linyphiidae	predator	Sieve	950
Centromerus serratus	Araneae	Linyphiidae	predator	Kempson	674
Cepea hortensis	Pulmonata	Helicidae	herbivore	Sieve	838
Cepea hortensis (juv)	Pulmonata	Helicidae	herbivore	Sieve	839
Cepea nemoralis	Pulmonata	Helicidae	herbivore	Sieve	844
Cepheus cepheiformes	Oribatida	Cepheidae	detritivore	McFayden	498
Ceratinella brevis	Araneae	Linyphiidae	predator	Sieve	931
Ceratinella scabrosa	Araneae	Linyphiidae	predator	Sieve	972
Ceratophysella armata	Collembola	Hypogastruridae	detritivore	McFayden	3
Ceratophysella denticulata	Collembola	Hypogastruridae	detritivore	McFayden	4
Ceratophysella gibbosa	Collembola	Hypogastruridae	detritivore	McFayden	5
Ceratophysella sp.	Collembola	Hypogastruridae	detritivore	McFayden	678
Ceratophysella succinea	Collembola	Hypogastruridae	detritivore	McFayden	389
Ceratozetes gracilis	Oribatida	Ceratozetidae	detritivore	McFayden	305
Chamobates borealis	Oribatida	Chamobatidae	detritivore	McFayden	306
Chamobates cuspidatus	Oribatida	Chamobatidae	detritivore	McFayden	307
Chamobates pusillus	Oribatida	Chamobatidae	detritivore	McFayden	500
Chamobates subglobulus	Oribatida	Chamobatidae	detritivore	McFayden	499
Chamobates voigtsi	Oribatida	Chamobatidae	detritivore	McFayden	308
Chelidurella guentheri	Dermaptera	Forficulidae	predator	Sieve	993
Chordeuma silvestre	Diplopoda	Chordeumatidae	predator	Kempson	384
Chordeumatidae (juv) {m}	Diplopoda	Chordeumatidae	detritivore	Kempson	754
Chordeumatidae (juv) {s}	Diplopoda	Chordeumatidae	detritivore	Kempson	755
Chrysomelidae sp.	Coleoptera	Chrysomeldiae	detritivore	Sieve	866
Chrysomelidae sp. (juv)	Coleoptera	Chrysomeldiae	herbivore	Sieve	896
Clausilia bidentata	Pulmonata	Clausiliidae	herbivore	Sieve	832
Clausilia bidentata (juv)	Pulmonata	Clausiliidae	detritivore	Sieve	833
Clubiona comta	Araneae	Clubionidae	predator	Combination	169
Clubiona pallidula	Araneae	Clubionidae	predator	Sieve	986
Clubionidae (juv)	Araneae	Clubionidae	predator	Combination	584
Coccinella septempunctata	Coleoptera	Coccinellidae	predator	Sieve	902
Cochlicopa lubrica	Pulmonata	Cochlicopidae	predator	Sieve	834
Cochlodina laminata	Pulmonata	Clausiliidae	detritivore	Sieve	823
Coelotes sp. (juv) {l}	Araneae	Amaurobiidae	predator	Combination	168
Coelotes sp. (juv) {xl}	Araneae	Amaurobiidae	predator	Combination	728
Coelotes terrestris	Araneae	Amaurobiidae	predator	Sieve	170
Coleoptera sp.	Coleoptera	Coleoptera spec	detritivore	Sieve	863
Coleoptera sp. (juv)	Coleoptera	Coleoptera	herbivore	Sieve	857
Conosoma testaceum	Coleoptera	Stapylinidae	predator	Combination	553
Cordalia sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	554
Cornodendrolaelaps cf cornutulus	Mesostigmata	Rhodacaridae	predator	McFayden	647
Corrinidae sp. (juv)	Araneae	Corinnidae	predator	Sieve	988
Cossoninae sp.	Coleoptera	Curculionidae	herbivore	Kempson	545
Crychus caraboides	Coleoptera	Carabidae	predator	Sieve	877
Cryphoeca sp. (juv)	Araneae	Hahniidae	predator	Kempson	197
Cryptops hortensis	Chilopoda	Cryptopidae	predator	Combination	521
Cryptopygus garretti	Collembola	Isotomidae	detritivore	McFayden	6
Cryptorhynchinae sp.	Coleoptera	Curculionidae	herbivore	Kempson	103
Cultroribula bicultrata	Oribatida	Astegistidae	detritivore	McFayden	309
Curculionidae sp.	Coleoptera	Curculionidae	herbivore	Sieve	855
Curculionidae sp. (juv)	Coleoptera	Curculionidae	herbivore	Kempson	106
Cychrus attenuatus	Coleoptera	Carabidae	predator	Sieve	868
Cylisticus sp.	Isopoda	Cylisticidae	detritivore	Sieve	910
Cymberemaeus cymba	Oribatida	Cymberemaeidae	detritivore	McFayden	608

Dalopius marginatus (juv) {l}	Coleoptera	Elateridae	herbivore	Kempson	723
Dalopius marginatus (juv) {m}	Coleoptera	Elateridae	herbivore	Kempson	118
Damaeobelba minutissima	Oribatida	Damaeidae	detritivore	McFayden	501
Damaeus auritus	Oribatida	Damaeidae	detritivore	McFayden	502
Damaeus onustus	Oribatida	Damaeidae	detritivore	McFayden	310
Damaeus riparius	Oribatida	Damaeidae	detritivore	McFayden	311
Dendrobaena octaedra	Lumbricidae	Lumbricidae	detritivore	Mustard	289
Dendrobaena octaedra (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	290
Dendrobaena pygmaea	Lumbricidae	Lumbricidae	detritivore	Mustard	293
Dendrodrilus rubidus	Lumbricidae	Lumbricidae	detritivore	Mustard	291
Dendrodrilus rubidus (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	292
Desoria violacea	Collembola	Isotomidae	detritivore	McFayden	7
Deuteraphorura inermis	Collembola	Onychiuridae	detritivore	McFayden	8
Deuterosminthurus pallipes	Collembola	Bourletiellidae	detritivore	McFayden	10
Deuterosminthurus sp.	Collembola	Bourletiellidae	detritivore	McFayden	9
Dictyna latens	Araneae	Dictynidae	predator	Sieve	953
Dictynidae sp. (juv)	Araneae	Dictynidae	predator	Sieve	979
Dicymbium brevisetosum	Araneae	Linyphiidae	predator	Sieve	964
Dicyrtoma fusca	Collembola	Sminthuridae	detritivore	McFayden	391
Dicyrtomina ornata	Collembola	Dicyrtomidae	detritivore	McFayden	679
Dinychus perforatus	Mesostigmata	Urodinychidae	predator	McFayden	203
Dinychus perforatus (juv)	Mesostigmata	Urodinychidae	predator	McFayden	204
Diplocephalus latifrons	Araneae	Linyphiidae	predator	Kempson	171
Diplocephalus picinus	Araneae	Linyphiidae	predator	Combination	172
Diplostyla concolor	Araneae	Linyphiidae	predator	Combination	472
Diplostyla concolor (juv)	Araneae	Linyphiidae	predator	Kempson	585
Discus rotundatus	Pulmonata	Patulidae	detritivore	Sieve	811
Discus rotundatus (juv)	Pulmonata	Patulidae	detritivore	Sieve	812
Dissorhina ornata	Oribatida	Oppiidae	predator	McFayden	312
Domene scabricollis	Coleoptera	Stapylinidae	predator	Combination	137
Donacochara speciosa	Araneae	Linyphiidae	predator	Sieve	968
Drusilla canaliculata	Coleoptera	Stapylinidae	predator	Sieve	779
Edwarzetes edwardsii	Oribatida	Ceratozetidae	detritivore	McFayden	609
Elater ferrugineus (juv)	Coleoptera	Elateridae	predator	Kempson	547
Elateridae sp.	Coleoptera	Elateridae	herbivore	Sieve	861
Elateridae sp1 (juv) {l}	Coleoptera	Elateridae	herbivore	Kempson	724
Elateridae sp1 (juv) {m}	Coleoptera	Elateridae	herbivore	Kempson	119
Ena montana	Pulmonata	Enidae	detritivore	Sieve	802
Ena montana (juv)	Pulmonata	Enidae	detritivore	Sieve	803
Eniochthonius minutissimus	Oribatida	Eniochthoniidae	detritivore	McFayden	313
Enoplognatha ovata	Araneae	Theridiidae	predator	Sieve	965
Entomobrya cf. multifasciata	Collembola	Entomobryidae	detritivore	McFayden	441
Entomobrya corticalis	Collembola	Entomobryidae	detritivore	McFayden	438
Entomobrya quinquelineata	Collembola	Entomobryidae	detritivore	McFayden	454
Entomobrya sp.	Collembola	Entomobryidae	detritivore	McFayden	11
Entomobryidae (juv).	Collembola	Entomobryidae	detritivore	McFayden	681
Epicrius canestrinii	Mesostigmata	Epicriidae	predator	McFayden	205
Epicrius cf. spinituberculatus	Mesostigmata	Epicriidae	predator	McFayden	648
Epicrius schusteri	Mesostigmata	Epicriidae	predator	McFayden	206
Epicrius sp. (juv)	Mesostigmata	Epicriidae	predator	McFayden	207
Epidamaeus setiger	Oribatida	Damaeidae	detritivore	McFayden	610
Erigonella hiemalis	Araneae	Linyphiidae	predator	Combination	466
Ero furcata	Araneae	Mimetidae	predator	Sieve	945
Erotylidae sp.	Coleoptera	Erotylidae	detritivore	Sieve	898
Euconulus fulvus	Pulmonata	Euconulidae	detritivore	Sieve	821
Eulohmannia ribagai	Oribatida	Eulohmanniidae	detritivore	McFayden	314
Euophrys frontalis	Araneae	Salticidae	predator	Sieve	936
Euophrys herbigrada	Araneae	Salticidae	predator	Sieve	974
Eupelops hirtus	Oribatida	Phenopelopidae	detritivore	McFayden	315
Eupelops plicatus	Oribatida	Phenopelopidae	detritivore	McFayden	316
Eupelops torulosus	Oribatida	Phenopelopidae	detritivore	McFayden	503
Eurocoelotes inermis	Araneae	Amaurobiidae	predator	Sieve	949

Euryopis flavomaculata	Araneae	Theridiidae	predator	Combination	479
Eusphalerum sp.	Coleoptera	Stapylinidae	predator	Combination	139
Euzetes globulus	Oribatida	Euzetidae	detritivore	McFayden	317
Evarcha arcuata	Araneae	Salticidae	predator	Sieve	989
Eviphis sp. (juv)	Mesostigmata	Eviphididae	predator	McFayden	419
Folsomia brevicauda	Collembola	Isotomidae	detritivore	McFayden	458
Folsomia fimetaria	Collembola	Isotomidae	detritivore	McFayden	12
Folsomia ksenemani	Collembola	Isotomidae	detritivore	McFayden	683
Folsomia litsteri	Collembola	Isotomidae	detritivore	McFayden	13
Folsomia quadrioculata	Collembola	Isotomidae	detritivore	McFayden	14
Folsomia sp. (juv)	Collembola	Isotomidae	detritivore	McFayden	682
Folsomia spinosa	Collembola	Isotomidae	detritivore	McFayden	15
Forficula auricularia	Dermaptera	Forficulidae	predator	Sieve	994
Fosseremus laciniatus	Oribatida	Damaeolidae	detritivore	McFayden	318
Friesea claviseta	Collembola	Neanuridae	predator	McFayden	476
Friesea mirabilis	Collembola	Neanuridae	predator	McFayden	16
Friesea truncata	Collembola	Neanuridae	predator	McFayden	17
Fuscozetes setosus	Oribatida	Ceratozetidae	detritivore	McFayden	611
Galumna lanceata	Oribatida	Galumnidae	detritivore	McFayden	319
Galumna tarsipennata	Oribatida	Galumnidae	detritivore	McFayden	504
Gamasina sp. (juv)	Mesostigmata	Gamasina	predator	McFayden	208
Geholaspis aeneus	Mesostigmata	Macrochelidae	predator	McFayden	209
Geholaspis longispinosus	Mesostigmata	Macrochelidae	predator	McFayden	421
Geholaspis longispinosus (juv)	Mesostigmata	Macrochelidae	predator	McFayden	420
Geholaspis mandibularis	Mesostigmata	Macrochelidae	predator	McFayden	210
Geholaspis mandibularis (juv.)	Mesostigmata	Macrochelidae	predator	McFayden	650
Geholaspis sp. (juv)	Mesostigmata	Macrochelidae	predator	McFayden	211
Geophilomorpha sp.	Chilopoda	Geophilomorpha spec	predator	Sieve	921
Geophilus electricus	Chilopoda	Geophilidae	predator	Kempson	76
Geophilus electricus (juv)	Chilopoda	Geophilidae	predator	Kempson	605
Geophilus flavus	Chilopoda	Geophilidae	predator	Kempson	78
Geophilus flavus (juv)	Chilopoda	Geophilidae	predator	Kempson	601
Geophilus insculptus	Chilopoda	Geophilidae	predator	Kempson	75
Geophilus ribauti	Chilopoda	Geophilidae	predator	Kempson	74
Geophilus ribauti (juv)	Chilopoda	Geophilidae	predator	Kempson	595
Geophilus studeri	Chilopoda	Geophilidae	predator	Kempson	596
Geophilus Studeri (juv)	Chilopoda	Geophilidae	predator	Kempson	594
Geophilus truncorum	Chilopoda	Geophilidae	predator	Kempson	527
Geostiba circellaris	Coleoptera	Stapylinidae	predator	Kempson	140
Geotrupidae sp.	Coleoptera	Geotrupidae	detritivore	Sieve	892
Gisianus flammeolus	Collembola	Katiannidae	detritivore	McFayden	18
Glomeris connexa	Diplopoda	Glomeridae	detritivore	Kempson	388
Glomeris conspersa {l}	Diplopoda	Glomeridae	detritivore	Kempson	390
Glomeris conspersa {xl}	Diplopoda	Glomeridae	detritivore	Kempson	756
Glomeris hexasticha	Diplopoda	Glomeridae	detritivore	Kempson	640
Glomeris marginata	Diplopoda	Glomeridae	detritivore	Kempson	392
Glomeris sp.	Diplopoda	Glomeridae	detritivore	Sieve	920
Glomeris sp. (juv) {m}	Diplopoda	Glomeridae	detritivore	Kempson	393
Glomeris sp. (juv) {xl}	Diplopoda	Glomeridae	detritivore	Kempson	757
Glomeris undulata	Diplopoda	Glomeridae	detritivore	Kempson	394
Gnaphosidae sp. (juv)	Araneae	Gnaphosidae	predator	Combination	173
Gonatium rubens	Araneae	Linyphiidae	predator	Sieve	969
Gongylidiellum latebricola	Araneae	Linyphiidae	predator	Combination	470
Gyrohypnus sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	141
Habrocerus capillaricornis	Coleoptera	Stapylinidae	predator	Combination	142
Hahnia pusilla	Araneae	Hahniidae	predator	Combination	175
Hahnia pusilla (juv)	Araneae	Hahniidae	predator	Kempson	174
Hahniidae sp. (juv)	Araneae	Hahniidae	predator	Combination	578
Haplodrassus silvstris	Araneae	Gnaphosidae	predator	Sieve	982
Haplodrassus soerenseni	Araneae	Gnaphosidae	predator	Kempson	478
Haplophthalmus mengei	Isopoda	Trichoniscidae	detritivore	Kempson	381
Harpactea lepida	Araneae	Dysderidae	predator	Combination	177

