What do Snails Do in Ecosystems?
It is a Matter of Traits

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Abstract

Current environmental changes demand the ability to predict possible consequences for ecosystems performing important functions regulating the Earth system, and providing essential services for human well-being. Indirect impacts can occur through changes in biotic communities. Functional traits determine organisms' performance, and thus their fitness in a given environment. Therefore, traits can be used to assess communities' response to environmental variation (via response traits) and their effects on ecosystem processes (via effect traits).

In this thesis, I used terrestrial snails as study organisms to examine different aspects of their response to environmental and spatial factors, and their potential effects on leaf litter decomposition, as mediated by their traits. I investigated which factors determine the assembly of communities and found that trait underdispersion was more common than trait overdispersion, indicating the dominance of environmental filtering over biotic interactions. Testing the relative importance of environmental and spatial factors, I found that both environment and space significantly contributed to the variation in community trait composition, whereby the environment had the strongest effect. This indicates that intrinsic population processes (e.g. dispersal) that are independent from the environment play only a subordinate role. Moreover, I conducted microcosm experiments to measure snail traits that affect leaf litter decomposition (consumption rate, faeces production and assimilation efficiency) testing two litter types differing in quality. With the observed relationship between species specific shell size and consumption rate as proxy I assessed snail communities' potential influence on leaf litter decomposition along an acidification gradient.

Several traits responded to environmental factors in all three observational studies (shell size, number of offspring, reproduction mode, and microhabitat occurrence), or in two of the three studies (survival of dry period, and humidity preference) suggesting some generality of certain trait-environment relationships. Three traits (shell size, calcium affinity, and self-fertilization) and one measure of functional diversity (functional richness) responded both to environmental variation, and influenced the snails' potential contribution to leaf litter decomposition.

Keywords: Gastropoda, soil invertebrates, functional traits, functional diversity, community assembly, consumption rate, leaf litter decomposition, ecosystem functioning

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Dedication

To the snails,
those gentle little creatures that taught me patience.

To my family,
on which I can always count on.

The crucial first step to survival in all organisms is habitat selection. If you get to the right place, everything else is likely to be easier.
Edward O. Wilson, *Biophilia*, 1984

Contents

List of Publications

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

I Astor, T., Strengbom, J., Berg, M.P., Lenoir, L., Marteinsdóttir, B., Bengtsson, J. (2014). Underdispersion and overdispersion of traits in terrestrial snail communities on islands. *Ecology and Evolution* 4(11), 2090-2102.

II Astor, T., von Proschwitz, T., Strengbom, J., Lenoir, L., Berg, M.P., Bengtsson, J. Environment contributes more than space to trait composition in terrestrial snail communities (manuscript).

III Astor, T., Lenoir, L., Berg, M.P. Measuring effect traits of a range of terrestrial snails – litter consumption, faeces production and scaling with shell size (submitted to Oecologia).

IV Astor, T., Strengbom, J., Lenoir, L., Bengtsson, J. Testing the response-and-effect trait framework on macro-invertebrate communities: land snail effects on litter consumption (manuscript)

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The contribution of Tina Astor to the papers included in this thesis was as follows:

I Main author, data analysis, idea and concept, co-authors: Joachim Strengbom, Matty P. Berg, Lisette Lenoir, Bryndís Marteinsdóttir, and Jan Bengtsson

II Main author, data handling and analysis, idea and concept together with Jan Bengtsson, Joachim Strengbom, Lisette Lenoir and Matty P. Berg, co-authors: Ted von Proschwitz, Joachim Strengbom, Lisette Lenoir, Matty P. Berg, M.P., and Jan Bengtsson

III Main author, practical work, idea and concept together with Matty P. Berg, co-authors: Lisette Lenoir and Matty P. Berg

IV Main author, data analysis, idea and concept together with Jan Bengtsson, Lisette Lenoir and Joachim Strengbom, co-authors: Joachim Strengbom, Lisette Lenoir, and Jan Bengtsson

Abbreviations

BDEF	biodiversity and ecosystem functioning
Ca	calcium
CR	consumption rate
CWM	community-weighted mean trait value
FD	functional diversity
FDis	functional dispersion
FEve	functional evenness
FRic	functional richness
MEM	Moran’s eigenvector maps
PCNM	principal coordinate of neighbour matrices
PCoA	Principal coordinate analysis
pRDA	partial redundancy analysis

1 Introduction

1.1 Contemporary community ecology

Within community ecology research interest is shifting from the question ‘how many species are present in communities and why’, to the question ‘species possessing which traits, and how much variation in traits is present in communities and why’. The advantage of using traits instead of species is that functional traits directly link organisms’ performance to environmental (both abiotic and biotic) conditions (Violle *et al.*, 2007), facilitating a more mechanistic understanding of underlying processes controlling species distribution patterns and community composition (Villéger *et al.*, 2008; McGill *et al.*, 2006). Trait-based approaches also allow for comparisons of large numbers of species and their interactions across different environments and scales even when the taxonomic knowledge is limited which is the case for many groups of organisms. For these reasons, traits can be used to achieve generality and predictability (Laliberté & Legendre, 2010; Villéger *et al.*, 2008; McGill *et al.*, 2006), for addressing major ecological questions, such as: a) how are species sorted along environmental gradients? b) what is the relative importance of different processes governing the assembly of communities? c) how does the performance of organisms scale up to the functioning of ecosystems? There is growing consensus that trait-based approaches are useful for answering these questions, and evidence has been found for different organisms and ecosystems, although most progress has been achieved within the field of plant ecology. In this thesis, I used terrestrial snails as study organisms and focussed on leaf litter decomposition as model ecosystem function to address these questions.

1.2 Definition of traits, trait composition and functional diversity

Functional traits are defined as any morphological, physiological and phenotypic features of an organism that determine its ability to grow, reproduce or survive, and thus directly or indirectly impact its fitness (Violle *et al.*, 2007; Petchey & Gaston, 2002).

The environment (abiotic and biotic) can act as a filter allowing only those species to persist in a community that possess specific combination of traits that enable them to cope with the prevailing conditions at a site (Keddy, 1992). These traits are also termed *response traits* (Laliberté & Legendre, 2010; Villéger *et al.*, 2008; Lavorel & Garnier, 2002; Petchey & Gaston, 2002; Keddy, 1992) and comprise functional traits that increase an organism's fitness towards environmental conditions. A characteristic feature of response traits on community-level is that their average values and distribution vary consistently due to environmental drivers. Examples include growth form and seedling growth rate of plants in response to fire (Lavorel & Garnier, 2002), growth form and life span of plants in response to grazing (Díaz *et al.*, 2007b), desiccation resistance of terrestrial isopods in response to water availability (Dias *et al.*, 2013b), drought tolerance and body size of sub-arctic collembolan communities in response to changes in climate (Makkonen *et al.*, 2011), and mobility and start of the flying season in bees in response to fire (Münkemüller *et al.*, 2011; Moretti *et al.*, 2009).

In contrast, *effect traits* are those traits that affect ecosystem functioning (Lavorel & Garnier, 2002; Díaz & Cabido, 2001), such as specific leaf area, leaf dry matter content, and nitrogen content, influencing litter decomposition, soil carbon and net primary productivity, consumption of leaf litter by macro-detritivores influencing leaf litter mass loss (Vos *et al.,* 2011 and Paper III of this thesis), or faeces and mucus production of gastropods facilitating decomposition (Theenhaus & Scheu, 1996; Jennings & Barkham, 1979; Newell, 1967).

Species can also induce changes in their environment via their traits, which, in turn, can modify subsequent responses (of the same or other species) to these new environmental conditions (Webb *et al.*, 2010; Suding *et al.*, 2008). An example are ecosystem engineers, organisms which modulate the availability of resources for other species (Jones *et al.*, 1994). Such impacts of species on the environment have received less attention although they may be equally important in determining the species' niche as the species' requirements to cope with given environmental conditions (Chase & Leibold, 2003).

The distribution of traits within a community (trait composition) can be described by the average trait values and the variation of trait values among species (Box 1). Both of these components of trait composition can determine the response of communities to environmental variation and their effect on ecosystem functioning.