Harpactea lepida (juv)	Araneae	Dysderidae	predator	Combination	176
Harpalinae sp.	Coleoptera	Carabidae	predator	Sieve	884
Harpalus affinis	Coleoptera	Carabidae	predator	Sieve	888
Harpalus latus	Coleoptera	Carabidae	predator	Kempson	87
Harpalus sp.	Coleoptera	Carabidae	predator	Combination	88
Helicidae sp. (juv)	Pulmonata	Helicidae	herbivore	Sieve	825
Helicigona lapicida	Pulmonata	Helicidae	detritivore	Sieve	804
Helicodonta obvoluta	Pulmonata	Helicodontidae	herbivore	Sieve	805
Helicodonta obvoluta (juv)	Pulmonata	Helicodontidae	herbivore	Sieve	806
Hermannia gibba	Oribatida	Hermanniidae	detritivore	McFayden	320
Heterothops dissimilis	Coleoptera	Stapylinidae	predator	Sieve	780
Heterothops dissimilis (juv)	Coleoptera	Stapylinidae	predator	Kempson	555
Heterothops sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	143
Histeridae sp.	Coleoptera	Histeridae	predator	Kempson	120
Histopona torpida	Araneae	Agelenidae	predator	Sieve	937
Holoparasitus stramenti	Mesostigmata	Pergamasinae	predator	McFayden	212
Hungarobelba pyrenaica	Oribatida	Belbodamaeidae	detritivore	McFayden	612
Hymenaphorura sp. (juv)	Collembola	Onychiuridae	detritivore	McFayden	684
Hypoaspididae sp. (juv)	Mesostigmata	Hypoaspididae	predator	McFayden	671
Hypoaspis aculeifer	Mesostigmata	Hypoaspididae	predator	McFayden	213
Hypoaspis aculeifer (juv)	Mesostigmata	Hypoaspididae	predator	McFayden	422
Hypochthonius luteus	Oribatida	Hypochthoniidae	predator	McFayden	321
Hypochthonius rufulus	Oribatida	Hypochthoniidae	predator	McFayden	322
Hypogastrura burkilli	Collembola	Hypogastruridae	detritivore	McFayden	19
Hypogastrura purpurescens	Collembola	Hypogastruridae	detritivore	McFayden	20
Isotoma cf viridis (juv)	Collembola	Isotomidae	detritivore	McFayden	686
Isotoma hiemalis	Collembola	Isotomidae	detritivore	McFayden	685
Isotomidae sp.	Collembola	Isotomidae	detritivore	McFayden	21
Isotomiella minor	Collembola	Isotomidae	detritivore	McFayden	22
Isotomurus palustris	Collembola	Isotomidae	detritivore	McFayden	23
Jugatala angulata	Oribatida	Ceratozetidae	detritivore	McFayden	613
Julidae sp.	Diplopoda	Julidae	detritivore	Combination	486
Julidae sp. (juv) {l}	Diplopoda	Julidae	detritivore	Kempson	758
Julidae sp. (juv) {m}	Diplopoda	Julidae	detritivore	Kempson	395
Lamprohiza splendidula (juv)	Coleoptera	Lampyridae	predator	Kempson	121
Lasioseius lawrencei	Mesostigmata	Podocinidae	predator	McFayden	423
Lathrididae sp.	Coleoptera	Lathrididae	detritivore	Kempson	635
Lathrimaeum atrocephalum	Coleoptera	Stapylinidae	predator	Sieve	781
Lathrobium brunnipes	Coleoptera	Stapylinidae	predator	Combination	556
Lathrobium fulvipenne	Coleoptera	Stapylinidae	predator	Sieve	782
Lathrobium sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	557
Lehmannia marginata	Pulmonata	Limacidae	detritivore	Sieve	846
Leioseius bicolor	Mesostigmata	Ascidae	predator	McFayden	214
Leioseius elongatus	Mesostigmata	Ascidae	predator	McFayden	424
Leitneria granulata	Mesostigmata	Halolaelapidae	predator	McFayden	464
Leitneria granulata (juv)	Mesostigmata	Halolaelapidae	predator	McFayden	215
Lepidocyrtus curvicolis	Collembola	Entomobryidae	detritivore	McFayden	687
Lepidocyrtus cyaneus	Collembola	Entomobryidae	detritivore	McFayden	24
Lepidocyrtus lanuginosus	Collembola	Entomobryidae	detritivore	McFayden	25
Lepidocyrtus lignorum	Collembola	Entomobryidae	detritivore	McFayden	688
Lepidocyrtus sp. (juv)	Collembola	Entomobryidae	detritivore	McFayden	689
Leptacinus sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	558
Leptogamasus cf. tectegynellus	Mesostigmata	Pergamasinae	predator	McFayden	425
Leptogamasus sp.	Mesostigmata	Pergamasinae	predator	McFayden	426
Leptogamasus sp. (juv)	Mesostigmata	Pergamasinae	predator	McFayden	200
Leptogamasus suecicus	Mesostigmata	Pergamasinae	predator	McFayden	216
Leptusa sp.	Coleoptera	Stapylinidae	predator	Combination	559
Leucoparyphus sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	560
Liacarus coracinus	Oribatida	Liacaridae	detritivore	McFayden	614
Liacarus subterraneus	Oribatida	Liacaridae	detritivore	McFayden	615
Liacarus xylariae	Oribatida	Liacaridae	detritivore	McFayden	324
Liebstadia humerata	Oribatida	Scheloribatidae	detritivore	McFayden	325

Liebstadia similis	Oribatida	Scheloribatidae	detritivore	McFayden	326
Ligidium hypnorum	Isopoda	Ligiidae	detritivore	Combination	379
Limacidae sp.	Pulmonata	Limacidae	detritivore	Sieve	822
Limax cinereoniger	Pulmonata	Limacidae	detritivore	Sieve	829
Linyphia hortensis	Araneae	Linyphiidae	predator	Sieve	946
Linyphiidae (juv)	Araneae	Linyphiidae	predator	Combination	178
Linyphiidae cf Erigoniinae (juv) {m}	Araneae	Linyphiidae	predator	Kempson	759
Linyphiidae cf Erigoniinae (juv) {s}	Araneae	Linyphiidae	predator	Kempson	465
Liocranidae sp. (juv)	Araneae	Liocranidae	predator	Sieve	976
Liodidae sp. {l}	Coleoptera	Liodidae	detritivore	Kempson	122
Liodidae sp. {s}	Coleoptera	Liodidae	detritivore	Kempson	549
Liogluta longiuscula	Coleoptera	Stapylinidae	predator	Combination	146
Lipothrix lubbocki	Collembola	Sminthuridae	detritivore	McFayden	26
Lithobius mutabilis (juv)	Chilopoda	Lithobiidae	predator	Kempson	599
Lithobius aeruginosus (juv)	Chilopoda	Lithobiidae	predator	Kempson	593
Lithobius aeruginosus {l}	Chilopoda	Lithobiidae	predator	Kempson	764
Lithobius aeruginosus {m}	Chilopoda	Lithobiidae	predator	Kempson	763
Lithobius aeruginosus {s}	Chilopoda	Lithobiidae	predator	Kempson	592
Lithobius aulacopus	Chilopoda	Lithobiidae	predator	Kempson	63
Lithobius calcaratus	Chilopoda	Lithobiidae	predator	Kempson	523
Lithobius calcaratus (juv)	Chilopoda	Lithobiidae	predator	Kempson	602
Lithobius cf. aulacopus (juv)	Chilopoda	Lithobiidae	predator	Kempson	64
Lithobius cf. crassipes (juv)	Chilopoda	Lithobiidae	predator	Kempson	59
Lithobius cf. dentatus (juv)	Chilopoda	Lithobiidae	predator	Kempson	68
Lithobius cf. mutabilis	Chilopoda	Lithobiidae	predator	Kempson	524
Lithobius cf. mutabilis (juv)	Chilopoda	Lithobiidae	predator	Kempson	66
Lithobius crassipes	Chilopoda	Lithobiidae	predator	Kempson	58
Lithobius curtipes (juv)	Chilopoda	Lithobiidae	predator	Kempson	522
Lithobius curtipes {l}	Chilopoda	Lithobiidae	predator	Kempson	702
Lithobius curtipes {m}	Chilopoda	Lithobiidae	predator	Kempson	701
Lithobius curtipes {s}	Chilopoda	Lithobiidae	predator	Kempson	60
Lithobius dentatus	Chilopoda	Lithobiidae	predator	Kempson	67
Lithobius erythrocephalus	Chilopoda	Lithobiidae	predator	Kempson	525
Lithobius forficatus	Chilopoda	Lithobiidae	predator	Kempson	528
Lithobius forficatus (juv)	Chilopoda	Lithobiidae	predator	Kempson	529
Lithobius lapidicola	Chilopoda	Lithobiidae	predator	Kempson	600
Lithobius melanops	Chilopoda	Lithobiidae	predator	Kempson	62
Lithobius mutabilis	Chilopoda	Lithobiidae	predator	Kempson	65
Lithobius muticus	Chilopoda	Lithobiidae	predator	Kempson	57
Lithobius piceus	Chilopoda	Lithobiidae	predator	Kempson	61
Lithobius sp.	Chilopoda	Lithobiidae	predator	Combination	73
Lithobius sp. (juv) {l}	Chilopoda	Lithobiidae	predator	Kempson	704
Lithobius sp. (juv) {m}	Chilopoda	Lithobiidae	predator	Kempson	69
Lithobius sp1 {l}	Chilopoda	Lithobiidae	predator	Kempson	705
Lithobius sp1 {s}	Chilopoda	Lithobiidae	predator	Kempson	70
Lithobius sp2 {l}	Chilopoda	Lithobiidae	predator	Kempson	706
Lithobius sp2 {s}	Chilopoda	Lithobiidae	predator	Kempson	71
Lithobius sp3 {m}	Chilopoda	Lithobiidae	predator	Kempson	707
Lithobius sp3 {xs}	Chilopoda	Lithobiidae	predator	Kempson	72
Lithobius subtilis	Chilopoda	Lithobiidae	predator	Kempson	603
Lithobius tricuspis	Chilopoda	Lithobiidae	predator	Kempson	597
Lumbricidae sp. (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	577
Lumbricus castaneus	Lumbricidae	Lumbricidae	detritivore	Mustard	278
Lumbricus rubellus (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	282
Lumbricus rubellus (juv) {xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	281
Lumbricus rubellus (juv) {xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	744
Lumbricus rubellus{xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	280
Lumbricus rubellus{xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	743
Lumbricus sp. (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	283
Lumbricus terrestris	Lumbricidae	Lumbricidae	detritivore	Mustard	284
Lumbricus terrestris (juv) {xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	285
Lumbricus terrestris (juv) {xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	745

Lumbricus terrestris (juv) {xxxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	746
Luperus	Coleoptera	Chrysomeldiae	herbivore	Sieve	852
Lycosidae sp. (juv)	Araneae	Lycosidae	predator	Sieve	973
Lysigamasus celticus	Mesostigmata	Pergamasinae	predator	McFayden	651
Lysigamasus cf arcuatus	Mesostigmata	Pergamasinae	predator	McFayden	653
Lysigamasus cf conus	Mesostigmata	Pergamasinae	predator	McFayden	217
Lysigamasus cf rostriforceps	Mesostigmata	Pergamasinae	predator	McFayden	652
Lysigamasus cf runcatellus	Mesostigmata	Pergamasinae	predator	McFayden	427
Lysigamasus cf wasmanni	Mesostigmata	Pergamasinae	predator	McFayden	659
Lysigamasus cornutus	Mesostigmata	Pergamasinae	predator	McFayden	218
Lysigamasus digitulus	Mesostigmata	Pergamasinae	predator	McFayden	654
Lysigamasus jugincola	Mesostigmata	Pergamasinae	predator	McFayden	428
Lysigamasus lapponicus	Mesostigmata	Pergamasinae	predator	McFayden	219
Lysigamasus minorleitneriae	Mesostigmata	Pergamasinae	predator	McFayden	655
Lysigamasus misellus	Mesostigmata	Pergamasinae	predator	McFayden	656
Lysigamasus parunciger	Mesostigmata	Pergamasinae	predator	McFayden	657
Lysigamasus puerilis	Mesostigmata	Pergamasinae	predator	McFayden	220
Lysigamasus puerilis (juv)	Mesostigmata	Pergamasinae	predator	McFayden	430
Lysigamasus runcatellus	Mesostigmata	Pergamasinae	predator	McFayden	429
Lysigamasus sp.	Mesostigmata	Pergamasinae	predator	McFayden	431
Lysigamasus sp. (juv)	Mesostigmata	Pergamasinae	predator	McFayden	201
Lysigamasus truncellus	Mesostigmata	Pergamasinae	predator	McFayden	658
Lysigamasus vagabundus	Mesostigmata	Pergamasinae	predator	McFayden	222
Macrargus rufus	Araneae	Linyphiidae	predator	Combination	473
Macrocheles cf. dentatus (juv)	Mesostigmata	Macrochelidae	predator	McFayden	223
Macrocheles cf. opacus aciculatus	Mesostigmata	Macrochelidae	predator	McFayden	224
Macrocheles dentatus	Mesostigmata	Macrochelidae	predator	McFayden	225
Macrocheles montanus	Mesostigmata	Macrochelidae	predator	McFayden	226
Macrocheles opacus	Mesostigmata	Macrochelidae	predator	McFayden	432
Macrocheles sp.	Mesostigmata	Macrochelidae	predator	McFayden	433
Macrochelidae (juv)	Mesostigmata	Macrochelidae	predator	McFayden	669
Macrogastra ventricosa	Pulmonata	Clausiliidae	detritivore	Sieve	840
Malthinus seriepunctatus (juv)	Coleoptera	Cantharidae	predator	Kempson	629
Malthodes sp. (juv)	Coleoptera	Cantharidae	predator	Kempson	82
Maro minutus	Araneae	Linyphiidae	predator	Combination	467
Megalothorax minimus	Collembola	Neelidae	detritivore	McFayden	27
Megaphyllum projectum	Diplopoda	Julidae	detritivore	Kempson	485
Melogona cf. voigti	Diplopoda	Chordeumatidae	detritivore	Kempson	378
Mesaphorura italica	Collembola	Tullbergiidae	predator	McFayden	690
Mesaphorura jarmiliae	Collembola	Tullbergiidae	predator	McFayden	512
Mesaphorura macrochaeta	Collembola	Tullbergiidae	predator	McFayden	691
Mesaphorura sp.	Collembola	Tullbergiidae	predator	McFayden	28
Mesaphorura sylvatica	Collembola	Tullbergiidae	predator	McFayden	692
Mesaphorura tenuisensillata	Collembola	Tullbergiidae	predator	McFayden	693
Mesaphorura yosii	Collembola	Tullbergiidae	predator	McFayden	641
Metabelba pulverosa	Oribatida	Damaeidae	detritivore	McFayden	330
Metaphorura affinis	Collembola	Tullbergiidae	predator	McFayden	29
Metellina segmentata	Araneae	Tetragnathidae	predator	Sieve	948
Micanurida forsslundi	Collembola	Neanuridae	predator	McFayden	694
Micranurida cf sensillata	Collembola	Neanuridae	predator	McFayden	30
Micranurida granulata	Collembola	Neanuridae	predator	McFayden	31
Micranurida pygmaea	Collembola	Neanuridae	predator	McFayden	32
Micranurida sp. (juv)	Collembola	Neanuridae	predator	McFayden	695
Micraphorura absoloni	Collembola	Onychiuridae	detritivore	McFayden	33
Micrargus herbigradus	Araneae	Linyphiidae	predator	Combination	179
Micreremus brevipes	Oribatida	Micreremidae	detritivore	McFayden	505
Micreremus gracilior	Oribatida	Micreremidae	detritivore	McFayden	506
Microlestes minutulus	Coleoptera	Carabidae	predator	Sieve	895
Microlestes sp.	Coleoptera	Carabidae	predator	Kempson	540
Microlinyphia pusilla	Araneae	Linyphiidae	predator	Sieve	960
Microneta viaria	Araneae	Linyphiidae	predator	Combination	180
Microppia minus	Oribatida	Oppiidae	predator	McFayden	331