Box 1 – Community trait composition

Average trait value

The average trait value is usually calculated for each trait as the average of trait values for all species present in a community, weighted by their relative abundances (also termed community-weighted trait mean, or CWM; Garnier *et al.*, 2004) and emphasizes the dominant trait value of a community. CWMs have been shown to be useful to detect shifts in environmental filters (Ackerly & Cornwell, 2007). If an ecosystem function is driven by the dominant species (and their respective traits), CWMs can be used to assess the impact of communities on ecosystem functioning. This idea arose from the mass ratio hypothesis (Grime, 1998), stating that a species` contribution to a function is proportional to its relative proportion in a community.

Variation of trait values

The variation of trait values within a community, or the degree to which species differ in their trait values can be quantified by different indices of functional diversity (FD) (Laliberté & Legendre, 2010; Villéger *et al.*, 2008; Petchey & Gaston, 2002). There is a general consensus that functional diversity is multi-facetted, consisting of three distinct components – functional richness, functional evenness and functional divergence (Mason *et al.*, 2005), and methods have been developed and advanced to calculate multivariate indices for each facet (Laliberté & Legendre, 2010; Villéger *et al.*, 2008). Functional richness reflects the range of trait variability in a community, functional evenness describes the evenness of abundance distributions across traits, and functional divergence represents the degree of dissimilarity in abundance distributions across traits (Mason *et al.*, 2005). FD can capture community response to environmental gradients (Pakeman, 2011a), depict different mechanisms of community assembly (Münkemüller *et al.*, 2011; Mouchet *et al.*, 2010), and influence ecosystem functioning, due to non-additive biotic interactions - either synergistic, through complementarity and facilitation, or antagonistic, through competition - promoting a more efficient resource use among coexisting species (Heemsbergen *et al.*, 2004; Petchey *et al.*, 2004; Tilman *et al.*, 1997).

1.3 Community assembly

How species assemble into communities and which response traits are involved in the assembly process is still a central question in community ecology (McGill *et al.*, 2006; Weiher & Keddy, 1995). Species are added to species pools by speciation and dispersal, and their abundances are influenced by random processes (drift), deterministic fitness differences (selection), and ongoing dispersal (Vellend, 2010). Generally, processes resulting in random patterns of community composition (Connor & Simberloff, 1979), such as neutral performance of individuals (Hubbell, 2001), are distinguished from processes resulting in deterministic or non-random patterns, usually termed assembly rules (Weiher & Keddy, 1995; Diamond, 1975; MacArthur & Levins, 1967).

The assembly of communities is thought to be a hierarchical process in which species have to pass a set of abiotic and biotic filters acting on subsequently finer spatio-temporal scales (Zobel, 1997) selecting species that are best adapted to local conditions. *Phylogenetic assembly*, being a result of constraints due to long-term historic pattern of speciation, extinction, and biogeographic migration, is distinguished from *ecological assembly*, comprising dispersal (both active and passive), abiotic and biotic processes (Götzenberger *et al.*, 2012; Lortie *et al.*, 2004; Belyea & Lancaster, 1999) (Figure 1).

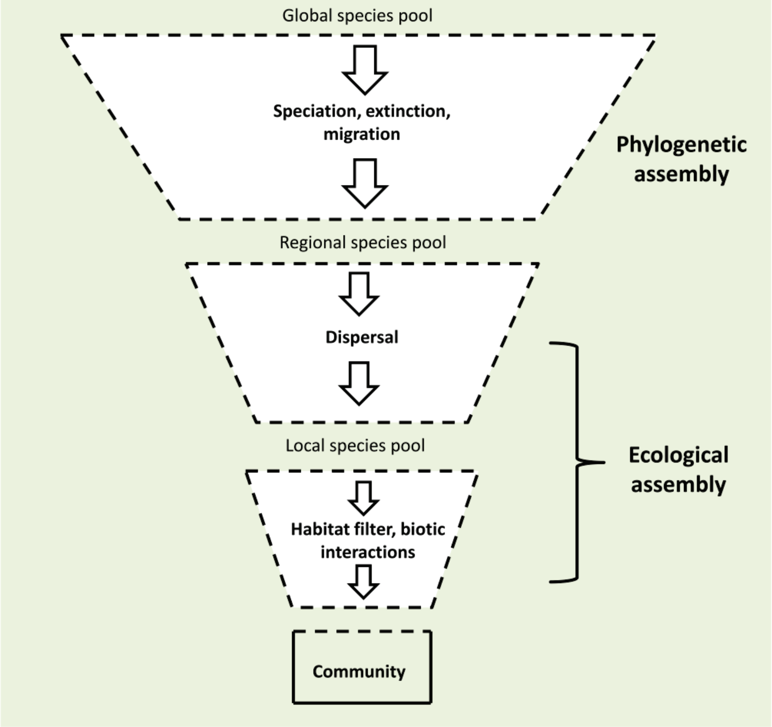

Figure 1. Different processes involved in community assembly and the spatial scales at which they are most predominant (adapted from Zobel, 1997, and Götzenberger *et al.* 2012).

In this thesis, I solely focus on the ecological part. During ecological assembly, species (via their traits) are hierarchically filtered by large-scale environmental factors, such as climate, followed by finer-scale environmental factors and biotic interactions (Díaz *et al.*, 1998; Weiher & Keddy, 1995). Local community composition thus represents the cumulative effect of all these processes (Figure 2).

In order to test for different deterministic assembly pattern, null model approaches, with the null hypothesis that the observed pattern is a result of pure chance, are usually used. Deterministic patterns of community composition are expressed through species being either more similar (underdispersed) or more different (overdispersed) to each other than expected from a random distribution (Figure 2). Traditionally, studies on community assembly were based on species occurrences and could only detect one of these patterns. In contrast, approaches based on traits allow for testing both patterns simultaneously (Naaf & Wulf, 2012; Cornwell & Ackerly, 2009; Ingram & Shurin, 2009).

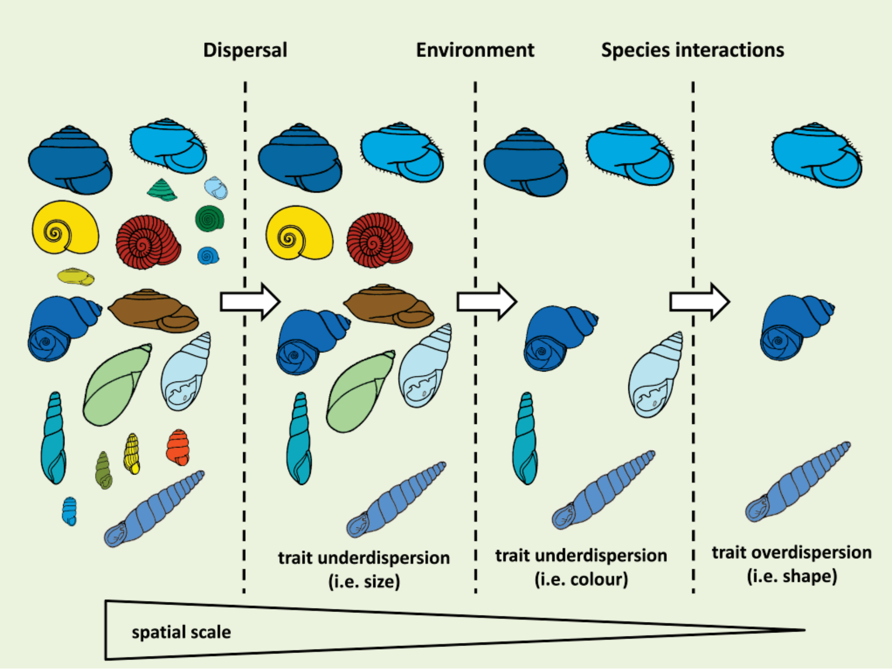

Figure 2. Hypothetical example to illustrate ecological assembly of snail communities. The dispersal filter may select large species from the regional species pool (leading to underdispersion in size). The environmental filter may select only species with a certain colour (leading to underdispersion in colour). Finally, at the community level, the species interaction filter may select species that are dissimilar in their shell shape (leading to overdispersion in shell shape).

The hypothesis that ecological assembly rules are the result of a set of hierarchical filters acting on the regional species pool filtering out species with non-appropriate response traits (Götzenberger *et al.*, 2012; Weiher & Keddy, 1995) is widely accepted. Traditionally, patterns of underdispersion and overdispersion have been ascribed to environmental filtering and niche partitioning, respectively (Weiher & Keddy, 1995). If species are primarily sorted by a common environmental filter, they should have certain traits in common that enable them to sustain the prevailing environmental conditions, resulting in under-dispersion of those traits (Silva & Batalha, 2008; Fukami *et al.*, 2005; Weiher & Keddy, 1995). Dispersal limitation is another mechanism resulting in underdispersion because species need certain traits to be able to disperse.

However, trait underdispersion can also occur due to predation (Abrams & Chen, 2002; Chase *et al.*, 2002; Zaret, 1980), natural enemies such as pathogens (Mitchell & Power, 2003), and competitive exclusion in the presence of a common limiting factor (Mayfield & Levine, 2010). Disentangling these alternative explanations would require carefully designed experiments that test for one mechanism ensuring to exclude all others. Such tests are very time consuming and would be a project on its own. Hence, I here focus on exploring the occurrence of underdispersion and overdispersion of traits, while ultimately identifying the underlying mechanisms goes beyond the scope of this thesis.

An explanation for overdispersion originates from the idea that species are more likely to coexist, when they are sufficiently different in traits related to resource requirements and resource acquisition. That traits are involved in maintaining species diversity through niche partitioning, has frequently been shown (Mason *et al.*, 2012; Kraft *et al.*, 2008; Stubbs & Wilson, 2004), and builds on the classical theory of limiting similarity (Diamond, 1975; MacArthur & Levins, 1967). However, the relative importance of the various processes that generate underdispersion or overdispersion and the underlying mechanisms are largely unknown.

1.4 Trait-environment relationship and the role of space

The prerequisite to develop generalizable predictions of impacts of environmental changes on community structure is that traits vary consistently along environmental gradients and among eco-regions. Within plant ecology major progress has been made in determining such sets of response traits that show robust relationships with environmental factors among sites and vegetation types (Díaz *et al.*, 2007a; Keith *et al.*, 2007; Ackerly, 2004).

Despite the early interest in the association between traits (which were previously termed characteristics) of terrestrial invertebrates and environmental factors in form of environmental stress (see Statzner *et al.*, 2001 for a summary), a consistent conceptual and methodological road map on which traits to focus on, and how to measure them is still lacking. However, awareness of the importance of trait-based approaches for terrestrial soil invertebrates is increasing (Pey *et al.*, 2014), databases collecting traits of different soil fauna groups are establishing (Bertelsmeier *et al.*, 2013; Salmon & Ponge, 2012; Makkonen *et al.*, 2011; Falkner *et al.*, 2001), and suggestions have been made to improve and expand the functional classification practice for terrestrial animals (Blaum *et al.*, 2011), for instance by including behavioural traits.

Soil organisms usually exhibit a patchy (spatially aggregated) distribution (Ettema & Wardle, 2002). These patchy distribution patterns can arise from true trait-environment relationships, environmental factors that are themselves spatially structured, or from intrinsic population processes, such as dispersal, reproduction and competition which are independent of environmental variation (Ettema & Wardle, 2002).

In analyses testing the relative importance of environmental factors and intrinsic population processes for explaining community composition, a large influence of pure spatial variables (after partialling out the effect of environmental variables) indicates that intrinsic population processes play an important role. Evidence is accumulating that both environmental, and spatial components jointly determine community composition in a variety of organisms, e.g. plants (Tuomisto *et al.*, 2003), micro-organisms (Heino *et al.*, 2010) and soil animals (Viketoft, 2013; Benefer *et al.*, 2010), including snails (Hájek *et al.*, 2011; Labaune & Magnin, 2001), and a recent meta-analysis comparing 158 datasets revealed that for most communities the environmental component explained the largest amount of variation in community composition, followed by the purely spatial component and the spatially structured environment (Cottenie, 2005).

1.5 Biodiversity and ecosystem functioning (BDEF) in a changing environment

The increasing use of natural resources by humans leads to a continuing depletion and simplification of ecosystems regulating the biogeochemical processes that support the Earth system (Millenium Ecosystem Assessment 2005). Alarmingly high rates of species loss (Pimm & Raven, 2000) due to global environmental changes including altered land use accompanied by habitat destructions have raised concern about the consequences for major ecosystem functions and services humans derive from them (Thompson & Starzomski, 2007; Chapin *et al.*, 2000).

Out of this concern, a research field has developed that seeks to unravel how changes in species distribution, composition and abundance influence ecosystem functioning (Naeem, 2002; Tilman *et al.*, 1997; Schulze & Mooney, 1993). Ecosystem functioning encompasses ecosystem properties (including both the size of the compartments and the rates of processes), ecosystem goods which possess a direct economic value, and ecosystem services, being those ecosystem processes that are essential for human well-being (Christensen *et al.*, 1996). The important role of functional traits in driving ecosystem processes has been emphasized due to their ability to improve the predictability of ecosystem processes (Hooper *et al.*, 2005; Naeem & Wright, 2003; Loreau *et al.*, 2001). Major aims pursued in current BDEF research are disentangling the relative importance of different components of trait composition (average trait values vs. variability in traits) for driving ecosystem functioning (Dias *et al.*, 2013a), developing strategies for assessing multiple ecosystem processes and services across different ecosystems and organisms (de Bello *et al.*, 2010), and including multi-trophic levels (Lavorel *et al.*, 2013).

1.6 Decomposition and the role of macro-detritivores

Leaf litter decomposition is a key ecosystem function controlling the cycling of energy and nutrients in below- and aboveground ecosystem compartments (Swift, 1979). It is driven by the interplay between physicochemical soil conditions, leaf litter quality and detrital food web structure in both terrestrial (Coûteaux *et al.*, 1995; Berg *et al.*, 1993) and aquatic biomes (Handa *et al.*, 2014; Tank *et al.*, 2010). The quality of leaf litter, expressed by chemical or physical traits, such as nitrogen concentration (Handa *et al.*, 2014; Wright *et al.*, 2004), lignin content (Aerts, 1997; Van Vuuren *et al.*, 1993), polyphenol and condensed tannin content (Valachovic *et al.*, 2004; Nicolai, 1988) and physical leaf toughness (Gallardo & Merino, 1993) has been shown to influence decomposition rates. Litter that decomposes faster is characterized by a high nitrogen content, low content of phenolic compounds and tannins and low physical leaf toughness.

Primary decomposers, such as microbes and fungi are mainly responsible for the actual carbon mineralization and nutrient cycling (Swift & Anderson, 1993), whereas soil microfauna (e.g. protozoa), mesofauna (e.g. mites, collembolan), and macrofauna (e.g. isopods, earthworms, snails) largely influence the rates at which these processes operate. In the following, I will discuss the role of soil macro-fauna for decomposition, because snails - used as study organisms in the present work –belong to this group.

Soil macro-detritivores feeding on leaf litter have been demonstrated to play an important role in decomposition processes (Handa *et al.*, 2014; Hättenschwiler & Gasser, 2005; Vasconcelos & Laurance, 2005; Heemsbergen *et al.*, 2004; Bradford *et al.*, 2002; Cárcamo *et al.*, 2000; Seastedt, 1984; Mason, 1970b). They can influence decomposition rates in various ways, such as fragmenting litter material (Hedde *et al.*, 2007; Coûteaux *et al.*, 2002), mixing of organic and mineral particles (Jones *et al.*, 1994), modifying organic matter chemistry during metabolic processes (Coulis *et al.*, 2009; Kadamannaya & Sridhar, 2009), and facilitating microbial activity (Maraun & Scheu, 1996; Theenhaus & Scheu, 1996; Petersen & Luxton, 1982), e.g. through the addition of nutrient rich faeces or mucus (Newell, 1967).