Microtritia minima	Oribatida	Euphthiracaroidae	detritivore	McFayden	507
Molops elatus	Coleoptera	Carabidae	predator	Kempson	89
Molops piceus	Coleoptera	Carabidae	predator	Sieve	885
Monachoides incarnatus	Pulmonata	Hygromiidae	detritivore	Sieve	818
Monachoides incarnatus (juv)	Pulmonata	Hygromiidae	detritivore	Sieve	819
Monocephalus fuscipes	Araneae	Linyphiidae	predator	Combination	588
Mycetoporus mulsanti	Coleoptera	Stapylinidae	predator	Kempson	561
Mycetoporus sp.	Coleoptera	Stapylinidae	predator	Combination	562
Nanhermannia elegantula	Oribatida	Nanhermanniidae	detritivore	McFayden	508
Nanhermannia nana	Oribatida	Nanhermanniidae	detritivore	McFayden	332
Nargus anisotomoides	Coleoptera	Catopidae	detritivore	Kempson	101
Nargus sp.	Coleoptera	Catopidae	detritivore	Kempson	544
Nargus wilkini	Coleoptera	Catopidae	detritivore	Kempson	102
Neanura muscorum	Collembola	Neanuridae	predator	McFayden	696
Neelides minutus	Collembola	Neelidae	detritivore	McFayden	34
Neobisium carcinoides	Pseudoscorpiones	Neobisidae	predator	Kempson	181
Neobisium sp.	Pseudoscorpiones	Neobisidae	predator	Combination	182
Neon reticulatus	Araneae	Salticidae	predator	Kempson	183
Neon reticulatus (juv)	Araneae	Salticidae	predator	Kempson	184
Neonaphorura dubosqi	Collembola	Tullbergiidae	predator	McFayden	697
Neotrichoppia confinis	Oribatida	Oppiidae	predator	McFayden	333
Neotullbergia ramicuspis	Collembola	Onychiuridae	detritivore	McFayden	698
Nesovitrea hammonis	Pulmonata	Oxychilidae	detritivore	Sieve	813
Nesovitrea hammonis (juv)	Pulmonata	Oxychilidae	detritivore	Sieve	814
Nitidulidae sp.	Coleoptera	Nitidulidae	herbivore	Sieve	878
Nothrus palustris	Oribatida	Nothridae	detritivore	McFayden	334
Nothrus silvestris	Oribatida	Nothridae	detritivore	McFayden	335
Notiophilus biguttatus	Coleoptera	Carabidae	predator	Combination	92
Notiophilus rufipes (juv)	Coleoptera	Carabidae	predator	Kempson	93
Notiophilus sp.	Coleoptera	Carabidae	predator	Sieve	874
Octolasion sp. (juv)	Lumbricidae	Lumbricidae	detritivore	Mustard	288
Octolasion tyrtaeum (juv) {xl}	Lumbricidae	Lumbricidae	detritivore	Mustard	287
Octolasion tyrtaeum (juv) {xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	748
Octolasion tyrtaeum{xxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	286
Octolasion tyrtaeum{xxxl}	Lumbricidae	Lumbricidae	detritivore	Mustard	747
Olophrum piceum	Coleoptera	Stapylinidae	predator	Kempson	563
Omalium sp.	Coleoptera	Stapylinidae	predator	Sieve	783
Oncopodura crassicornis	Collembola	Oncopoduridae	detritivore	McFayden	35
Oniscidae sp. (juv)	Isopoda	Oniscidae	detritivore	Kempson	377
Oniscus asellus	Isopoda	Oniscidae	detritivore	Combination	380
Onychiuridae	Collembola	Onychiuridae	detritivore	McFayden	36
Oodes helipioides	Coleoptera	Carabidae	predator	Sieve	897
Ophidiotrichus tectus	Oribatida	Oribatellidae	detritivore	McFayden	336
Oppiella acuminata	Oribatida	Oppiidae	predator	McFayden	509
Oppiella falcata	Oribatida	Oppiidae	predator	McFayden	337
Oppiella fallax	Oribatida	Oppiidae	predator	McFayden	510
Oppiella marginedentata	Oribatida	Oppiidae	predator	McFayden	340
Oppiella nova	Oribatida	Oppiidae	predator	McFayden	338
Oppiella obsoleta	Oribatida	Oppiidae	predator	McFayden	341
Oppiella propinqua	Oribatida	Oppiidae	predator	McFayden	511
Oppiella subpectinata	Oribatida	Oppiidae	predator	McFayden	339
Orchesella bifasciata	Collembola	Entomobryidae	detritivore	McFayden	37
Oribatella calcarata	Oribatida	Oribatellidae	detritivore	McFayden	342
Oribatida sp. (juv)	Oribatida	Oribatida	detritivore	McFayden	323
Oribatula tibialis	Oribatida	Oribatulidae	detritivore	McFayden	343
Othius punctulatus	Coleoptera	Stapylinidae	predator	Combination	148
Othius sp. (juv) {m}	Coleoptera	Stapylinidae	predator	Kempson	150
Othius sp. (juv) {s}	Coleoptera	Stapylinidae	predator	Kempson	769
Othius subuliformis	Coleoptera	Stapylinidae	predator	Combination	149
Otiorhynchus sp.	Coleoptera	Curculionidae	herbivore	Combination	104
Otioryhnchinae sp.	Coleoptera	Curculionidae	herbivore	Sieve	872
Oxypoda annularis	Coleoptera	Stapylinidae	predator	Combination	151

Oxypoda livipennis	Coleoptera	Stapylinidae	predator	Sieve	784
Oxypoda sp.	Coleoptera	Stapylinidae	predator	Combination	564
Oxytelus sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	152
Ozyptila particola	Araneae	Thomisidae	predator	Sieve	987
Ozyptila sp. (juv)	Araneae	Thomisidae	predator	Kempson	675
Ozyptila trux	Araneae	Thomisidae	predator	Sieve	967
Pachygnatha degeeri	Araneae	Tetragnathidae	predator	Sieve	984
Pachylaelaps bellicosus	Mesostigmata	Pachylaelapidae	predator	McFayden	434
Pachylaelaps cf. bellicosus (juv)	Mesostigmata	Pachylaelapidae	predator	McFayden	435
Pachylaelaps cf. vexillifer	Mesostigmata	Pachylaelapidae	predator	McFayden	660
Pachylaelaps fuscinuliger	Mesostigmata	Pachylaelapidae	predator	McFayden	227
Pachylaelaps laeuchlii	Mesostigmata	Pachylaelapidae	predator	McFayden	436
Pachylaelaps longisetosus	Mesostigmata	Pachylaelapidae	predator	McFayden	228
Pachylaelaps regularis	Mesostigmata	Pachylaelapidae	predator	McFayden	229
Pachylaelaps sp. (juv)	Mesostigmata	Pachylaelapidae	predator	McFayden	437
Pachylaelaps tesselatus	Mesostigmata	Pachylaelapidae	predator	McFayden	230
Pachyseius angustus	Mesostigmata	Macrochelidae	predator	McFayden	231
Pachyseius humeralis	Mesostigmata	Macrochelidae	predator	McFayden	232
Palliduphantes pallidus	Araneae	Linyphiidae	predator	Sieve	955
Pamagaeus bipustulatus	Coleoptera	Carabidae	predator	Sieve	900
Pantelozetes paolii	Oribatida	Thyrisomidae	detritivore	McFayden	344
Parachipteria punctata	Oribatida	Achipteriidae	detritivore	McFayden	616
Paragamasus sp.	Mesostigmata	Pergamasinae	predator	McFayden	670
Parasitidae (juv) {s}	Mesostigmata	Parasitidae	predator	McFayden	734
Parasitidae (juv) {xs}	Mesostigmata	Parasitidae	predator	McFayden	233
Paratullbergia callipygos	Collembola	Tullbergiidae	predator	McFayden	38
Paratullbergia macdougalli	Collembola	Tullbergiidae	predator	McFayden	772
Paratullbergia sp.	Collembola	Tullbergiidae	predator	McFayden	39
Pardosa lugubris	Araneae	Lycosidae	predator	Sieve	952
Pardosa sp. (juv)	Araneae	Lycosidae	predator	Kempson	590
Parisotoma notabilis	Collembola	Isotomidae	detritivore	McFayden	40
Pelecopsis radicicola	Araneae	Linyphiidae	predator	Combination	992
Pella sp.	Coleoptera	Stapylinidae	predator	Sieve	785
Pergalumna nervosa	Oribatida	Galumnidae	detritivore	McFayden	513
Pergamasinae (juv) {s}	Mesostigmata	Pergamasinae	predator	McFayden	735
Pergamasinae (juv) {xs}	Mesostigmata	Pergamasinae	predator	McFayden	234
Pergamasinae (male)	Mesostigmata	Pergamasinae	predator	McFayden	235
Pergamasus crassipes	Mesostigmata	Pergamasinae	predator	McFayden	236
Pergamasus norvegicus	Mesostigmata	Pergamasinae	predator	McFayden	439
Pergamasus quisquiliarum	Mesostigmata	Pergamasinae	predator	McFayden	440
Pergamasus septentrionalis	Mesostigmata	Pergamasinae	predator	McFayden	661
Pergamasus sp. (juv) {m}	Mesostigmata	Pergamasinae	predator	McFayden	736
Pergamasus sp. (juv) {s}	Mesostigmata	Pergamasinae	predator	McFayden	237
Phalacridae sp.	Coleoptera	Phalacridae	herbivore	Sieve	867
Phalangiidae sp. (juv)	Opiliones	Phalangiidae	predator	Combination	185
Philodromidae sp. (juv)	Araneae	Philodromidae	predator	Sieve	978
Philodromus dispar	Araneae	Philodromidae	predator	Sieve	977
Philonthus carbonarius	Coleoptera	Stapylinidae	predator	Combination	636
Philonthus sp.	Coleoptera	Stapylinidae	predator	Combination	153
Philoscia muscorum	Isopoda	Philosciidae	detritivore	Sieve	914
Phthiracarus affinis	Oribatida	Phthiracaridae	detritivore	McFayden	514
Phthiracarus anonymus	Oribatida	Phthiracaridae	detritivore	McFayden	345
Phthiracarus borosetosus	Oribatida	Phthiracaridae	detritivore	McFayden	346
Phthiracarus cf crenophilus	Oribatida	Phthiracaridae	detritivore	McFayden	617
Phthiracarus clavatus	Oribatida	Phthiracaridae	detritivore	McFayden	347
Phthiracarus compressus	Oribatida	Phthiracaridae	detritivore	McFayden	348
Phthiracarus crinitus	Oribatida	Phthiracaridae	detritivore	McFayden	618
Phthiracarus ferrugineus	Oribatida	Phthiracaridae	detritivore	McFayden	619
Phthiracarus globosus	Oribatida	Phthiracaridae	detritivore	McFayden	349
Phthiracarus italicus	Oribatida	Phthiracaridae	detritivore	McFayden	620
Phthiracarus laevigatus	Oribatida	Phthiracaridae	detritivore	McFayden	515
Phthiracarus lentulus	Oribatida	Phthiracaridae	detritivore	McFayden	350

Phthiracarus longulus	Oribatida	Phthiracaridae	detritivore	McFayden	351
Phthiracarus stramineus	Oribatida	Phthiracaridae	detritivore	McFayden	621
Phyllobius callacartus	Coleoptera	Curculionidae	herbivore	Sieve	854
Phyllobius oblongus	Coleoptera	Curculionidae	herbivore	Sieve	876
Phyllobius pyri	Coleoptera	Curculionidae	herbivore	Sieve	891
Phyllobius sp.	Coleoptera	Curculionidae	herbivore	Sieve	853
Phytoseinae sp. (juv)	Mesostigmata	Phytoseinae	predator	McFayden	238
Pilogalumna crassiclava	Oribatida	Galumnidae	detritivore	McFayden	516
Pilogalumna tenuiclava	Oribatida	Galumnidae	detritivore	McFayden	352
Platybunus sp.	Opiliones	Phalangiidae	predator	Kempson	471
Platynothrus peltifer	Oribatida	Camisiidae	detritivore	McFayden	353
Plectophoreus fischeri	Coleoptera	Pselaphidae	predator	Kempson	124
Pocadicnemis juncea	Araneae	Linyphiidae	predator	Sieve	951
Poecilus sp. (juv)	Coleoptera	Carabidae	predator	Kempson	541
Polydesmidae sp.	Diplopoda	Polydesmidae	detritivore	Combination	396
Polydesmus angustus	Diplopoda	Polydesmidae	detritivore	Kempson	484
Polydesmus angustus (juv)	Diplopoda	Polydesmidae	detritivore	Kempson	487
Polydesmus complanatus	Diplopoda	Polydesmidae	detritivore	Kempson	488
Polydesmus complanatus (juv)	Diplopoda	Polydesmidae	detritivore	Kempson	483
Polydesmus denticulatus	Diplopoda	Polydesmidae	detritivore	Kempson	642
Polydesmus inconstans	Diplopoda	Polydesmidae	detritivore	Kempson	480
Polydesmus sp. (juv)	Diplopoda	Polydesmidae	detritivore	Kempson	398
Polyxenus lagurus	Diplopoda	Polyxenidae	detritivore	Kempson	489
Porcellio conspersum	Isopoda	Porcellionidae	detritivore	Sieve	917
Porcellio dilatatus	Isopoda	Porcellionidae	detritivore	Kempson	643
Porcellio montanus	Isopoda	Porcellionidae	detritivore	Kempson	644
Porcellio sp.	Isopoda	Porcellionidae	detritivore	Sieve	915
Porcellio spinicornis	Isopoda	Porcellionidae	detritivore	Kempson	376
Porobelba spinosa	Oribatida	Damaeidae	detritivore	McFayden	355
Porrhomma microphthalmum	Araneae	Linyphiidae	predator	Sieve	944
Proisotoma minima	Collembola	Isotomidae	detritivore	McFayden	41
Proisotoma minuta	Collembola	Isotomidae	detritivore	McFayden	359
Protaphorura armata	Collembola	Onychiuridae	detritivore	McFayden	42
Protaphorura aurantiaca	Collembola	Onychiuridae	detritivore	McFayden	43
Protaphorura fimata	Collembola	Onychiuridae	detritivore	McFayden	360
Protaphorura quadriocellata	Collembola	Onychiuridae	detritivore	McFayden	362
Protaphorura sp.	Collembola	Onychiuridae	detritivore	McFayden	361
Proteroiulus fuscus	Diplopoda	Blaniulidae	detritivore	Kempson	482
Prozercon cf traeghardi	Mesostigmata	Zerconidae	predator	McFayden	662
Prozercon fimbriatus	Mesostigmata	Zerconidae	predator	McFayden	239
Prozercon fimbriatus (juv)	Mesostigmata	Zerconidae	predator	McFayden	240
Prozercon kochi	Mesostigmata	Zerconidae	predator	McFayden	443
Pseudachorutes cf dubius	Collembola	Neanuridae	predator	McFayden	44
Pseudachorutes subcrassus	Collembola	Neanuridae	predator	McFayden	45
Pseudanurophorus binoculatus	Collembola	Isotomidae	detritivore	McFayden	363
Pseudoparasitus placentulus	Mesostigmata	Hypoaspididae	predator	McFayden	444
Pseudoparasitus placentulus (juv)	Mesostigmata	Hypoaspididae	predator	McFayden	445
Pseudosinella alba	Collembola	Entomobryidae	detritivore	McFayden	364
Pseudosinella decipiens	Collembola	Entomobryidae	detritivore	McFayden	773
Pseudosinella immaculata	Collembola	Entomobryidae	detritivore	McFayden	46
Pseudosinella ksenemani	Collembola	Entomobryidae	detritivore	McFayden	367
Pterostichinae sp.	Coleoptera	Carabidae	predator	Sieve	893
Pterostichus burmeisteri	Coleoptera	Carabidae	predator	Kempson	95
Pterostichus chamaeleon (juv)	Coleoptera	Carabidae	predator	Kempson	542
Pterostichus longicollis	Coleoptera	Carabidae	predator	Kempson	96
Pterostichus oblongopunctatus	Coleoptera	Carabidae	predator	Kempson	97
Pterostichus sp.	Coleoptera	Carabidae	predator	Combination	543
Pterostichus strenuus	Coleoptera	Carabidae	predator	Kempson	98
Ptiliidae sp.	Coleoptera	Ptiliidae	detritivore	Sieve	873
Pulmonata sp. (juv)	Pulmonata	Pulmonata	detritivore	Sieve	835
Quadroppia hammerae	Oribatida	Quadroppiidae	detritivore	McFayden	622
Quadroppia monstruosa	Oribatida	Quadroppiidae	detritivore	McFayden	356