Recently, it has been suggested that both leaf litter identity and macro-detritivore identity interactively influence decomposition rates (Vos *et al.*, 2011; Hättenschwiler & Gasser, 2005). Such effects can be generated by selective feeding of macro-detritivores on litters with certain traits in litter mixtures (Hättenschwiler & Bretscher, 2001; Zimmer & Topp, 2000).

1.7 The response-and-effect trait framework

Due to rapid species loss and deterioration of ecosystems, ecologists are in urgent need to understand how changes in the environment alter community structure and assembly and how these changes, in turn, influence ecosystem functioning. Such information is needed in order to be able to predict possible consequences of environmental change and for decision makers and stakeholders to initiate target-oriented protection and restoration actions.

Researchers developed a framework that links species' responses to environmental variation to their influence on ecosystem processes through functional traits (Suding *et al.*, 2008; Lavorel & Garnier, 2002) representing one possible way to accomplish this challenging task. The basic assumption of the framework is that there are traits that respond to environmental factors (response traits), and traits that influence ecosystem functioning (effect traits). If these traits overlap (i.e. the same trait operates as response- and effect trait, or response- and effect traits are correlated) it is possible to predict how changes in the environment influence ecosystem functioning mediated by the biotic communities (Lavorel & Garnier, 2002) (Figure 3).

2 Thesis Aims

The general aim of this thesis is to apply trait-based approaches to terrestrial snails in order to examine different aspects of their responses to environmental variation (including community assembly), and their potential effects on leaf litter mass loss (Figure 3).

The specific objectives are to:

- Identify traits that are involved in community assembly and examine the relative importance of environmental filtering and niche partitioning (Paper I)

- Examine how response trait composition is related to environmental factors (Paper I and II) and if trait composition is best explained by environmental or spatial determinants using a regional scale dataset (Paper II)

- Measure effect traits of snails in relation to leaf litter mass loss (consumption rate, faeces production and assimilation efficiency) (Paper III)

- Examine how environmental change along an acidification gradient influences snail communities' response traits, and if changes in these traits can be linked to the potential influence of snail communities on leaf litter mass loss (effect traits) (Paper IV)

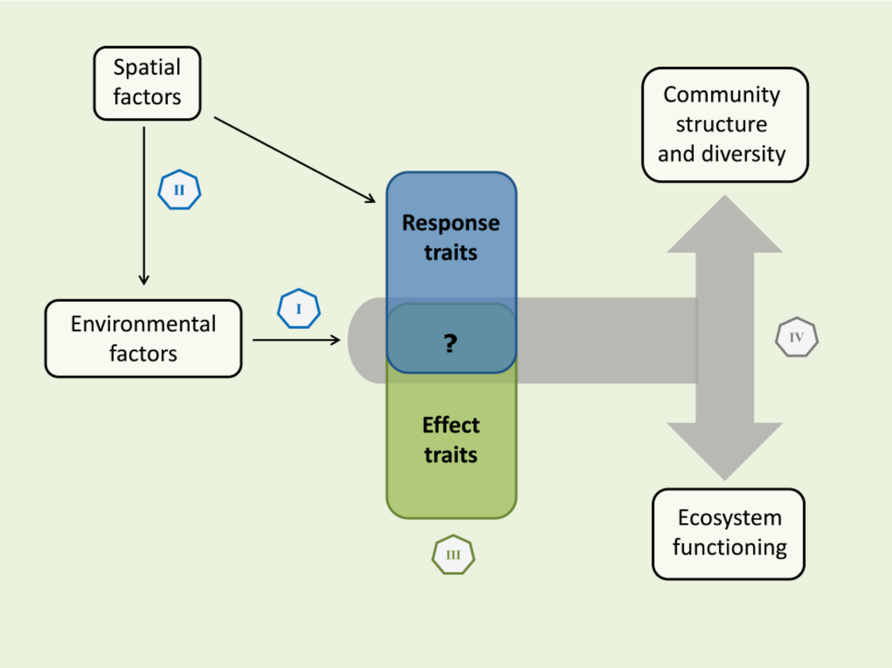

Figure 3. Schematic figure showing how the four thesis articles (Roman numerals) feed into the response-and-effect trait framework of Lavorel *et al.* (2002).

3 Methods

3.1 Study organisms

Gastropods (comprising terrestrial snails and slugs) represent a highly diverse order including about 35 000 species divided into 112 families worldwide (van Bruggen *et al.*, 1995; Solem, 1984). Gastropods can be divided into Prosobranchs – having no lung, one pair of tentacles and an operculum (chitinoid cap to seal the shell mouth) and Stylommatophoran pulmonates – having a lung, two pairs of tentacles and lacking an operculum. Stylommatophorans form the great majority of terrestrial gastropods.

The majority of terrestrial gastropods are detritivores, feeding on decaying plant litter along with associated microorganisms, but feeding strategies also comprise omnivory, herbivory and carnivory (Barker, 2001). Their local occurrence is determined by several factors, such as pH and calcium content (Martin & Sommer, 2004; Nekola & Smith, 1999), drainage (Paul, 1978), altitude (Cowie *et al.*, 1995), shelter possibilities (South, 1965), humidity (Martin & Sommer, 2004), plant composition, and plant diversity (Barker & Mayhill, 1999).

The roles of terrestrial gastropods in ecosystems are diverse. They have been reported to influence macro-nutrient cycling in moisture stressed environments, by re-allocating nitrogen to the soil (Jones & Shachak, 1994; Jones & Shachak, 1990). Highly selective feeding of some gastropod species can lead to an alteration of plant composition due to increased selective pressure caused by changes in nitrogen and phosphorous contents in the soil (Thompson *et al.*, 1993). Because they can fix calcium through intra- and extracellular biomineralization (Simkiss, 1976) they might contribute to the retention of calcium in the upper soil layer and their shells provide an important calcium source for birds (Graveland & van der Wal, 1996). Gastropods have a high capability to accumulate metals in their body (Dallinger, 1993) and can therefore be used as biological indicators of polluted habitats (Dallinger *et al.*, 2004). Finally, gastropods have been reported to accelerate leaf litter decomposition by fragmenting the litter, and facilitating colonization by microbes through the excretion of nutrient rich faeces and mucus which provide suitable habitats for microbes (Jennings & Barkham, 1979; Newell, 1967).

3.2 Trait database

The database "Shelled Gastropods of Western Europe" (Falkner *et al.*, 2001) currently represents the most extensive collection of snail traits, containing information (in form of ranked multi-choice variables, for more details on how these categories were treated see the papers) on a wide range of traits and characteristics related to morphology, life-history, environmental tolerance, habitat-, and diet preferences (Falkner *et al.*, 2001). All information on response traits was gathered from this trait database. An overview of all traits and their categories extracted from the database and used in this thesis are given in Table 1. From the trait 'reproduction periods' the number of reproduction periods per year were counted and used as trait instead of the original information. The entries for ecosystem occurrences, micro-habitat occurrences and food preferences were converted to binary multi-choice variables because not all categories could be used, due to redundancy. For Paper II and IV, the occurrences in the respective categories were used to calculate ecosystem-, microhabitat-, and diet niche width with the Shannon Index (Shannon, 1948).

In Paper IV, maximum shell sizes were obtained from a determination key (Kerney & Cameron, 1979) and shell volume was calculated, assuming an elliptic cone as approximation for the shape of the shells.

Note that only snails were considered in this thesis because there is no comparable trait information available for slugs.

Table 1. *Traits obtained from the Database on Shelled Gastropoda of Western Europe (Falkner et al., 2001) with their original categories.*

	Traits	**Original categories**	**Used in Paper**
Life-history	max. shell size	<2.5mm; 2.5-5mm; 5-15mm; >15mm	I, II
	age at maturity	< 1year; 1 year; >1year	I, II
	number of offspring	1-10; 11-100	I, II, IV
	reproduction mode	cross-fertilization, self-fertilization	I, II, IV
	reproduction periods	Jan/Feb; Mar/Apr; May/Jun; Jul/Aug; Sept/Oct; Nov/Dec	I, II
Morphology	shell shape	depressed; globose/conical; oblong	I, II, III
Environmental tolerance	humidity preference	dry; moist; wet	I, II
	survival of dry period	days; weeks; months	I, II
	inundation tolerance	low; moderate; high	I, II
	soil Ca affinity	calcareous soil; non-calcareous soil	I, II, IV
Habitat and diet	ecosystem occurrence	deciduous forest; scrub; mixed forest; coniferous forest; tall herb; thermophilous forest fringe; unimproved grassland; heathland; coastal dunes; inland dunes; cliff/rock; scree/walls; hedge; fen; reed; water edge	I, II, IV
	micro-habitat occurrence	trees; shrubs/bushes/saplings; herbs; mosses; timber; forest litter; stones; strand debris; sand; soil; bare rock; root zone; crevices; caves	I, II, IV
	food preference	deciduous forest litter; fungi; lichens; live mosses; live algae, higher live plants; carnivorous/saprophagous	I, II IV

3.3 Study systems and sampling

For the present work I used three existing sets of snail community data surveyed with different spatial resolution and extent (Paper I, II and IV). In Paper III, I conducted a microcosm feeding experiment in the laboratory.

3.3.1 Paper I

The dataset used to test for different assembly patterns of snail communities (i.e. trait underdispersion indicating environmental filtering, and trait-overdispersion indicating niche partitioning) comprised species abundances of

17 islands located in the central part of Lake Mälaren, Sweden (Figure 6 B), within an area of approximately 1062 km^2 (Nilsson *et al.*, 1988). The islands are covered with mature, unmanaged forest to varying degree (Figure 4). In the original study, ground-living snails were sampled on five occasions from May to September 1981 on each island. Within 10 × 10 m plots (1 plot on the smallest, and four plots on the largest islands) litter and the upper soil layer were collected from five to seven randomly placed 0.1 m^2 squares. The counts from each small square were lumped together to give one count per species for each 10 × 10 m plot. After drying the litter at 50°C the material was sieved and hand-sorted. Along with the snail abundance data, I used a part of the environmental variables recorded in the original study (island size, distance to the mainland, habitat diversity, plant diversity, amount of deciduous and coniferous forest, and tree cover).

Figure 4. Examples of different vegetation cover on the islands.

3.3.2 Paper II

For this study, I utilized a part of the on-going long-term survey of snail species occurrences in Sweden conducted by the Gothenburg Natural History Museum. The standard sampling procedure (von Proschwitz, 1996; Waldén, 1965) is carried out by the same person each year from April to October. An amount of 15-20 litres of fresh ground litter, representative for the respective site, was sieved (8 x 8 mm mesh) in the field. After air-drying the material it was sieved into smaller fractions and snails were hand-sorted. In some sites snails were only collected by manual search for 45 minutes. All snails were identified to species using a magnification of 6-50x. Additionally, a description of the site's geomorphology, structure, and vegetation was always carried out on the site.

For my analysis I considered snail occurrence data of 622 sites surveyed in the period between 1960 and 2012 and distributed within the area of the Province of Skåne, South Sweden (Figure 6 D).

3.3.3 Paper III

During time of leaf abscission in October 2012, leaves of *Betula pendula* were collected in the vicinity of the Swedish University of Agricultural Sciences, Uppsala, Sweden (Lat. 59°50' N, Long. 17°38' E), and *Fraxinus excelsior* leaves were collected in the vicinity of the VU University, Amsterdam, the Netherlands (Lat. 52°33' N, Long. 04°86' E).The litter material was dried and stored at room temperature.

During April and May 2013, ten snail species (i.e. *Arianta arbustorum*, *Discus rotundatus*, *Oxychilus cellarius*, *Oxychilus draparnaudi*, *Trochulus hispidus*, *Cochlodina laminata*, *Cornu aspersum*, *Monachoides incarnatus*, *Balea biplicata*, and *Merdigera obscura*) were collected on four sites in the Netherlands: Zwolle (park, Lat. 52°32' N, Long. 06°05' E), Maastricht (forest, Lat. 50°48' N, Long. 05°41' E), Amsterdam (park, Lat. 52°19' N, Long. 04°51' E), and Santpoort (dune forest, Lat. 52°26' N, Long 4°36'). The animals were allowed to acclimatize in a climate room at 15°C, 75% humidity, a 12/12 h light:dark regime and provided with the experimental food (either *Fraxinus* or *Betula* leaves) for one week, prior to the experiment.

For the first experimental trial, aiming at measuring traits that potentially influence leaf litter mass loss and testing the relationship between consumption rate and shell size, ten snail species were tested on one litter type. For the second trial, testing if litter quality influences the amount and rank order of consumption, four snail species were fed on both litter types. Additionally, a control treatment with leaf litter but without snails was included. All treatments (including the control) were replicated ten times. Litter was provided in form of standardized leaf discs (Figure 5) that were produced with a punching device. Prior to the start of the experiment the leaf discs were dried at 50 °C for 48 h and weighed. At the end of the experiment, the leaf discs and faeces were separated, dried at 50°C for 48 h and weighed again. The snail individuals were weighed alive before and after the experiment. Thereafter, they were transferred to a jar filled with liquid nitrogen and vacuum freeze-dried for 48 h to obtain their dry weights. Litter mass loss was calculated as $mg_{litter\ mass\ loss}\ d^{-1}$, and as $mg_{litter\ mass\ loss}\ g_{snail\ dry\ weight}^{-1}\ d^{-1}$. Differences between treatments were analysed using one- and two-way ANOVAs and the relationship between consumption rate and shell size was tested using linear regression.

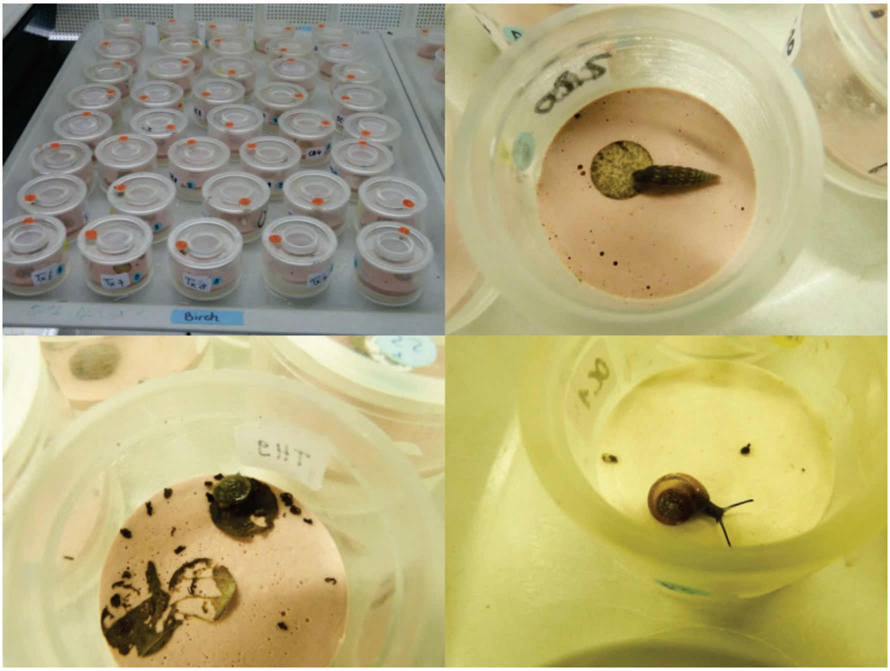

Figure 5. **Top left**: tray with plastic containers filled with a moistened layer of plaster of Paris and cealed with a lid with an opening covered by a net. Each container contained one individual snail and leaf discs of one litter type (in this case *Betula*). **Top right**: *Balea biplicata* with a *Betula* leaf disc at the start of the experiment. **Bottom left**: *Trochulus hispidus* feeding on *Fraxinus* leaf discs during the experiment. **Bottom right**: *Oxychilus cellarius* separated after the end of the experiment.