Quadroppia quadricarinata	Oribatida	Quadroppiidae	detritivore	McFayden	357
Quedius cinctus	Coleoptera	Stapylinidae	predator	Sieve	786
Quedius fuliginosus	Coleoptera	Stapylinidae	predator	Sieve	787
Quedius molochinus	Coleoptera	Stapylinidae	predator	Sieve	788
Quedius sp.	Coleoptera	Stapylinidae	predator	Sieve	789
Quedius sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	154
Rhagonycha lignosa	Coleoptera	Cantharidae	predator	Kempson	83
Rhodacarellus kreuzi	Mesostigmata	Rhodacaridae	predator	McFayden	241
Rhodacarus agrestis	Mesostigmata	Rhodacaridae	predator	McFayden	663
Rhodacarus agrestis (juv)	Mesostigmata	Rhodacaridae	predator	McFayden	672
Rhodacarus coronatus	Mesostigmata	Rhodacaridae	predator	McFayden	448
Rhodacarus coronatus (juv)	Mesostigmata	Rhodacaridae	predator	McFayden	447
Rhodacarus sp.	Mesostigmata	Rhodacaridae	predator	McFayden	449
Rhynchaeninae sp1	Coleoptera	Curculionidae	herbivore	Kempson	634
Rhynchaenus fagi	Coleoptera	Curculionidae	herbivore	Sieve	882
Rhysotritia duplicata	Oribatida	Euphthiracaroidae	detritivore	McFayden	517
Robertus lividus	Araneae	Theridiidae	predator	Combination	186
Robertus lividus (juv) {l}	Araneae	Theridiidae	predator	Kempson	762
Robertus lividus (juv) {m}	Araneae	Theridiidae	predator	Kempson	587
Robertus scoticus	Araneae	Theridiidae	predator	Kempson	579
Robertus sp.	Araneae	Theridiidae	predator	Kempson	591
Robertus sp. (juv) {l}	Araneae	Theridiidae	predator	Kempson	733
Robertus sp. (juv) {m}	Araneae	Theridiidae	predator	Kempson	187
Rugilus rufipes	Coleoptera	Stapylinidae	predator	Sieve	790
Saaristoa abnormis	Araneae	Linyphiidae	predator	Sieve	963
Saloca diceros	Araneae	Linyphiidae	predator	Combination	188
Salticidae sp. (juv)	Araneae	Salticidae	predator	Sieve	947
Scarabeidae sp. (juv)	Coleoptera	Scarabeidae	herbivore	Sieve	889
Scheloribates initialis	Oribatida	Scheloribatidae	detritivore	McFayden	518
Scheloribates laevigatus	Oribatida	Scheloribatidae	detritivore	McFayden	358
Schendyla nemorensis	Chilopoda	Schendylidae	predator	Kempson	77
Schendyla nemorensis (juv)	Chilopoda	Schendylidae	predator	Kempson	604
Scolopendrella cf. subnuda {m}	Symphyla	Scolopendrellidae	detritivore	Kempson	719
Scolopendrella cf. subnuda {s}	Symphyla	Scolopendrellidae	detritivore	Kempson	81
Scolytidae sp.	Coleoptera	Scolytidae	herbivore	Sieve	880
Scutigerella immaculata {m}	Symphyla	Scutigerellidae	detritivore	Kempson	718
Scutigerella immaculata {s}	Symphyla	Scutigerellidae	detritivore	Kempson	717
Scutigerella immaculata {xs}	Symphyla	Scutigerellidae	detritivore	Kempson	80
Scydmaenidae sp1 {m}	Coleoptera	Scydmanidae	predator	Kempson	128
Scydmaenidae sp1 {xxl}	Coleoptera	Scydmanidae	predator	Kempson	725
Scydmaenidae sp2	Coleoptera	Scydmanidae	predator	Kempson	129
Serica sp. (juv)	Coleoptera	Scarabeidae	herbivore	Kempson	550
Sitona sp.	Coleoptera	Curculionidae	herbivore	Sieve	870
Sminthuridae (juv).	Collembola	Sminthurididae	detritivore	McFayden	368
Sminthurides sp.	Collembola	Sminthurididae	detritivore	McFayden	47
Sminthurinus aureus	Collembola	Katiannidae	detritivore	McFayden	48
Sminthurinus niger	Collembola	Katiannidae	detritivore	McFayden	369
Sminthurinus sp. (juv)	Collembola	Katiannidae	detritivore	McFayden	49
Sminthurus viridis	Collembola	Sminthuridae	detritivore	McFayden	50
Sphaeridia pumilis	Collembola	Sminthurididae	detritivore	McFayden	370
Sphaerozetes piriformes	Oribatida	Ceratozetidae	detritivore	McFayden	623
Staphylinidae sp. (juv) {l}	Coleoptera	Stapylinidae	predator	Kempson	771
Staphylinidae sp. (juv) {s}	Coleoptera	Stapylinidae	predator	Kempson	162
Staphylinus erythropterus	Coleoptera	Stapylinidae	predator	Sieve	791
Steganacarus herculeanus	Oribatida	Phthiracaridae	detritivore	McFayden	519
Steganacarus magnus	Oribatida	Phthiracaridae	detritivore	McFayden	365
Stenaphorura denisi	Collembola	Tullbergiidae	predator	McFayden	51
Stenaphorura quadrispina	Collembola	Tullbergiidae	predator	McFayden	327
Stenus clavicornis	Coleoptera	Stapylinidae	predator	Combination	565
Stenus fuscicornis	Coleoptera	Stapylinidae	predator	Kempson	155
Stenus humilis	Coleoptera	Stapylinidae	predator	Kempson	566
Stenus impressus	Coleoptera	Stapylinidae	predator	Combination	567

Stenus mendicus	Coleoptera	Stapylinidae	predator	Kempson	568
Stenus sp.	Coleoptera	Stapylinidae	predator	Combination	569
Stilicus rufipes	Coleoptera	Stapylinidae	predator	Kempson	570
Stilicus sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	156
Strigamia acuminata	Chilopoda	Dignathodontidae	predator	Combination	79
Strigamia acuminata (juv)	Chilopoda	Dignathodontidae	predator	Kempson	598
Suctobelba altvateri	Oribatida	Suctobelbidae	predator	McFayden	366
Suctobelba trigona	Oribatida	Suctobelbidae	predator	McFayden	624
Suctobelbella sp.	Oribatida	Suctobelbidae	predator	McFayden	625
Supraphorura furcifera	Collembola	Onychiuridae	detritivore	McFayden	52
Synuchus nivalis	Coleoptera	Carabidae	predator	Sieve	899
Tachinus scapularis	Coleoptera	Stapylinidae	predator	Kempson	637
Tachypodoiulus niger	Diplopoda	Julidae	detritivore	Combination	399
Tachyporus obtusus	Coleoptera	Stapylinidae	predator	Combination	157
Tachyusa sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	158
Tapinocyba insecta	Araneae	Linyphiidae	predator	Combination	189
Tapinocyba pallens	Araneae	Linyphiidae	predator	Combination	190
Tapinocyba praecox	Araneae	Linyphiidae	predator	Combination	468
Tectocepheus minor	Oribatida	Tectocepheidae	detritivore	McFayden	371
Tectocepheus velatus alatus	Oribatida	Tectocepheidae	detritivore	McFayden	372
Tectocepheus velatus sarekensis	Oribatida	Tectocepheidae	detritivore	McFayden	373
Tectocepheus velatus	Oribatida	Tectocepheidae	detritivore	McFayden	626
Tenebrionidae sp.	Coleoptera	Tenebrionidae	detritivore	Kempson	573
Tenebrionidae sp. (juv)	Coleoptera	Tenebrionidae	detritivore	Kempson	572
Tenuiphantes flavipes	Araneae	Linyphiidae	predator	Kempson	469
Tenuiphantes mengei	Araneae	Linyphiidae	predator	Sieve	939
Tenuiphantes tenebricola	Araneae	Linyphiidae	predator	Kempson	191
Tenuiphantes tenuis	Araneae	Linyphiidae	predator	Sieve	940
Theridiidae sp. (juv)	Araneae	Theridiidae	predator	Sieve	942
Thomisidae sp. (juv)	Araneae	Thomisidae	predator	Sieve	954
Tomocerus baudoti	Collembola	Tomoceridae	detritivore	McFayden	328
Tomocerus flavescens	Collembola	Tomoceridae	detritivore	McFayden	53
Tomocerus minor	Collembola	Tomoceridae	detritivore	McFayden	329
Tomocerus minutus	Collembola	Tomoceridae	detritivore	McFayden	54
Tomocerus vulgaris	Collembola	Tomoceridae	detritivore	McFayden	55
Trachelipus rathkei	Isopoda	Trachelipidae	detritivore	Kempson	490
Trachelipus ratzeburgii	Isopoda	Trachelipidae	detritivore	Sieve	912
Trachelipus sp.	Isopoda	Trachelipidae	detritivore	Sieve	916
Trachytes aegrota	Mesostigmata	Trachytidae	predator	McFayden	242
Trachytes aegrota (juv) {s}	Mesostigmata	Trachytidae	predator	McFayden	737
Trachytes aegrota (juv) {xs}	Mesostigmata	Trachytidae	predator	McFayden	243
Trachytes pauperior (juv)	Mesostigmata	Trachytidae	predator	McFayden	245
Trachytes pauperior{s}	Mesostigmata	Trachytidae	predator	McFayden	738
Trechinae sp.	Coleoptera	Carabidae	predator	Sieve	869
Trechus sp. (juv)	Coleoptera	Carabidae	predator	Kempson	100
Trichia striolata	Pulmonata	Helicidae	detritivore	Sieve	816
Trichia striolata (juv)	Pulmonata	Helicidae	detritivore	Sieve	817
Trichoniscus pusillus {l}	Isopoda	Trichoniscidae	detritivore	Kempson	751
Trichoniscus pusillus {m}	Isopoda	Trichoniscidae	detritivore	Kempson	750
Trichoniscus pusillus {s}	Isopoda	Trichoniscidae	detritivore	Kempson	375
Trichoniscus pygmaeus	Isopoda	Trichoniscidae	detritivore	Kempson	645
Trichoniscus sp.	Isopoda	Trichoniscidae	detritivore	Sieve	911
Trichoribates novus	Oribatida	Ceratozetidae	detritivore	McFayden	627
Trichouropoda cf. obscura (juv)	Mesostigmata	Trematuridae	predator	McFayden	664
Trichouropoda ovalis	Mesostigmata	Trematuridae	predator	McFayden	450
Trimium brevicorne	Coleoptera	Pselaphidae	predator	Kempson	125
Tritegeus bisulcatus	Oribatida	Cepheidae	detritivore	McFayden	374
Trochosa sp. (juv)	Araneae	Lycosidae	predator	Kempson	475
Trogulus nepaeformis	Opiliones	Trogulidae	predator	Kempson	589
Trogulus sp. (juv)	Opiliones	Trogulidae	predator	Combination	586
Trogulus tricarinatus	Opiliones	Trogulidae	predator	Kempson	192
Trombidiidae	Prostigmata	Trombidiidae	predator	Kempson	193

Tropiphorus sp.	Coleoptera	Curculionidae	herbivore	Kempson	105
Troxochrus nasutus	Araneae	Linyphiidae	predator	Kempson	581
Urodiaspis shcherbakae	Mesostigmata	Urodinychidae	predator	McFayden	451
Urodiaspis tecta	Mesostigmata	Urodinychidae	predator	McFayden	452
Urodiaspis tecta (juv)	Mesostigmata	Urodinychidae	predator	McFayden	246
Uropoda athiasae	Mesostigmata	Uropodidae	predator	McFayden	247
Uropoda athiasae (juv)	Mesostigmata	Uropodidae	predator	McFayden	673
Uropoda cassidea	Mesostigmata	Uropodidae	predator	McFayden	248
Uropoda cassidea (juv)	Mesostigmata	Uropodidae	predator	McFayden	249
Uropoda cf splendida (juv)	Mesostigmata	Uropodidae	predator	McFayden	250
Uropoda minima	Mesostigmata	Uropodidae	predator	McFayden	251
Uropoda minima (juv)	Mesostigmata	Uropodidae	predator	McFayden	252
Uropodina sp. (juv)	Mesostigmata	Uropodidae	predator	McFayden	253
Uroseius cylindricus	Mesostigmata	Polyaspidae	predator	McFayden	254
Uroseius cylindricus (juv)	Mesostigmata	Polyaspidae	predator	McFayden	255
Veigaia agilis	Mesostigmata	Veigaiaidae	predator	McFayden	256
Veigaia cerva	Mesostigmata	Veigaiaidae	predator	McFayden	257
Veigaia cerva (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	258
Veigaia cf agilis (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	259
Veigaia cf mollis (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	665
Veigaia cf propingua (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	455
Veigaia exigua	Mesostigmata	Veigaiaidae	predator	McFayden	260
Veigaia exigua (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	261
Veigaia kochi (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	262
Veigaia nemorensis	Mesostigmata	Veigaiaidae	predator	McFayden	263
Veigaia nemorensis (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	264
Veigaia planicola	Mesostigmata	Veigaiaidae	predator	McFayden	456
Veigaia planicola (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	457
Veigaia sp. (juv)	Mesostigmata	Veigaiaidae	predator	McFayden	265
Velleius sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	571
Vitrea diaphana	Pulmonata	Pristilomatidae	detritivore	Sieve	836
Vitrea diaphana (juv)	Pulmonata	Pristilomatidae	detritivore	Sieve	837
Vulgarogamasus kraepelini	Mesostigmata	Parasitidae	predator	McFayden	460
Vulgarogamasus kraepelini (juv)	Mesostigmata	Parasitidae	predator	McFayden	459
Vulgarogamasus remberti	Mesostigmata	Parasitidae	predator	McFayden	666
Vulgarogamasus sp.	Mesostigmata	Parasitidae	predator	McFayden	461
Vulgarogamasus sp. (juv)	Mesostigmata	Parasitidae	predator	McFayden	202
Walckenaeria antica	Araneae	Linyphiidae	predator	Sieve	941
Walckenaeria atrotibialis	Araneae	Linyphiidae	predator	Sieve	957
Walckenaeria corniculans	Araneae	Linyphiidae	predator	Sieve	962
Walckenaeria cucullata	Araneae	Linyphiidae	predator	Combination	194
Walckenaeria cuspidata	Araneae	Linyphiidae	predator	Sieve	966
Walckenaeria dysderoides	Araneae	Linyphiidae	predator	Combination	195
Walckenaeria furcillata	Araneae	Linyphiidae	predator	Sieve	935
Walckenaeria nudipalpis	Araneae	Linyphiidae	predator	Sieve	943
Willemia anophthalma	Collembola	Hypogastruridae	detritivore	McFayden	56
Willemia aspinata	Collembola	Hypogastruridae	detritivore	McFayden	279
Xantholininae sp. (juv)	Coleoptera	Stapylinidae	predator	Kempson	161
Xantholinus laevigatus	Coleoptera	Stapylinidae	predator	Combination	159
Xantholinus sp. (juv) {m}	Coleoptera	Stapylinidae	predator	Kempson	160
Xantholinus sp. (juv) {s}	Coleoptera	Stapylinidae	predator	Kempson	770
Xantholinus tricolor	Coleoptera	Stapylinidae	predator	Kempson	638
Xenillus tegeocranus	Oribatida	Liacaridae	detritivore	McFayden	520
Xenyella sp.	Collembola	Hypogastruridae	detritivore	McFayden	303
Xenylla grisea	Collembola	Hypogastruridae	detritivore	McFayden	774
Xysticus cristatus	Araneae	Thomisidae	predator	Sieve	985
Xysticus erraticus	Araneae	Thomisidae	predator	Sieve	980
Xysticus lanio	Araneae	Thomisidae	predator	Kempson	196
Zercon cf gurensis	Mesostigmata	Zerconidae	predator	McFayden	266
Zercon cf peltatus	Mesostigmata	Zerconidae	predator	McFayden	462
Zercon cf peltatus (juv)	Mesostigmata	Zerconidae	predator	McFayden	463
Zercon cf romagniolus	Mesostigmata	Zerconidae	predator	McFayden	667

Zercon cf triangularis	Mesostigmata	Zerconidae	predator	McFayden	668
Zercon sp. (juv)	Mesostigmata	Zerconidae	predator	McFayden	268
Zerconidae sp. (juv)	Mesostigmata	Eviphididae	predator	McFayden	649
Zerconopsis remiger	Mesostigmata	Ascidae	predator	McFayden	270
Zora spinimana	Araneae	Zoridae	predator	Sieve	981
Zora spinimana (juv)	Araneae	Zoridae	predator	Sieve	975
Zyras sp.	Coleoptera	Stapylinidae	predator	Sieve	792

Table 4.S2: Leaf litter elemental contents of 48 forest sites.