3.3.4 Paper IV

This study is based on published snail distribution data of 20 forest sites in South Småland, Sweden (Figure 6 C), that were originally collected to investigate the effects of acidification on snail species richness and abundance (Wäreborn, 1992). In the original study, 55 forest sites were sampled in the period 1964-1966 (Wäreborn, 1969). Twenty of these sites were re-visited in the period 1987-1988 and data were collected with the same standard methods (Wäreborn, 1992). For my analyses, I utilized information on snail species abundances and soil calcium content. Samples on each site were taken between the middle of June and the end of August within a 10 × 20 m square. From these squares forest litter and the upper soil layer was collected and sieved (10

× 10 mm mesh sieve) until a volume of 3-4 litres was reached. The material was air-dried and snails were hand sorted using a magnifying glass. Species abundances (living snails) per site were re-calculated to a volume of 3 litres. For the calcium analysis the sieved and air-dried litter and soil material was ashed and extracted with hot 7.5 M HCl (Wäreborn, 1969). Ca was expressed as mg g^{-1} of ash-free dry weight.

I used eight traits (shell volume, calcium affinity, number of offspring, number of reproduction periods, degree of self-fertilization, diet-, microhabitat- and ecosystem niche width) and three multivariate functional diversity indices (functional richness, functional evenness and functional dispersion) to test if they were related to soil Ca content.

To obtain an estimate of the snail's potential contribution to leaf litter mass loss, I made use of the consumption rate – shell size relationship obtained in Paper III to predict the consumption rates of all snail species present in the 20 forest sites. The total consumption rate of each community was then calculated by multiplying the abundance of each species with its predicted consumption rates and the sum of these values was calculated for each community.

With linear mixed effect models, I examined how individual traits (CWM) and FD indices of the communities differ depending on soil Ca content, and which of those influence community-wide consumption rates. The response-and-effect trait framework suggests that the traits and FD indices that both respond to Ca content, and influence community-wide consumption are candidates to predict consequences of acidification on leaf litter mass loss mediated by snail communities.

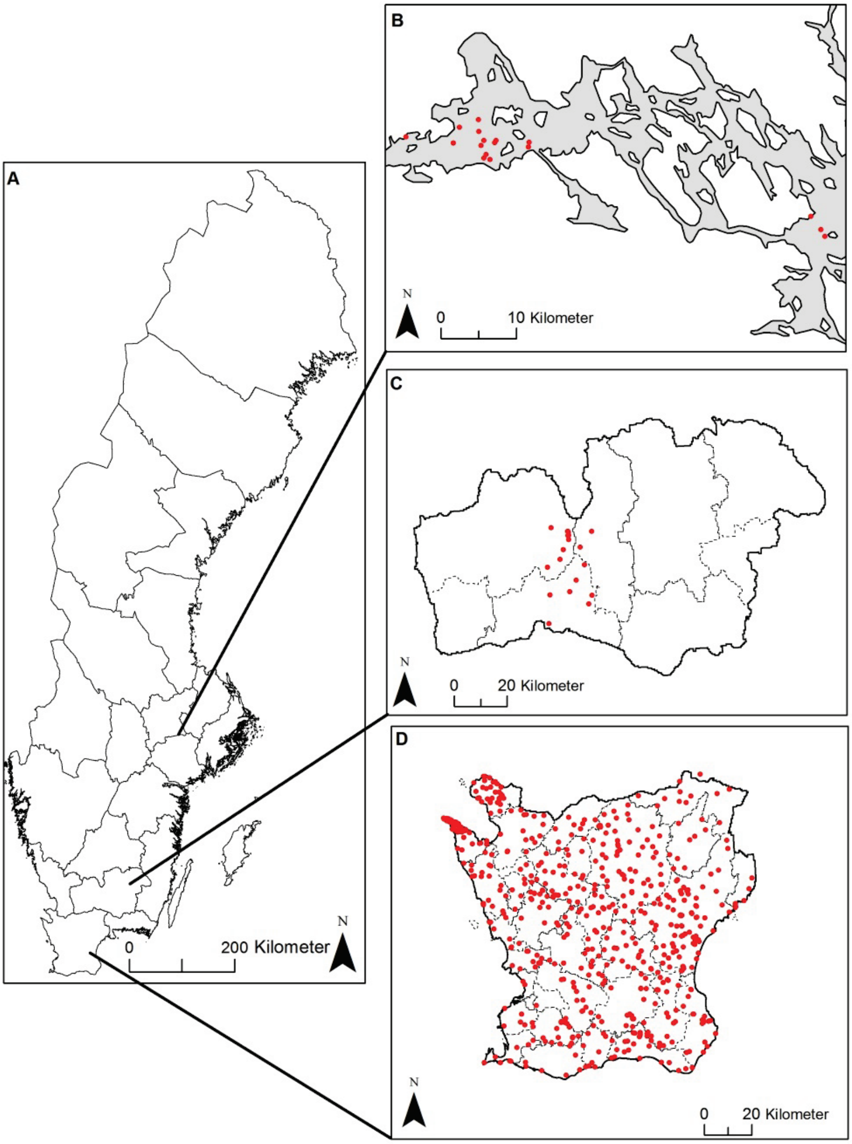

Figure 6. Study areas and sampling sites of the three data sets used in this thesis. **(A)** Sweden, **(B)** 17 islands on lake Mälaren (Nilsson *et al.*, 1988) used in Paper I, **(C)** 20 sites in south Småland (Wäreborn, 1992; Wäreborn, 1969) used in Paper IV, **(D)** 622 sites in Skåne (von Proschwitz, 1996; Waldén, 1986) used in Paper II.

3.4 Data Analysis

3.4.1 CWM

The community-weighted mean trait value is calculated for single traits as the sum of the trait values for each species weighted by their relative abundances (Garnier *et al.*, 2004):

$$CWM = \sum_{i=1}^{n} a_i \times t_i$$

where n is the number of species in a community, a_i is the relative abundance of species i, and t_i is the trait value for speices i.

CWMs were used in Paper I to examine trait composition along environmental gradients, in Paper II to examine trait composition in relation to environmental and spatial variables, and in paper IV to link the response of traits to soil Ca content to their effect on community-wide consumption rates (Table 2).

3.4.2 FD indices

Functional diversity indices used in this thesis include functional richness (FRic) (Villéger *et al.*, 2008; Cornwell *et al.*, 2006), functional evenness (FEve) (Villéger *et al.*, 2008), functional dispersion (FDis) (Laliberté & Legendre, 2010) and Rao's quadratic entropy index (Q) (Botta-Dukat, 2005), representing different facets of functional diversity.

Functional richness (FRic)

Functional richness represents the volume of the trait space occupied by the species in a community and is calculated from species occurrence data as the minimum convex hull volume including all species (Cornwell *et al.*, 2006). It can be considered as a multivariate analogue of the range.

Functional eveness (FEve)

Functional evenness represents the regularity of the abundance distribution in the volume of trait space. It measures the regularity of abundance distribution along the minimum spanning tree which links all species in the multi-dimensional trait space.

First, the length of each branch l is divided by the sum of the abundances of the two species linked by the branch giving a weighted evenness, EW:

$$EW_l = \frac{d_{i,j}}{a_i + a_j}$$

where $d_{i,j}$ is the euclidean distance between species i and j, and a_i and a_j are the relative abundances of the two species, respectively. Then, the partial weighted evenness, PEW, is calculated for each branch by dividing the EW_l values by the sum of all EW_l values of the tree.

Finally, functional evenness is calculated as:

$$FEve = \frac{\sum_{l=1}^{S}\left(PEW_l \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

where S is the total number of branches. The index is constrained between 0 and 1 and equals 1 when all PEW_l values are equal to $1/(S-1)$.

Functional dissimilarity

In this thesis I used two indices that express functional dissimilarity.

The *Rao index* (Rao hereafter) is defined as the extent of trait dissimilarity among species in a community and is calculated as the sum of trait dissimilarities among all pairs of species weighted by the product of their relative abundances.