plot ID	C total	N	Al	Ca	Cu	Fe	K	Mg	Mn	Na	P	Zn	S
AEW 1	465.28	18.17	1.57	5.39	0.01	1.17	1.11	0.46	2.17	0.05	0.85	0.05	1.46
AEW 2	432.81	16.27	3.80	16.95	0.03	2.47	1.42	0.88	1.52	0.07	0.64	0.05	1.21
AEW 3	410.78	15.56	8.14	14.91	0.04	5.55	2.53	1.19	0.68	0.09	0.76	0.08	1.17
AEW 4	411.67	15.60	3.46	19.67	0.01	2.48	1.30	1.45	0.31	0.13	0.85	0.05	1.24
AEW 5	440.83	15.68	8.36	17.93	0.01	5.57	1.97	1.55	0.74	0.09	0.42	0.05	0.91
AEW 6	439.37	14.62	3.68	19.37	0.02	2.47	1.67	1.14	0.63	0.07	0.71	0.04	1.04
AEW 7	445.05	19.38	2.43	18.37	0.02	1.58	1.24	1.42	0.94	0.05	0.87	0.05	1.44
AEW 8	434.33	15.70	2.71	24.38	0.01	1.52	1.41	0.98	0.73	0.03	0.77	0.04	1.16
AEW 9	418.71	13.92	5.59	19.92	0.01	3.97	1.41	1.18	0.64	0.06	0.54	0.04	3.62
AEW 11	365.38	16.04	8.57	5.44	0.03	6.53	2.69	1.29	2.46	0.12	0.96	0.06	1.20
AEW 17	456.05	16.54	1.34	19.35	0.01	1.00	1.06	1.43	0.35	0.06	0.81	0.04	1.17
AEW 18	378.49	13.09	6.74	12.13	0.01	5.93	2.21	1.42	0.98	0.09	0.85	0.05	0.85
AEW 25	427.74	13.49	2.99	19.73	0.02	2.31	1.14	1.24	0.77	0.11	0.52	0.04	1.02
AEW 27	447.02	20.51	1.98	19.52	0.03	1.21	0.97	1.46	1.44	0.04	0.86	0.06	1.80
AEW 30	408.38	13.98	9.90	21.13	0.02	5.12	2.09	1.75	0.32	0.15	0.75	0.05	1.12
AEW 49	411.90	13.95	5.98	27.36	0.02	3.43	1.38	1.41	0.50	0.05	0.48	0.07	1.02
HEW 1	373.29	12.56	11.02	26.71	0.02	7.54	3.31	10.47	0.67	0.17	0.65	0.05	0.99
HEW 2	426.36	14.44	5.70	14.94	0.03	4.34	3.49	2.23	0.18	0.16	0.85	0.05	1.26
HEW 3	463.78	15.70	1.41	13.07	0.01	1.17	1.63	0.87	0.92	0.06	0.71	0.05	1.17
HEW 4	385.48	11.41	9.18	23.90	0.02	8.36	2.33	1.89	0.60	0.14	0.50	0.06	1.05
HEW 5	412.35	14.04	8.07	19.12	0.01	4.01	2.46	1.70	0.83	0.10	0.54	0.05	1.07
HEW 6	428.54	16.42	2.51	14.73	0.01	2.41	2.30	1.57	1.48	0.12	1.00	0.05	1.19
HEW 10	406.41	12.30	8.45	19.17	0.02	5.71	3.44	1.88	0.55	0.09	0.56	0.04	0.92
HEW 11	345.93	13.68	16.67	15.49	0.02	9.97	4.40	2.99	1.06	0.15	0.83	0.07	1.11
HEW 12	379.45	14.83	4.85	12.99	0.02	4.35	2.03	1.32	1.44	0.09	0.76	0.07	1.15
HEW 13	425.86	17.50	4.48	18.01	0.01	3.26	2.67	1.66	0.24	0.11	0.84	0.05	1.39
HEW 16	366.91	13.25	10.14	17.73	0.02	7.35	3.78	2.46	1.18	0.12	0.82	0.05	1.04
HEW 17	434.51	16.97	1.92	17.09	0.00	1.43	1.71	1.27	2.15	0.06	0.64	0.06	1.35
HEW 21	401.24	15.74	4.91	14.70	0.02	3.57	2.05	2.55	0.49	0.14	0.60	0.05	1.19
HEW 22	354.39	13.01	7.30	14.58	0.00	5.71	2.27	1.59	1.18	0.11	0.52	0.05	0.93
HEW 36	395.77	13.43	6.35	16.74	0.01	4.68	2.59	1.51	0.81	0.10	0.58	0.04	0.94
HEW 47	410.02	15.75	3.22	18.13	0.02	2.44	1.89	1.27	1.02	0.08	0.77	0.05	1.17
SEW 1	411.47	11.38	2.52	5.86	0.02	3.53	1.68	0.73	1.14	0.08	0.64	0.05	0.93
SEW 2	489.78	12.30	0.65	7.69	0.01	0.83	0.78	0.44	1.45	0.03	0.54	0.04	0.85
SEW 3	458.04	13.39	0.75	4.68	0.01	1.20	2.25	0.88	1.24	0.07	0.79	0.04	1.05
SEW 4	454.49	15.54	0.79	10.55	0.01	1.63	1.02	0.83	2.87	0.06	0.78	0.05	1.24
SEW 5	431.14	16.31	0.50	10.43	0.01	0.98	1.20	1.04	2.16	0.04	0.84	0.04	1.12
SEW 6	422.42	15.41	1.98	11.50	0.01	2.83	1.58	1.27	3.38	0.10	0.94	0.06	1.12
SEW 7	324.54	11.99	2.08	9.68	0.01	4.85	1.05	0.91	2.14	0.10	0.63	0.03	0.88
SEW 8	396.64	13.47	1.03	11.54	0.02	2.84	1.22	0.94	2.90	0.13	0.70	0.03	0.97
SEW 9	377.16	12.44	0.82	10.08	0.02	2.39	1.29	0.72	3.85	0.06	0.76	0.03	0.90
SEW 18	470.02	14.97	0.54	4.74	0.00	0.81	1.57	0.69	1.19	0.07	0.71	0.05	1.17
SEW 35	413.80	14.67	1.33	10.24	0.01	2.63	1.24	1.08	3.87	0.07	0.76	0.05	1.05
SEW 36	412.83	14.33	0.83	12.67	0.02	2.05	1.38	1.07	3.73	0.05	0.84	0.05	1.06
SEW 37	365.41	12.59	1.17	9.17	0.01	2.77	1.09	0.88	2.24	0.06	0.72	0.04	0.89
SEW 41	413.77	13.95	1.47	9.73	0.01	2.11	1.18	0.98	3.04	0.06	0.74	0.04	1.05
SEW 43	418.41	13.76	0.91	13.65	0.01	1.88	1.48	0.95	2.69	0.09	0.82	0.05	0.98
SEW 48	454.53	12.82	0.47	12.31	0.01	0.80	1.10	1.19	3.67	0.06	0.70	0.04	0.93

Table 4.S3: Pearson product-moment correlation coefficients for Carbon-to-element ratios. After calculating the Carbon-to-nutrient ratios the stoichiometric variables were log_{10} transformed and normalized prior to analysis. Please note that we tested for variance inflation factors (VIF) separately after testing for collinearity.

	VIF	C:N	C:P	C:Al	C:Ca	C:Fe	C:K	C:Na	C:S	C:Mn	C:Mg
C:N	2.8	1	0.50	0.41	0.29	0.26	0.22	0.18	0.66	-0.05	0.39
C:P	1.8	0.50	1	0.02	-0.07	0.13	0.21	0.22	0.34	0.07	0.20
C:Al	6.3	0.41	0.02	1	0.57	**0.83**	0.63	0.52	0.41	-0.34	0.60
C:Ca	3.9	0.29	-0.07	0.57	1	0.51	0.27	0.23	0.23	-0.30	0.70
C:Fe	7.3	0.26	0.13	**0.83**	0.51	1	0.73	0.72	0.27	-0.15	0.67
C:K	4.3	0.22	0.21	0.63	0.27	0.73	1	0.74	0.21	-0.25	0.71
C:Na	3.3	0.18	0.22	0.52	0.23	0.72	0.74	1	0.19	-0.20	0.64
C:S	1.9	0.66	0.34	0.41	0.23	0.27	0.21	0.19	1	-0.18	0.33
C:Mn	1.5	-0.05	0.07	-0.34	-0.30	-0.15	-0.25	-0.20	-0.18	1	-0.31
C:Mg	6.0	0.39	0.20	0.60	0.70	0.67	0.71	0.64	0.33	-0.31	1

Table 4.S4: Pearson product-moment correlation coefficients for contents of single elements in the leaf litter. VIF indicates variance inflation factors. After calculating the Carbon-to-nutrient ratios the stoichiometric variables were log_{10} transformed and normalized prior to analysis.

	VIF	C	N	P	Al	Ca	Fe	K	Na	S	Mn	Mg
C	3.6	1	0.46	0.05	-0.54	-0.10	-0.74	-0.45	-0.55	0.18	-0.04	-0.31
N	2.5	0.46	1	0.47	-0.22	0.08	-0.41	-0.21	-0.28	0.35	-0.07	-0.15
P	2.3	0.05	0.47	1	-0.20	-0.31	-0.19	0.05	0.01	0.03	0.29	-0.07
Al	17.4	-0.54	-0.22	-0.20	1	0.46	**0.92**	**0.82**	0.67	0.00	-0.50	0.53
Ca	2.3	-0.10	0.08	-0.31	0.46	1	0.30	0.23	0.24	0.18	-0.56	0.46
Fe	20.4	-0.74	-0.41	-0.19	**0.92**	0.30	1	**0.78**	0.72	-0.09	-0.32	0.50
K	4.9	-0.45	-0.21	0.05	**0.82**	0.23	**0.78**	1	0.69	-0.11	-0.42	0.51
Na	2.7	-0.55	-0.28	0.01	0.67	0.24	0.72	0.69	1	-0.14	-0.33	0.55
S	1.2	0.18	0.35	0.03	0.00	0.18	-0.09	-0.11	-0.14	1	-0.17	-0.05
Mn	2.3	-0.04	-0.07	0.29	-0.50	-0.56	-0.32	-0.42	-0.33	-0.17	1	-0.27
Mg	1.9	-0.31	-0.15	-0.07	0.53	0.46	0.50	0.51	0.55	-0.05	-0.27	1

Table 4.S5: Model selection procedure.

random type	co-variables	run	model type	df*	AIC	delta AIC
simple			Null 1	4	10479.31	193.72
	C:X ratios	**with Fe**	Increase 1	8	10458.08	172.49
			Decrease 1	**13**	**10285.59**	**0**
			Full 1	22	10300.78	15.19
	C:X ratios	with Al	Increase 1	8	10458.08	172.49
			Decrease 1	15	10287.26	1.67
			Full 1	22	10298.62	13.03
complex			Null 2	6	6739.19	69.78
	C:X ratios	with Fe	Increase 2	8	7754.70	1085.29
			Decrease 2	15	6671.64	2.23
			Full 2	24	6684.32	14.91
	C:X ratios	**with Al**	Increase 2	8	7754.70	1085.29
			Decrease 2	**12**	**6669.41**	**0**
			Full 2	24	6685.00	15.59
simple			Null 3	4	10479.31	195.92
	Elements (X)	**with Fe**	Increase 3	7	10467.66	184.28
			Decrease 3	**16**	**10283.80**	**0.42**
			Full 3	24	10297.48	14.09
	Elements (X)	with Al	Increase 3	7	10467.66	184.28
			Decrease 3	17	10283.39	0
			Full 3	24	10295.82	12.43

Table 4.S6: The linear mixed effects models with the complex random structure.

Model		Estimate	SE*	df†	t-value	p-value	low.ci‡	up.ci§
Null	Intercept	1.35	0.18	4881	7.4	0	0.99	1.71
	Body mass	0.76	0.01	4881	70.0	0	0.74	0.78
Best	Intercept	1.35	0.18	4873	7.4	0	0.99	1.70
	Body mass	0.75	0.01	4873	70.2	0	0.73	0.78
	C:N	-0.03	0.01	4873	-2.7	0.01	-0.05	-0.01
	C:P	0.02	0.01	4873	2.1	0.03	<0.01	0.04
	C:Ca	0.01	0.01	4873	0.9	0.37	-0.01	0.03
	C:K	0.01	0.01	4873	0.7	0.46	-0.01	0.03
	Mass x C:N	-0.01	0.01	4873	-0.9	0.35	-0.02	0.01
	Mass x C:P	< -0.01	0.01	4873	-0.2	0.82	-0.01	0.01
	Mass x C:Ca	-0.04	0.01	4873	-6.1	0	-0.05	-0.03
	Mass x C:K	-0.02	0.01	4873	-2.4	0.02	-0.03	< -0.01

*Standard errors, †denominator degrees of freedom, ‡lower and §upper 95% confidence intervals. Units were [$\log_{10}$ (mg)] for body mass, [$\log_{10}$ (mg/m²)] for biomass and normalized [$\log_{10}$ (mg/g)] for C:X ratios (please see methods for details). Note that every term included in the final model was of importance for the general model selection based on stepAIC.

Table 4.S7: The linear mixed effects models with single elements as co-variables.

Model		Estimate	SE*	df†	t-value	p-value	low.ci‡	up.ci§
Null	Intercept	1.48	0.01	4955	140.4	0	1.46	1.50
	Mass	0.32	0.01	4955	47.7	0	0.31	0.33
Best	Intercept	1.45	0.01	4941	138.1	0	1.43	1.47
	Mass	0.30	0.01	4941	45.4	0	0.29	0.32
	C	-0.02	0.02	4941	-1.1	0.27	-0.07	0.02
	N	0.04	0.01	4941	2.5	0.01	0.01	0.07
	P	-0.04	0.01	4941	-2.8	<0.01	-0.07	-0.01
	Ca	0.05	0.01	4941	3.5	<0.001	0.02	0.08
	Fe	< -0.01	0.03	4941	-0.2	0.87	-0.06	0.05
	K	0.01	0.02	4941	0.7	0.47	-0.02	0.05
	Mn	0.01	0.01	4941	0.5	0.61	-0.02	0.03
	Mass x C	-0.06	0.01	4941	-4.3	0	-0.09	-0.03
	Mass x N	0.01	0.01	4941	0.8	0.41	-0.01	0.03
	Mass x P	< -0.01	0.01	4941	-0.2	0.84	-0.02	0.02
	Mass x Ca	0.08	0.01	4941	8.2	0	0.06	0.10
	Mass x Fe	-0.03	0.02	4941	-1.9	0.06	-0.07	<0.01
	Mass x K	0.02	0.01	4941	2.0	0.05	<0.01	0.04
	Mass x Mn	-0.03	0.01	4941	-3.0	<0.01	-0.04	-0.01

*Standard errors, †denominator degrees of freedom, ‡lower and §upper 95% confidence intervals. Units were [$\log_{10}$ (mg)] for body mass, [$\log_{10}$ (mg/m²)] for biomass and normalized [$\log_{10}$ (mg/g)] for elements (please see methods for details). Note that every term included in the final model was of importance for the general model selection based on stepAIC.

Table 4.S8: AIC comparison of the best linear mixed effects models containing co-variables with the allometric null model for predators.

Model	df	AIC	deltaAIC
Null	4	5746.67	46.03
Single element	13	5700.64	0
Null	4	5746.67	40.03
Ratios	12	5706.63	0

Table 4.S9: Results of the best linear mixed effects models for predators.

Model		Estimate	SE*	df†	t-value	p-value	low.ci‡	up.ci§
with ratios	Intercept	1.27	0.01	2907	100.5	0	1.25	1.30
	Mass	0.24	0.01	2907	25.3	0	0.22	0.26
	C:N	-0.03	0.02	2907	-1.7	0.09	-0.06	<0.01
	C:P	0.05	0.02	2907	2.9	<0.01	0.02	0.08
	C:Ca	-0.04	0.02	2907	-2.8	0.01	-0.08	-0.01
	C:K	-0.01	0.01	2907	-0.6	0.55	-0.04	0.02
	C:Mn	-0.05	0.02	2907	-3.2	<0.01	-0.08	-0.02
	Mass x C:N	<0.01	0.01	2907	0.4	0.72	-0.02	0.03
	Mass x C:P	-0.02	0.01	2907	-1.3	0.21	-0.04	0.01
	Mass x C:Ca	-0.06	0.01	2907	-5.0	0	-0.08	-0.04
	Mass x C:K	-0.02	0.01	2907	-1.4	0.16	-0.04	0.01
	Mass x C:Mn	-0.01	0.01	2907	-1.3	0.19	-0.04	0.01
with single elements	Intercept	1.27	0.01	2905	100.4	0	1.25	1.30
	Mass	0.24	0.01	2905	25.3	0	0.22	0.26
	C	-0.05	0.02	2905	-2.0	0.05	-0.09	< -0.001
	N	0.03	0.02	2905	1.7	0.09	-0.01	0.07
	P	-0.05	0.02	2905	-3.2	<0.01	-0.08	-0.02
	Ca	0.04	0.02	2905	2.2	0.03	<0.01	0.07
	Fe	-0.02	0.02	2905	-0.9	0.37	-0.07	0.03
	Mn	0.03	0.02	2905	1.9	0.05	< -0.001	0.07
	Mass x C	-0.06	0.02	2905	-3.2	<0.01	-0.09	-0.02
	Mass x N	-0.01	0.01	2905	-0.4	0.69	-0.03	0.02
	Mass x P	0.01	0.01	2905	0.8	0.43	-0.01	0.03
	Mass x Ca	0.05	0.01	2905	4.0	<0.001	0.03	0.07
	Mass x Fe	-0.03	0.02	2905	-1.4	0.18	-0.06	0.01
	Mass x Mn	< -0.01	0.01	2905	-0.4	0.70	-0.03	0.02

Supporting information - Chapter 5

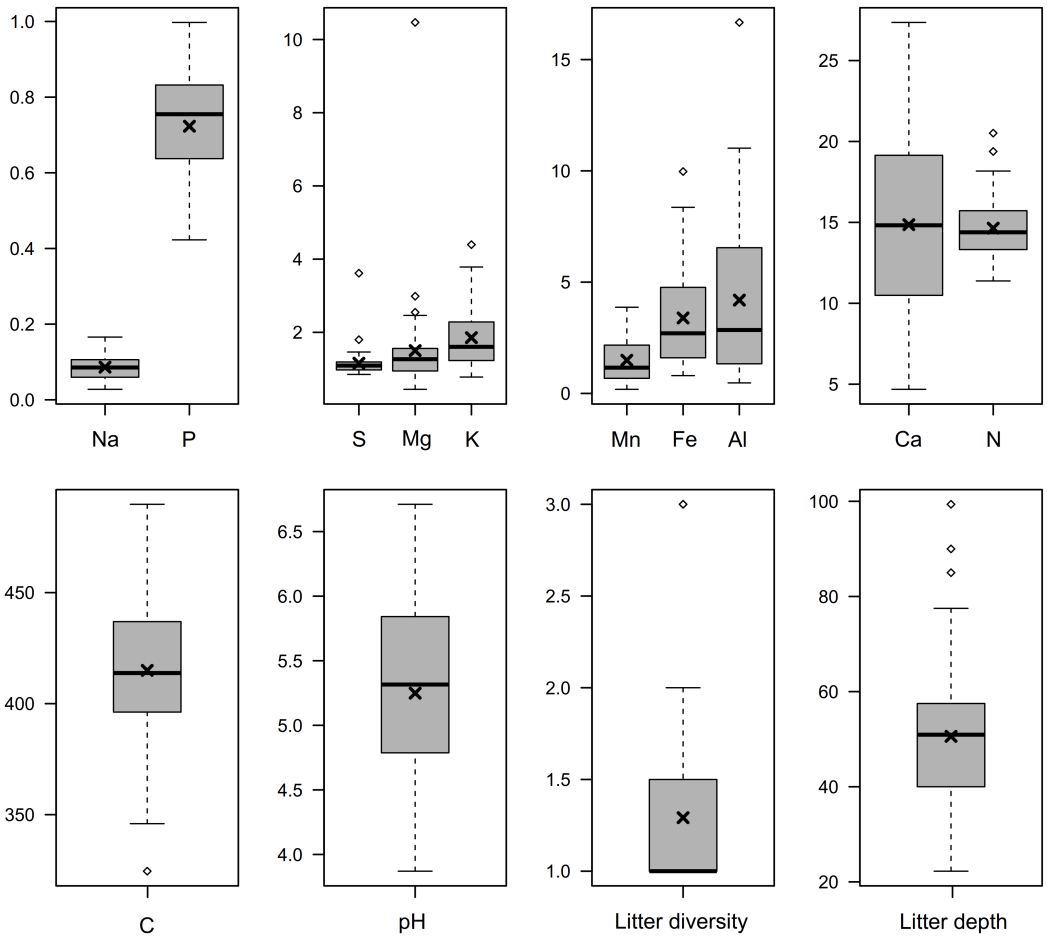

Figure 5.S1: Variation in leaf litter characteristics across the 48 forest sites (N = 1 per site). Shown are the litter elemental contents in milligram per gram dry mass, their corresponding ratios, the pH (0.01M $CaCl_2$), litter diversity (species richness) and litter depth in millimeter. Bars show medians, grey boxes show the first and third quartiles, whiskers show the 1.5 fold interquartile ranges, and open diamonds are outliers. Crosses indicate the calculated group means.

Table 5.S1: Pearson´s product-moment correlation coefficients. Stoichiometric variables were $\log_{10}$ transformed and normalized prior to analysis. Abbreviations: VIF = variance inflation factors, Depth = litter depth, Div = leaf litter species richness, Type = forest type.

	VIF	pH	Div	Depth	C:N	C:P	C:Al	C:Ca	C:Fe	C:K	C:Na	C:S	C:Mn	C:Mg
pH	3.8	**1**	0.34	-0.34	-0.20	0.09	-0.52	**-0.78**	-0.45	-0.38	-0.32	-0.27	0.40	-0.72
Div	1.7	***	**1**	-0.18	0.08	0.05	-0.16	-0.27	-0.12	-0.31	-0.20	-0.05	0.41	-0.33
Depth	1.5	***	*	**1**	-0.16	-0.13	0.27	0.24	0.30	0.21	0.08	-0.14	-0.19	0.24
C:N	3.1	***	ns	***	**1**	0.50	0.41	0.29	0.26	0.22	0.18	0.66	-0.05	0.39
C:P	1.8	***	ns	***	***	**1**	0.02	-0.07	0.13	0.21	0.22	0.34	0.07	0.20
C:Al	**6.4**	***	***	***	***	ns	**1**	0.57	**0.83**	0.63	0.52	0.41	-0.34	0.60
C:Ca	5.3	***	***	***	***	***	***	**1**	0.51	0.27	0.23	0.23	-0.30	0.70
C:Fe	**8.3**	***	***	***	***	***	***	***	**1**	0.73	0.72	0.27	-0.15	0.67
C:K	5.3	***	***	***	***	***	***	***	***	**1**	0.74	0.21	-0.25	0.71
C:Na	3.9	***	***	***	***	***	***	***	***	***	**1**	0.19	-0.20	0.64
C:S	2.1	***	***	***	***	***	***	***	***	***	***	**1**	-0.18	0.33
C:Mn	1.7	***	***	***	**	***	***	***	***	***	***	***	**1**	-0.31
C:Mg	**7.3**	***	***	***	***	***	***	***	***	***	***	***	***	**1**

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.1$, ns = not significant.

Table 5.S2: Results of the most parsimonious linear mixed effects models for the ecological and phylogenetical groups. Part A.

Group	Parameters	Estimate	SE*	den.df.*	t-value	p-value	low.ci*	up.ci*
Arachnida	Intercept	0.74	0.05	745	16.13	0	0.65	0.83
	Mass	0.61	0.06	745	9.61	0	0.48	0.73
	Beech70	0.14	0.07	745	2.18	0.03	0.01	0.27
	Unm.beech	0.19	0.07	745	2.81	0.01	0.06	0.31
	Conifer	-0.08	0.06	745	-1.17	0.24	-0.20	0.05
	C:N	-0.05	0.03	745	-1.49	0.14	-0.11	0.01
	C:P	0.03	0.03	745	0.80	0.42	-0.04	0.09
	C:Al	0.09	0.04	745	2.12	0.03	0.01	0.18
	C:K	-0.08	0.04	745	-1.77	0.08	-0.17	0.01
	Mass x Beech70	-0.12	0.09	745	-1.36	0.18	-0.30	0.06
	Mass x Unm.beech	-0.17	0.09	745	-1.86	0.06	-0.36	0.01
	Mass x Conifer	-0.10	0.10	745	-1.01	0.31	-0.30	0.10
	Mass x C:N	-0.06	0.05	745	-1.20	0.23	-0.15	0.04
	Mass x C:P	0.09	0.05	745	1.80	0.07	-0.01	0.18
	Mass x C:Al	0.05	0.07	745	0.68	0.49	-0.09	0.18
	Mass x C:K	-0.09	0.06	745	-1.36	0.18	-0.21	0.04
Coleoptera predacious	Intercept	0.96	0.03	603	37.18	0	0.91	1.02
	Mass	0.65	0.02	603	27.52	0	0.60	0.70
Chilopoda	Intercept	1.39	0.03	368	42.54	0	1.32	1.45
	Mass	0.83	0.04	368	18.85	0	0.75	0.92
	C:N	-0.04	0.03	368	-1.24	0.22	-0.10	0.02
	C:Ca	-0.06	0.04	368	-1.54	0.13	-0.14	0.02
	C:Mn	-0.05	0.04	368	-1.38	0.17	-0.12	0.02
	Mass x C:N	-0.02	0.04	368	-0.50	0.62	-0.10	0.06
	Mass x C:Ca	-0.05	0.06	368	-0.92	0.36	-0.16	0.06
	Mass x C:Mn	-0.04	0.05	368	-0.81	0.42	-0.13	0.05

* Standard errors (SE), denominator degrees of freedom (den.df), lower (low.ci) and upper 95% confidence intervals (up.ci) are given. Forest types are indicated with: conifer = coniferous, beech70 = old managed beech and unm.beech = unmanaged beech. Please see methods for further explanation.

Table 5.S2: Results of the most parsimonious linear mixed effects models for the ecological and phylogenetical groups. Part B.

Group	Parameters	Estimate	SE*	den.df.*	t-value	p-value	low.ci*	up.ci*
Isopoda	Intercept	0.78	0.13	107	6.05	0	0.52	1.04
	Mass	0.27	0.20	107	1.40	0.17	-0.12	0.67
	Beech70	0.43	0.18	107	2.36	0.02	0.07	0.80
	Unm.beech	0.65	0.19	107	3.46	<0.001	0.28	1.03
	Conifer	0.12	0.21	107	0.55	0.59	-0.31	0.54
	Litter div	-0.14	0.08	107	-1.81	0.07	-0.30	0.01
	pH	0.30	0.13	107	2.28	0.02	0.04	0.56
	C:P	0.02	0.07	107	0.31	0.76	-0.13	0.17
	C:Ca	0.25	0.19	107	1.35	0.18	-0.12	0.62
	C:Na	-0.06	0.09	107	-0.71	0.48	-0.24	0.11
	Mass x Beech70	-0.43	0.28	107	-1.50	0.14	-0.99	0.14
	Mass x Unm.beech	0.02	0.27	107	0.08	0.94	-0.50	0.55
	Mass x Conifer	-0.10	0.33	107	-0.30	0.77	-0.76	0.56
	Mass x Litter div	0.26	0.12	107	2.19	0.03	0.02	0.49
	Mass x pH	-0.20	0.23	107	-0.89	0.37	-0.66	0.25
	Mass x C:P	-0.15	0.12	107	-1.32	0.19	-0.38	0.08
	Mass x C:Ca	-0.27	0.27	107	-1.00	0.32	-0.81	0.27
	Mass x C:Na	0.19	0.13	107	1.51	0.13	-0.06	0.45
Diplopoda	Intercept	1.32	0.06	154	22.00	0	1.20	1.44
	Mass	0.67	0.04	154	16.04	0	0.59	0.76
	Litter depth	-0.10	0.08	154	-1.27	0.21	-0.25	0.05
	C:P	-0.07	0.06	154	-1.08	0.28	-0.19	0.06
	C:Ca	0.02	0.07	154	0.22	0.82	-0.12	0.15
	Mass x Litter depth	0.01	0.05	154	0.21	0.84	-0.09	0.11
	Mass x C:P	-0.01	0.04	154	-0.13	0.90	-0.09	0.08
	Mass x C:Ca	-0.07	0.05	154	-1.52	0.13	-0.17	0.02

* Standard errors (SE), denominator degrees of freedom (den.df), lower (low.ci) and upper 95% confidence intervals (up.ci) are given. Forest types are indicated with: conifer = coniferous, beech70 = old managed beech and unm.beech = unmanaged beech. Please see methods for further explanation.

Table 5.S2: Results of the most parsimonious linear mixed effects models for the ecological and phylogenetical groups. Part C.

Group	Parameters	Estimate	SE*	den.df.*	t-value	p-value	low.ci*	up.ci*
Oribatida	Intercept	2.19	0.09	950	24.42	0	2.02	2.37
	Mass	0.53	0.05	950	10.54	0	0.43	0.63
	Beech70	0.14	0.14	950	1.03	0.31	-0.13	0.41
	Unm.beech	0.13	0.13	950	0.99	0.32	-0.13	0.39
	Conifer	-0.02	0.13	950	-0.20	0.85	-0.27	0.22
	C:Mn	0.00	0.05	950	0.04	0.97	-0.10	0.11
	C:Na	0.03	0.08	950	0.39	0.70	-0.13	0.19
	Litter depth	-0.02	0.05	950	-0.36	0.72	-0.11	0.08
	C:Fe	-0.07	0.08	950	-0.82	0.41	-0.22	0.09
	Litter div	0.02	0.05	950	0.30	0.77	-0.08	0.12
	C:P	0.04	0.05	950	0.72	0.47	-0.06	0.14
	Mass x Beech70	0.08	0.08	950	1.04	0.30	-0.07	0.23
	Mass x Unm.beech	0.16	0.07	950	2.13	0.03	0.01	0.30
	Mass x Conifer	-0.12	0.07	950	-1.68	0.09	-0.26	0.02
	Mass x C:Mn	0.03	0.03	950	1.16	0.25	-0.02	0.09
	Mass x C:Na	-0.02	0.04	950	-0.55	0.58	-0.11	0.06
	Mass x Litter depth	-0.04	0.03	950	-1.32	0.19	-0.09	0.02
	Mass x C:Fe	-0.01	0.05	950	-0.13	0.90	-0.09	0.08
	Mass x Litter div	0.03	0.03	950	1.01	0.31	-0.03	0.08
	Mass x C:P	0.01	0.03	950	0.21	0.83	-0.05	0.06
Mesostigmata	Intercept	2.41	0.05	720	46.53	0	2.31	2.51
	Mass	0.83	0.03	720	27.63	0	0.77	0.89
	pH	-0.04	0.09	720	-0.46	0.65	-0.23	0.14
	C:P	0.02	0.07	720	0.37	0.71	-0.11	0.16
	C:N	-0.04	0.06	720	-0.60	0.55	-0.16	0.09
	C:K	0.04	0.08	720	0.55	0.58	-0.11	0.20
	C:Na	-0.06	0.08	720	-0.80	0.42	-0.22	0.09
	C:Ca	0.00	0.10	720	0.03	0.98	-0.18	0.19
	Litter depth	-0.07	0.06	720	-1.24	0.21	-0.18	0.04
	Mass x pH	0.00	0.06	720	0.00	1.00	-0.11	0.11
	Mass x C:P	-0.02	0.04	720	-0.51	0.61	-0.10	0.06
	Mass x C:N	0.00	0.04	720	0.03	0.97	-0.07	0.07
	Mass x C:K	0.00	0.05	720	-0.06	0.95	-0.09	0.09
	Mass x Na	-0.01	0.05	720	-0.27	0.78	-0.10	0.08
	Mass x C:Ca	-0.02	0.06	720	-0.40	0.69	-0.13	0.09
	Mass x Litter depth	-0.05	0.03	720	-1.67	0.10	-0.12	0.01

* Standard errors (SE), denominator degrees of freedom (den.df), lower (low.ci) and upper 95% confidence intervals (up.ci) are given. Forest types are indicated with: conifer = coniferous, beech70 = old managed beech and unm.beech = unmanaged beech. Please see methods for further explanation.