It is calculated as:

$$Q = \sum_{i=1}^{n}\sum_{j=1}^{n} d_{i,j} \times a_i a_j$$

where n is the number of species in a community, a_i is the relative abundance of species i, a_j is the relative abundance of species j in a community, and $d_{i,j}$ is the dissimilarity (i.e. distance) between species i and j.

Multivariate dispersion was originally proposed as a measure for beta diversity (Anderson *et al.*, 2006) and was extended to a functional diversity index called *functional dispersion* (Laliberté & Legendre, 2010) which measures the average dissimilarity (i.e. distance) of individual species to the centroid of all species in the community (Laliberté & Legendre, 2010).

It is calculated as:

$$FDis = \frac{\sum_{i=1}^{n} a_i d_i}{\sum_{i=1}^{n} a_i}$$

where n is the number of species in a community, a_i is the abundance of species i in a community and d_i is the distance of species i to the abundance weighted centroid of all species in a multi-dimensional trait space such that the centroid is shifted toward the more abundant species. FDis can be computed with any dissimilarity/distance (*d*) measure (e.g. euclidean).

Rao was used in Paper I to test for the relative importance of different assembly pattern. Functional richness, evenness and dispersion were used in Paper IV to link the response of FD to soil Ca content to its effect on community-wide consumption (Table 2).

3.4.3 Null model approach

Null models are often used to test observed patterns of community assembly against random pattern of community assembly. Different mathematical algorithms have been developed to generate random samples from species occurrence data where row and column totals are treated as either fixed sums, equiprobable or proportional (Gotelli, 2000).

In Paper I, I applied two different null-models to generate random pattern of species occurrences and abundances. In the first null model, communities (species × plots matrix) were randomized by reshuffling the species identity *among* islands while keeping the same number of species per site and the frequency at which species occurred in the entire region using the trial swap method of Miklós and Podani (2004). In the second null model, we randomized the species abundances only *within* islands maintaining species richness per island.

For each random community, the Rao Index was calculated and the mean value resulting from the random communities was compared to the observed value of Rao, using the standard effect size (SES; Gotelli and McCabe, 2002) calculated as the observed Rao minus the mean of the expected Rao divided by standard deviation of expected Rao under the random distribution.

Trait underdispersion (indicating environmental filtering) was identified when the observed Rao value was lower than the one generated by the random communities, whereas trait overdispersion (indicating niche partitioning) was identified when the observed Rao value was higher than the one generated from the random communities.

3.4.4 CWM-RDA

CWM-RDA is a multivariate method for examining the community functional response to environmental gradients (Kleyer *et al.*, 2012). It is basically a redundancy analysis (RDA, a canonical ordination) of the plot by CWM matrix constrained by environmental variables. CWM-RDA was used in Paper I to examine the trait environment relationship that is explaining part of the observed assembly pattern, and in Paper II to examine the relative importance of environmental and spatial variables for community trait composition.

3.4.5 Variation partitioning and PCNM

Variation partitioning is frequently used in ecological research in a multivariate context to quantify the variation in community structure explained by different sets of explanatory variables, while controlling for the respective other sets of variables (Peres-Neto *et al.*, 2006; Borcard *et al.*, 1992). In Paper II, I carried out variation partitioning of trait composition using Partial Redundancy Analysis (pRDA) of the plot by CWM matrix constrained by environmental and spatial variables. This allowed for quantifying the unique and shared contributions of environmental and spatial variables to the variation in trait composition.

To generate spatial variables at different scales, I carried out an analysis of PCNM (Principal Coordinate of Neighbour Matrices) (Borcard *et al.*, 2004; Borcard & Legendre, 2002), which belongs to the wider family of methods called MEM (Moran's eigenvector maps) (Dray *et al.*, 2006). A Euclidean distance matrix was constructed from the geographical coordinates of the sites and truncated to retain only the distances among close neighbours. Then, a Principal Coordinates Analysis (PCoA) was computed and eigenvalues with positive spatial correlation (Moran`s I) were retained. These eigenvalues, along with environmental variables served as explanatory variables in the partial redundancy analyses.

To ensure that only significant variables entered the model, we, prior to variation partitioning, performed a forward selection of the environmental and spatial variables. From initially thirteen environmental variables (representing habitat characteristics, soil characteristics, and climatic variables) eight were retained, and from initially 186 PCNM eigenvectors, seventeen, representing mainly broad-scale spatial structures, were retained.

3.4.6 Linear mixed effect models

In Paper IV, I used linear mixed effect models (LME) to

- Examine the relationship of CWMs and FD to soil Ca content (response to environment)
- Examine the relation of CWMs and FD to community-wide consumption rates (effect on ecosystem functioning)

In both analyses, 'plot' was added as random factor. Since each plot was sampled twice (in the 1960s and 1980s) the observations within each plot are not independent from each other and are therefore likely to exhibit a higher correlation than observations among plots. We accounted for this correlation structure in the models which resulted in an LME with a repeated measurement structure.

In the first analyses, single CWMs or FD indices were used as response variables and ‘Ca content’ and ‘sampling period’ were added as fixed effects.

In the second model, community-wide consumption rates were used as response variables and single CWMs or FD indices and ‘sampling period’ were added as fixed effects. Sampling period was added because the relationship between community-wide consumption rate and CWM (or FD) can differ between the two periods. In addition to the single trait models, we also tested a model with multiple traits (or FD indices) to find out which traits showed the strongest effect on community-wide consumption rate.

Table 2. *The different trait based measures used in this thesis and their application in the four papers.*

Measure	Used in Paper	Methods
CWM	I	CWM-RDA
	II	CWM-RDA and variation partitioning
	IV	linear mixed effect models
FRic	IV	linear mixed effect models
FEve	IV	linear mixed effect models
FDis	IV	linear mixed effect models
Rao	I	null models testing for deterministic assembly pattern

4 Results

4.1 Paper I

Key findings: Trait underdispersion was the dominant pattern of community assembly and could be linked to environmental filtering whereas only weak evidence was found for trait overdispersion linked to niche partitioning.

Trait underdispersion (Figure 7):

> Maximum shell size, age at maturity, number of offspring, reproduction mode, humidity preference, survival of dry period, ecosystem occurrence, and microhabitat occurrence.

Most important environmental variables:

> Location on dry esker ridge, tree cover, productivity of ground vegetation, and habitat diversity

Trait overdispersion in (Figure 8):