Table 5.S2: Results of the most parsimonious linear mixed effects models for the ecological and phylogenetical groups. Part D.

Group	Parameters	Estimate	SE*	den.df.*	t-value	p-value	low.ci*	up.ci*
Lumbricidae	Intercept	1.09	0.21	149	5.22	0	0.68	1.50
	Mass	0.88	0.08	149	10.47	0	0.71	1.04
	Beech70	0.36	0.29	149	1.26	0.21	-0.21	0.93
	Unm.beech	0.06	0.30	149	0.20	0.84	-0.54	0.66
	Conifer	-0.27	0.33	149	-0.80	0.42	-0.92	0.39
	C:P	0.19	0.14	149	1.39	0.17	-0.08	0.46
	C:Fe	-0.24	0.31	149	-0.79	0.43	-0.85	0.37
	C:K	-0.27	0.25	149	-1.05	0.29	-0.76	0.23
	C:Na	0.24	0.19	149	1.27	0.21	-0.13	0.61
	C:S	-0.24	0.13	149	-1.86	0.06	-0.50	0.01
	Mass x Beech70	-0.08	0.12	149	-0.65	0.52	-0.31	0.16
	Mass x Unm.beech	0.04	0.13	149	0.35	0.73	-0.21	0.30
	Mass x Conifer	0.14	0.13	149	1.02	0.31	-0.13	0.40
	Mass x C:P	-0.04	0.06	149	-0.72	0.47	-0.15	0.07
	Mass x C:Fe	0.13	0.13	149	1.05	0.30	-0.12	0.39
	Mass x C:K	0.05	0.10	149	0.50	0.62	-0.15	0.25
	Mass x C:Na	-0.12	0.08	149	-1.57	0.12	-0.27	0.03
	Mass x C:S	0.07	0.05	149	1.31	0.19	-0.04	0.18
Collembola	Intercept	0.99	0.34	672	2.92	0	0.32	1.65
	Mass	0.05	0.16	672	0.35	0.73	-0.25	0.36
	Beech70	0.34	0.46	672	0.75	0.46	-0.56	1.25
	Unm.beech	0.40	0.52	672	0.78	0.44	-0.61	1.42
	Conifer	0.65	0.44	672	1.48	0.14	-0.21	1.51
	Litter depth	-0.29	0.15	672	-1.92	0.06	-0.60	0.01
	C:Al	0.64	0.22	672	2.94	<0.01	0.21	1.07
	C:Mn	-0.08	0.20	672	-0.37	0.71	-0.48	0.32
	C:Na	-0.56	0.22	672	-2.54	0.01	-1.00	-0.13
	Mass x Beech70	0.15	0.21	672	0.71	0.48	-0.27	0.57
	Mass x Unm.beech	0.17	0.24	672	0.71	0.48	-0.30	0.64
	Mass x Conifer	0.21	0.20	672	1.03	0.30	-0.19	0.61
	Mass x Litter depth	-0.15	0.07	672	-2.15	0.03	-0.29	-0.01
	Mass x C:Al	0.27	0.10	672	2.72	0.01	0.08	0.47
	Mass x C:Mn	-0.02	0.09	672	-0.20	0.84	-0.20	0.17
	Mass x C:Na	-0.27	0.10	672	-2.65	0.01	-0.48	-0.07

* Standard errors (SE), denominator degrees of freedom (den.df), lower (low.ci) and upper 95% confidence intervals (up.ci) are given. Forest types are indicated with: conifer = coniferous, beech70 = old managed beech and unm.beech = unmanaged beech. Please see methods for further explanation.

Table 5.S2: Results of the most parsimonious linear mixed effects models for the ecological and phylogenetical groups. Part E.

Group	Parameters	Estimate	SE*	den.df.*	t-value	p-value	low.ci*	up.ci*
Gastropoda	Intercept	0.15	0.22	131	0.68	0.50	-0.29	0.59
Snails	Mass	0.97	0.11	131	8.89	0	0.75	1.18
	Beech70	0.18	0.28	131	0.65	0.52	-0.37	0.73
	Unm.beech	0.29	0.40	131	0.72	0.47	-0.50	1.07
	Conifer	-0.03	0.33	131	-0.09	0.93	-0.68	0.62
	pH	0.12	0.12	131	1.02	0.31	-0.11	0.36
	C:N	0.01	0.18	131	0.06	0.95	-0.35	0.38
	C:K	0.04	0.24	131	0.16	0.88	-0.43	0.50
	C:Mn	0.23	0.11	131	2.08	0.04	0.01	0.45
	C:Na	0.24	0.23	131	1.03	0.30	-0.22	0.69
	C:S	-0.19	0.29	131	-0.66	0.51	-0.77	0.39
	Mass x Beech70	-0.03	0.14	131	-0.18	0.85	-0.30	0.25
	Mass x Unm.beech	0.01	0.20	131	0.06	0.96	-0.38	0.40
	Mass x Conifer	0.07	0.17	131	0.41	0.68	-0.27	0.41
	Mass x pH	-0.03	0.07	131	-0.52	0.60	-0.17	0.10
	Mass x C:N	-0.04	0.09	131	-0.44	0.66	-0.22	0.14
	Mass x C:K	0.04	0.12	131	0.36	0.72	-0.19	0.27
	Mass x C:Mn	-0.11	0.06	131	-1.80	0.07	-0.23	0.01
	Mass x C:Na	-0.16	0.11	131	-1.39	0.17	-0.38	0.07
	Mass x C:S	0.11	0.14	131	0.80	0.43	-0.17	0.39
Gastropoda	Intercept	0.50	0.23	31	2.21	0.03	0.04	0.97
Slugs	Mass	0.90	0.09	31	9.66	0	0.71	1.09
Coleoptera	Intercept	0.58	0.07	71	8.62	0	0.45	0.72
non-predacious	Mass	0.96	0.09	71	10.79	0	0.78	1.13
	C:P	0.12	0.08	71	1.44	0.15	-0.05	0.28
	Mass x C:P	0.16	0.19	71	0.83	0.41	-0.22	0.53

* Standard errors (SE), denominator degrees of freedom (den.df), lower (low.ci) and upper 95% confidence intervals (up.ci) are given. Forest types are indicated with: conifer = coniferous, beech70 = old managed beech and unm.beech = unmanaged beech. Please see methods for further explanation.

Supporting information - Chapter 6

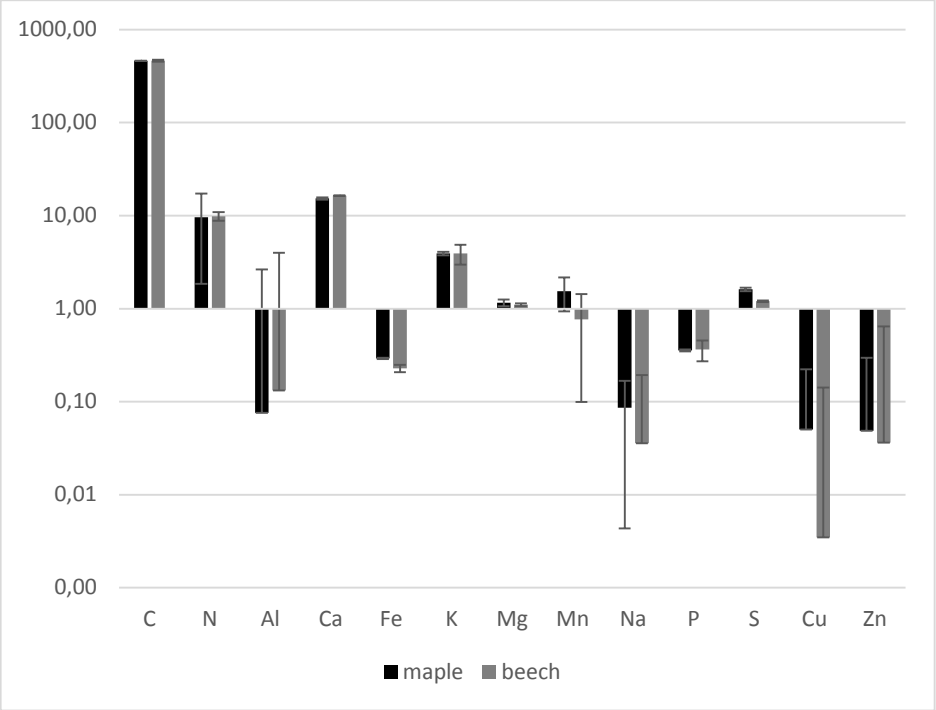

Figure 6.S1: Elemental contents of the leaf litter species maple (black bars) and beech (grey bars) given in [mg g^{-1}] dry weight. Bars correspond to average values of two samples per species containing three leaves each. Thus, the standard deviations shown indicate the real sample values. The y-axis is logarithmic scaled (log_{10}) and centered to ten [(log_{10} (10) = 1]. For values larger than one bars point upwards, whereas for values smaller than one the bars point downwards.

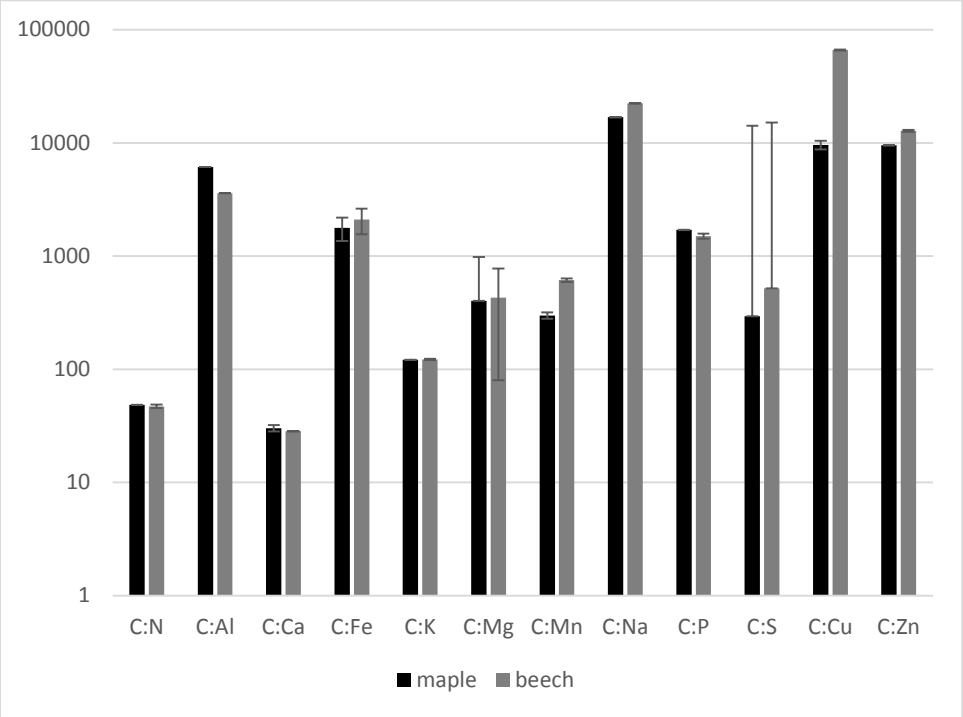

Figure 6.S2: Elemental contents of the leaf litter species maple (black bars) and beech (grey bars) expressed in C:X ratios. Bars correspond to average values of two samples per species containing three leaves each. Thus, the standard deviations shown indicate the ratio values per sample.

Table 5.S1: Estimates of the best linear mixed effects model examining interactive effects of mesh size (macro-mesh & micro-mesh), leaf litter species (beech & maple) and forest type (conifer, beech young, beech old and beech unmanaged) on the final leaf litter mass. The marginal coefficient of determination (R^2) corresponds to the fixed effects, the conditional R^2 corresponds to fixed and random effects in the model.

Parameter type	Parameter (Predictor level)	Estimate	Std.Error	DF*	t-value	p-value
	Intercept (Macro-mesh x Maple x Beech old)	0.34	0.03	178	11.09	0
Mesh size	Micro-mesh	0.12	0.04	178	2.93	0.004
Leaf species	Beech litter	0.21	0.04	178	5.37	0
Forest type	Beech young	-0.07	0.04	27	-1.59	0.123
Forest type	Beech unmanaged	0.03	0.04	27	0.63	0.537
Forest type	Conifer	-0.21	0.04	27	-4.91	0
2-way -interaction	Micro-mesh x Beech litter	-0.11	0.06	178	-1.92	0.057
2-way -interaction	Micro-mesh x Beech young	0.06	0.06	178	1.12	0.264
2-way -interaction	Micro-mesh x Beech unmanaged	0.01	0.06	178	0.21	0.832
2-way -interaction	Micro-mesh x Conifer	0.21	0.06	178	3.83	<0.01
2-way -interaction	Beech litter x Beech young	0.08	0.06	178	1.43	0.153
2-way -interaction	Beech litter x Beech unmanaged	-0.01	0.06	178	-0.25	0.801
2-way -interaction	Beech litter x Conifer	0.22	0.06	178	3.85	<0.01
3-way-interaction	Micro-mesh x Beech litter x Beech young	-0.10	0.08	178	-1.25	0.215
3-way-interaction	Micro-mesh x Beech litter x Beech unmanaged	-0.02	0.08	178	-0.29	0.776
3-way-interaction	Micro-mesh x Beech litter x Conifer	-0.20	0.08	178	-2.52	0.013
R^2	marginal	0.53				
R^2	conditional	0.57				

Table 5.S2: Results of the posthoc test of the best linear mixed effects model examining interactive effects of macro-mesh size (macro) and micro-mesh (micro), beech leaf litter (beech) and maple leaf litter (maple) and forest type (conifer, beech young, beech old and beech unmanaged) on the final leaf litter mass. Multiple comparisons of mean by Tukey contrasts. Linear hypotheses: contrast of treatments == 0.

Treatment (Factor level interaction)	vs.	Treatment (Factor level interaction)	Estimate	Std. Error	z value	Pr(>|z|)	
Macro x Maple x Beech young	-	Macro x Maple x Beech old	-0.07	0.04	-1.59	0.969	
Macro x Maple x Beech young	-	Micro x Maple x Beech old	-0.18	0.04	-4.28	<0.01	**
Macro x Maple x Beech young	-	Macro x Beech x Beech old	-0.28	0.04	-6.52	<0.01	***
Macro x Maple x Beech young	-	Micro x Beech x Beech old	-0.29	0.04	-6.6	<0.01	***
Macro x Maple x Beech unmanaged	-	Macro x Maple x Beech old	0.03	0.04	0.63	1	
Macro x Maple x Beech unmanaged	-	Micro x Maple x Beech old	-0.09	0.04	-2.07	0.783	
Macro x Maple x Beech unmanaged	-	Macro x Beech x Beech old	-0.19	0.04	-4.31	<0.01	**
Macro x Maple x Beech unmanaged	-	Micro x Beech x Beech old	-0.19	0.04	-4.42	<0.01	**
Macro x Maple x Beech unmanaged	-	Macro x Maple x Beech young	0.1	0.04	2.22	0.681	
Macro x Maple x Beech unmanaged	-	Micro x Maple x Beech young	-0.08	0.04	-1.92	0.865	
Macro x Maple x Beech unmanaged	-	Macro x Beech x Beech young	-0.2	0.04	-4.58	<0.01	***
Macro x Maple x Beech unmanaged	-	Micro x Beech x Beech young	-0.17	0.04	-3.97	<0.01	**
Macro x Maple x Conifer	-	Macro x Maple x Beech old	-0.21	0.04	-4.91	<0.01	***
Macro x Maple x Conifer	-	Micro x Maple x Beech old	-0.33	0.04	-7.61	<0.01	***
Macro x Maple x Conifer	-	Macro x Beech x Beech old	-0.42	0.04	-9.85	<0.01	***
Macro x Maple x Conifer	-	Micro x Beech x Beech old	-0.43	0.04	-9.88	<0.01	***
Macro x Maple x Conifer	-	Macro x Maple x Beech young	-0.14	0.04	-3.32	0.067	.
Macro x Maple x Conifer	-	Micro x Maple x Beech young	-0.32	0.04	-7.38	<0.01	***
Macro x Maple x Conifer	-	Macro x Beech x Beech young	-0.43	0.04	-10.12	<0.01	***
Macro x Maple x Conifer	-	Micro x Beech x Beech young	-0.41	0.04	-9.58	<0.01	***
Macro x Maple x Conifer	-	Macro x Maple x Beech unmanaged	-0.24	0.04	-5.54	<0.01	***
Macro x Maple x Conifer	-	Micro x Maple x Beech unmanaged	-0.37	0.04	-8.61	<0.01	***
Macro x Maple x Conifer	-	Macro x Beech x Beech unmanaged	-0.44	0.04	-10.15	<0.01	***
Macro x Maple x Conifer	-	Micro x Beech x Beech unmanaged	-0.43	0.04	-9.93	<0.01	***
Macro x Beech x Beech old	-	Macro x Maple x Beech old	0.21	0.04	5.37	<0.01	***
Macro x Beech x Beech old	-	Micro x Maple x Beech old	0.1	0.04	2.44	0.512	
Macro x Beech x Beech young	-	Macro x Maple x Beech old	0.22	0.04	5.2	<0.01	***
Macro x Beech x Beech young	-	Micro x Maple x Beech old	0.11	0.04	2.51	0.458	
Macro x Beech x Beech young	-	Macro x Beech x Beech old	0.01	0.04	0.27	1	
Macro x Beech x Beech young	-	Micro x Beech x Beech old	<0.01	0.04	0.09	1	
Macro x Beech x Beech young	-	Macro x Maple x Beech young	0.29	0.04	7.4	<0.01	***
Macro x Beech x Beech young	-	Micro x Maple x Beech young	0.11	0.04	2.82	0.253	
Macro x Beech x Beech unmanaged	-	Macro x Maple x Beech old	0.22	0.04	5.23	<0.01	***
Macro x Beech x Beech unmanaged	-	Micro x Maple x Beech old	0.11	0.04	2.54	0.4383	
Macro x Beech x Beech unmanaged	-	Macro x Beech x Beech old	0.01	0.04	0.3	1	
Macro x Beech x Beech unmanaged	-	Micro x Beech x Beech old	0.01	0.04	0.12	1	
Macro x Beech x Beech unmanaged	-	Macro x Maple x Beech young	0.29	0.04	6.82	<0.01	***
Macro x Beech x Beech unmanaged	-	Micro x Maple x Beech young	0.11	0.04	2.62	0.379	
Macro x Beech x Beech unmanaged	-	Macro x Beech x Beech young	0	0.04	0.03	1	
Macro x Beech x Beech unmanaged	-	Micro x Beech x Beech young	0.03	0.04	0.69	1	
Macro x Beech x Beech unmanaged	-	Macro x Maple x Beech unmanaged	0.2	0.04	5.02	<0.01	***

Macro x Beech x Beech unmanaged	-	Micro x Maple x Beech unmanaged	0.07	0.04	1.81	0.911	
Macro x Beech x Conifer	-	Macro x Maple x Beech old	0.22	0.04	5.02	<0.01	***
Macro x Beech x Conifer	-	Micro x Maple x Beech old	0.1	0.04	2.33	0.5965	
Macro x Beech x Conifer	-	Macro x Beech x Beech old	0	0.04	0.09	1	
Macro x Beech x Conifer	-	Micro x Beech x Beech old	< -0.01	0.04	-0.09	1	
Macro x Beech x Conifer	-	Macro x Maple x Beech young	0.28	0.04	6.61	<0.01	***
Macro x Beech x Conifer	-	Micro x Maple x Beech young	0.11	0.04	2.42	0.5308	
Macro x Beech x Conifer	-	Macro x Beech x Beech young	-0.01	0.04	-0.18	1	
Macro x Beech x Conifer	-	Micro x Beech x Beech young	0.02	0.04	0.48	1	
Macro x Beech x Conifer	-	Macro x Maple x Beech unmanaged	0.19	0.04	4.4	<0.01	**
Macro x Beech x Conifer	-	Micro x Maple x Beech unmanaged	0.06	0.04	1.45	0.987	
Macro x Beech x Conifer	-	Macro x Beech x Beech unmanaged	-0.01	0.04	-0.21	1	
Macro x Beech x Conifer	-	Micro x Beech x Beech unmanaged	-0.01	0.04	-0.13	1	
Macro x Beech x Conifer	-	Macro x Maple x Conifer	0.43	0.04	10.82	<0.01	***
Macro x Beech x Conifer	-	Micro x Maple x Conifer	0.1	0.04	2.48	0.484	
Micro x Maple x Beech old	-	Macro x Maple x Beech old	0.12	0.04	2.93	0.198	
Micro x Maple x Beech young	-	Macro x Maple x Beech old	0.11	0.04	2.53	0.443	
Micro x Maple x Beech young	-	Micro x Maple x Beech old	-0.01	0.04	-0.12	1	
Micro x Maple x Beech young	-	Macro x Beech x Beech old	-0.1	0.04	-2.33	0.598	
Micro x Maple x Beech young	-	Micro x Beech x Beech old	-0.11	0.04	-2.47	0.489	
Micro x Maple x Beech young	-	Macro x Maple x Beech young	0.18	0.04	4.45	<0.01	***
Micro x Maple x Beech unmanaged	-	Macro x Maple x Beech old	0.15	0.04	3.64	0.024	*
Micro x Maple x Beech unmanaged	-	Micro x Maple x Beech old	0.04	0.04	0.91	0.999	
Micro x Maple x Beech unmanaged	-	Macro x Beech x Beech old	-0.06	0.04	-1.36	0.993	
Micro x Maple x Beech unmanaged	-	Micro x Beech x Beech old	-0.07	0.04	-1.52	0.98	
Micro x Maple x Beech unmanaged	-	Macro x Maple x Beech young	0.22	0.04	5.25	<0.01	***
Micro x Maple x Beech unmanaged	-	Micro x Maple x Beech young	0.04	0.04	1.02	0.999	
Micro x Maple x Beech unmanaged	-	Macro x Beech x Beech young	-0.07	0.04	-1.63	0.962	
Micro x Maple x Beech unmanaged	-	Micro x Beech x Beech young	-0.04	0.04	-0.98	0.999	
Micro x Maple x Beech unmanaged	-	Macro x Maple x Beech unmanaged	0.13	0.04	3.28	0.079	.
Micro x Maple x Conifer	-	Macro x Maple x Beech old	0.12	0.04	2.75	0.298	
Micro x Maple x Conifer	-	Micro x Maple x Beech old	0	0.04	0.05	1	
Micro x Maple x Conifer	-	Macro x Beech x Beech old	-0.09	0.04	-2.19	0.702	
Micro x Maple x Conifer	-	Micro x Beech x Beech old	-0.1	0.04	-2.33	0.596	
Micro x Maple x Conifer	-	Macro x Maple x Beech young	0.19	0.04	4.34	<0.01	**
Micro x Maple x Conifer	-	Micro x Maple x Beech young	0.01	0.04	0.17	1	
Micro x Maple x Conifer	-	Macro x Beech x Beech young	-0.11	0.04	-2.46	0.497	
Micro x Maple x Conifer	-	Micro x Beech x Beech young	-0.08	0.04	-1.83	0.904	
Micro x Maple x Conifer	-	Macro x Maple x Beech unmanaged	0.09	0.04	2.12	0.748	
Micro x Maple x Conifer	-	Micro x Maple x Beech unmanaged	-0.04	0.04	-0.86	1	
Micro x Maple x Conifer	-	Macro x Beech x Beech unmanaged	-0.11	0.04	-2.49	0.477	
Micro x Maple x Conifer	-	Micro x Beech x Beech unmanaged	-0.1	0.04	-2.38	0.563	
Micro x Maple x Conifer	-	Macro x Maple x Conifer	0.33	0.04	8.34	<0.01	***
Micro x Beech x Beech old	-	Macro x Maple x Beech old	0.22	0.04	5.47	<0.01	***
Micro x Beech x Beech old	-	Micro x Maple x Beech old	0.1	0.04	2.59	0.402	
Micro x Beech x Beech old	-	Macro x Beech x Beech old	0.01	0.04	0.19	1	

Micro x Beech x Beech young	-	Macro x Maple x Beech old	0.2	0.04	4.61	<0.01	***
Micro x Beech x Beech young	-	Micro x Maple x Beech old	0.08	0.04	1.88	0.881	
Micro x Beech x Beech young	-	Macro x Beech x Beech old	-0.02	0.04	-0.39	1	
Micro x Beech x Beech young	-	Micro x Beech x Beech old	-0.02	0.04	-0.56	1	
Micro x Beech x Beech young	-	Macro x Maple x Beech young	0.26	0.04	6.79	<0.01	***
Micro x Beech x Beech young	-	Micro x Maple x Beech young	0.09	0.04	2.15	0.73	
Micro x Beech x Beech young	-	Macro x Beech x Beech young	-0.03	0.04	-0.72	1	
Micro x Beech x Beech unmanaged	-	Macro x Maple x Beech old	0.22	0.04	5.08	<0.01	***
Micro x Beech x Beech unmanaged	-	Micro x Maple x Beech old	0.11	0.04	2.43	0.521	
Micro x Beech x Beech unmanaged	-	Macro x Beech x Beech old	0.01	0.04	0.22	1	
Micro x Beech x Beech unmanaged	-	Micro x Beech x Beech old	<0.01	0.04	0.04	1	
Micro x Beech x Beech unmanaged	-	Macro x Maple x Beech young	0.29	0.04	6.65	<0.01	***
Micro x Beech x Beech unmanaged	-	Micro x Maple x Beech young	0.11	0.04	2.51	0.458	
Micro x Beech x Beech unmanaged	-	Macro x Beech x Beech young	0	0.04	-0.05	1	
Micro x Beech x Beech unmanaged	-	Micro x Beech x Beech young	0.03	0.04	0.6	1	
Micro x Beech x Beech unmanaged	-	Macro x Maple x Beech unmanaged	0.19	0.04	4.85	<0.01	***
Micro x Beech x Beech unmanaged	-	Micro x Maple x Beech unmanaged	0.07	0.04	1.7	0.947	
Micro x Beech x Beech unmanaged	-	Macro x Beech x Beech unmanaged	< -0.01	0.04	-0.08	1	
Micro x Beech x Conifer	-	Macro x Maple x Beech old	0.24	0.04	5.41	<0.01	***
Micro x Beech x Conifer	-	Micro x Maple x Beech old	0.12	0.04	2.76	0.291	
Micro x Beech x Conifer	-	Macro x Beech x Beech old	0.02	0.04	0.55	1	
Micro x Beech x Conifer	-	Micro x Beech x Beech old	0.02	0.04	0.37	1	
Micro x Beech x Conifer	-	Macro x Maple x Beech young	0.3	0.04	6.97	<0.01	***
Micro x Beech x Conifer	-	Micro x Maple x Beech young	0.13	0.04	2.84	0.246	
Micro x Beech x Conifer	-	Macro x Beech x Beech young	0.01	0.04	0.28	1	
Micro x Beech x Conifer	-	Micro x Beech x Beech young	0.04	0.04	0.94	0.999	
Micro x Beech x Conifer	-	Macro x Maple x Beech unmanaged	0.21	0.04	4.79	<0.01	***
Micro x Beech x Conifer	-	Micro x Maple x Beech unmanaged	0.08	0.04	1.89	0.877	
Micro x Beech x Conifer	-	Macro x Beech x Beech unmanaged	0.01	0.04	0.26	1	
Micro x Beech x Conifer	-	Micro x Beech x Beech unmanaged	0.01	0.04	0.33	1	
Micro x Beech x Conifer	-	Macro x Maple x Conifer	0.45	0.04	11.12	<0.01	***
Micro x Beech x Conifer	-	Micro x Maple x Conifer	0.12	0.04	2.94	0.196	
Micro x Beech x Conifer	-	Macro x Beech x Conifer	0.02	0.04	0.5	1	

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„*Unbowed, Unbent, Unbroken*“ - House Martell, G.R.R. Martin

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Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertation selbstständig angefertigt, und die benutzten Quellen und Hilfsmittel vollständig angegeben habe.
Weiterhin erkläre ich, bisher noch keinen Promotionsversuch unternommen zu haben und dass die Dissertation weder in ähnlicher noch in gleicher Form einer anderen Prüfungsbehörde vorgelegt wurde.

Göttingen, im September 2014 David Ott

Curriculum Vitae

The CV is available in the print version only.

List of publications

Publications in peer-reviewed journals

Ott, D., Digel, C., Rall, B. C., Maraun, M., Scheu, S. & Brose, U. (2014): Unifying elemental stoichiometry and metabolic theory. *Ecology Letters*, **17**, 1247-1256.

Ott, D., Digel, C, Klarner, B. Maraun, M., Pollierer, M., Rall, B. C., Scheu, S., Seelig G. & Brose, U. (2014): Litter elemental stoichiometry as determinant of biomass densities of forest soil invertebrates. *Oikos*, **123**, 1212-1223.

Ehnes R. B., Pollierer M. M., Erdmann G., Klarner B., Eitzinger B., Digel C., **Ott D.**, Maraun M., Scheu S., Brose U. (2014): Lack of energetic equivalence in forest soil invertebrates. *Ecology,* **95(2)**: 527-37.

Ott, D., Rall, B. C. & Brose, U. (2012): Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. *Philosophical Transactions of the Royal Society B,* **367(1605)**, 3025-3032.

Rall, B. C., Kalinkat, G., Vucic-Pestic, O., **Ott, D.**, & Brose, U. (2011): Taxonomic versus allometric constraints on nonlinear interaction strengths. *Oikos*, **120(4)**, 483-492.

Diploma Thesis

Ott, D. (2010): Examination of mechanisms of predator diversity on ecosystem functioning with biological control agents, Technische Universität Darmstadt (TUD), Germany

Conference contributions and workshops

02/2014	Ott, D.: Stoichiometry of food webs. Jena Experiment Aboveground-Belowground Network Workshop (*invited talk*).
11/2013	sDiv workshop Stoichiometric constraints of biodiversity – functioning relationships (sTOICHFUN), German Centre for Integrative Biodiversity Research (iDiv), Leipzig (*attended by invitation*).
06/2013	Ott, D.: Tracks in the mist ... litter decomposition in the context of soil food webs. PhD course / Summer School on Functioning of Boreal Forest Ecosystems, Umea°, Sweden (*talk*).
09/2012	Ott, D., Rall, B.C. & Brose, U.: Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. Gesellschaft für Ökologie 42th Annual Meeting, University of Lüneburg, Germany (*talk*).
11/2012	Conference on Biodiversity and Society / Tagung Biodiversität und Gesellschaft - Gesellschaftliche Dimensionen von Schutz und Nutzung biologischer Vielfalt, Göttingen, Germany (*attended*).
09/2012	Ott, D., Rall, B.C. & Brose, U.: Climate change effects on macrofaunal litter decomposition: the interplay of temperature, body masses and stoichiometry. Tagung der Deutschen Bodenkundlichen Gesellschaft (DBG) Kommission III, Bodenbiologie und Bodenökologie, University of Hohenheim, Germany (*talk*).
06/2012	Ott, D., Rall, B.C. & Brose, U.: Climate change effects on macrofaunal litter decomposition, Web of Life in a changing world, University of Montpellier, France (*poster*).
03/2012	Multitrophic Interactions Workshop II, Göttingen, Germany (*attended*).
02/2012	Ott, D., Spindler, K., Rall, B.C. & Brose, U.: Effects of leaf litter diversity and stoichiometry on macrofaunal litter processing. 9th Assembly of the Biodiversity Exploratories, Mainz, Germany (*poster*).
09/2011	Ott, D., Spindler, K., Rall, B.C. & Brose, U.: Effects of leaf litter diversity and stoichiometry on macrofaunal litter processing. Gesellschaft für Ökologie 41th Annual Meeting, University of Oldenburg, Germany (*poster*).
04/2011	Sizemic Meeting Changing Climate, Physiological Adaptation, Ecosystem Resilience and Body Size Constraints, Hamburg, Germany (*attended*).
09/2010	Ott D. & Brose U.: Examination of mechanisms of predator diversity on ecosystem functioning with biological control agents, Gesellschaft für Ökologie 40th Annual Meeting, Giessen, Germany (*talk*).
09/2010	Ott D. & Brose U.: Classic system – new insights: Interaction strengths of aphid predators, British Ecological Society Annual Meeting, University of Leeds, UK (*poster*).
03/2010	Multitrophic Interactions Workshop, Göttingen, Germany (*attended*).