> Number of reproduction periods, and shell shape

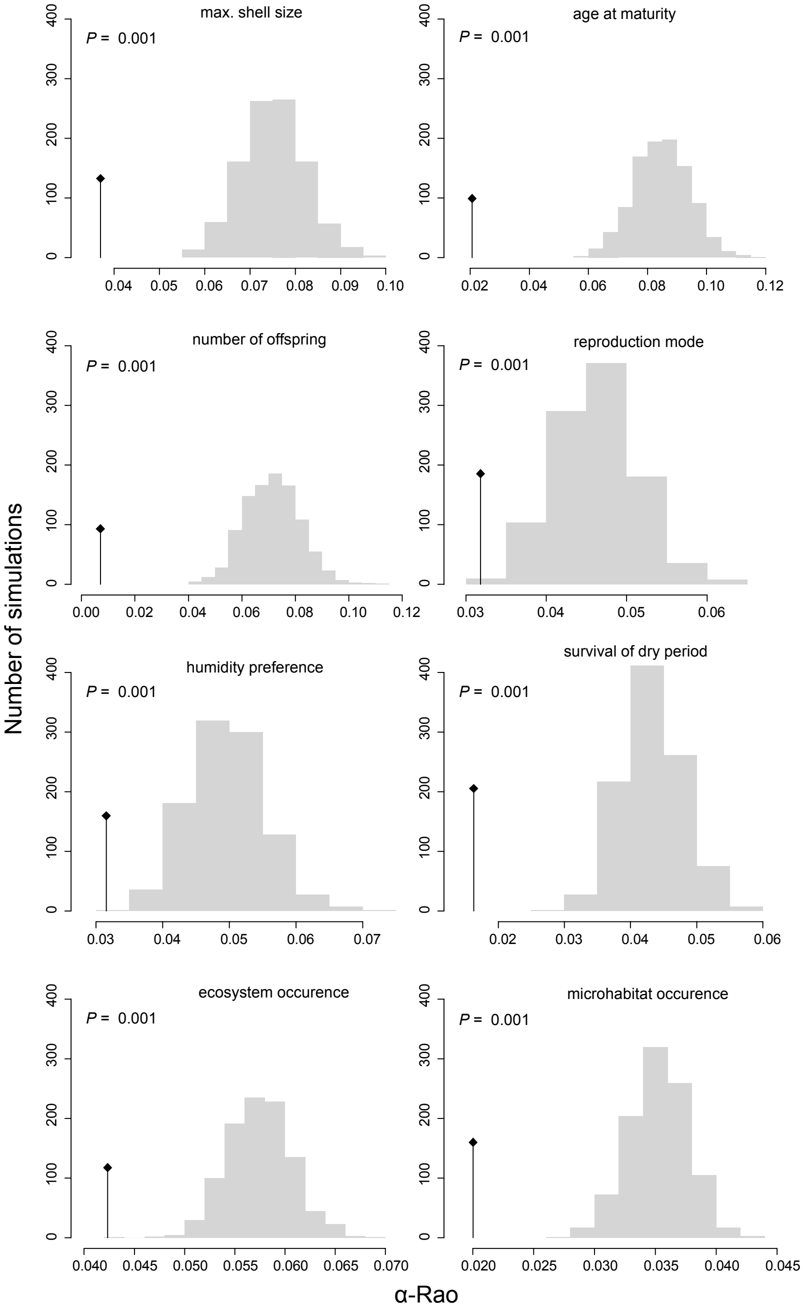

Figure 7. Observed (vertical line with a diamond symbol) versus expected Rao values resulting from a null species distribution (grey bars), shown for eight traits. Significant *P*-values imply that the observed value is significantly lower than the expected values, signifying trait underdispersion.

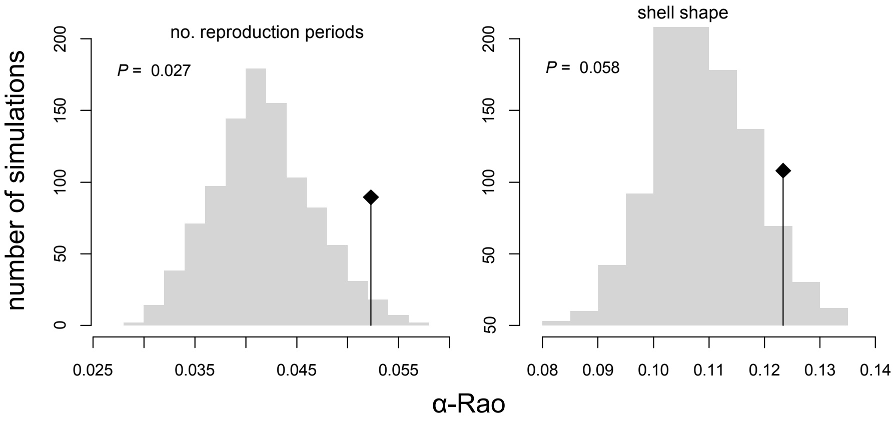

Figure 8. Observed (vertical line with a diamond symbol) versus expected Rao values resulting from a null species distribution (grey bars), shown for two traits. Significant *P*-values imply that the observed value is significantly larger than the expected values, signifying trait overdispersion.

4.2 Paper II

Key findings: Both environment, and space significantly contributed to community trait composition but the environmental fraction had the highest share.

Environmnental variables involved:

Wetland, fen, deciduous forest, pH, haplic podzol, stones, wet, and grazing

All fractions together (environment and space) explained 41.7% of the variation, leaving 58.3% unexplained variation (Figure 9). Environmental variables alone contributed most to the total variation (24.9%) followed by the fraction that is shared by environment and space (12.9%) and space alone (4.2%) (Figure 9).

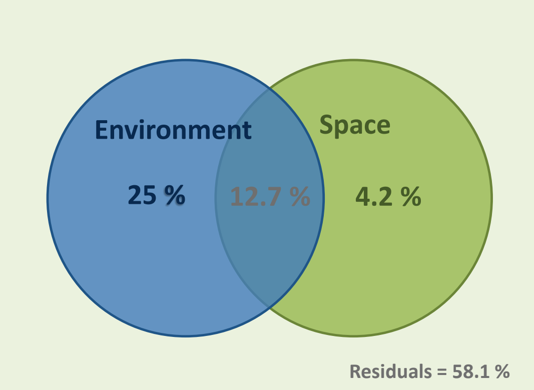

Figure 9. Unique and shared contribution of environmental and spatial variable to the variation in trait composition of terrestrial snail communities in the province of Skåne, south Sweden. (n=622), expressed as percentage of total variation in community-weighted mean trait values (CWM).

4.3 Paper III

Key findings: Species specific consumption rates can be predicted by shell size (Figure 10). The absolute amount of leaf litter consumed by the four tested snails differed between the two litter types, but relative consumption rates across species were the same for both litter types.

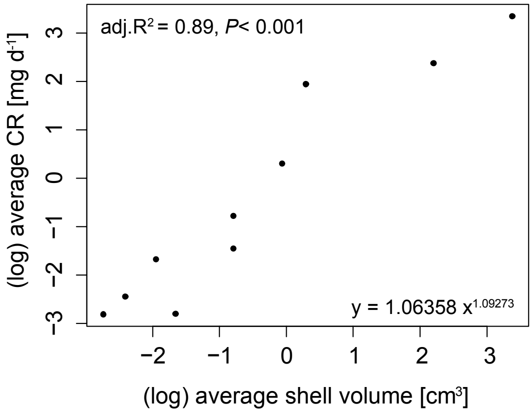

Figure 10. Relationship between species specific consumption rates (CR), and shell volume based on ten snail species (average values of 10 replicates per species) fed on *F.excesior* leaf litter.

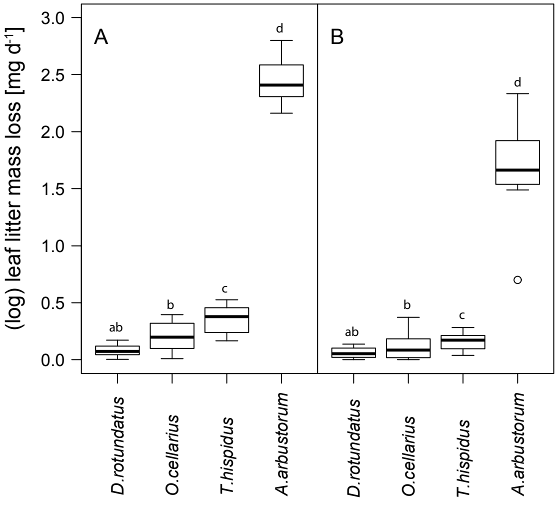

Figure 11. Boxplots showing the species specific consumption rates (CR) among species within the two litter types. (A) F. excelsior, (B) *B. pendula*. Different letters indicate a significant difference ($P < 0.05$). Boxplots show median values (central line), 25% and 75% quartiles (box) and the ranges (whiskers).

4.4 Paper IV

Key findings: Six of eight traits, namely shell volume, number of reproduction periods, number of offspring, degree of self-fertilization, calcium affinity, and microhabitat niche width, and one of three FD indices, namely functional richness, successfully captured the effects of soil calcium content on community-wide consumption rate mediated by the snail communities. Additionally, diet niche width and functional evenness were significantly related to community-wide consumption rate, but not to soil Ca content.

The best model explaining community-wide consumption rate, including both the pre-selected CWMs and FD indices, comprised three CWMs (shell volume, calcium affinity, and self-fertilization) and one FD index (functional richness), all having a positive relationship to community-wide consumption rate.

5 Discussion

The four presented articles of this thesis cover different aspects associated with the response-and-effect trait framework in which functional traits are used to explain how communities respond to environmental variation (via response traits) and how they, in turn, impact ecosystem functions, such as decomposition (via effect traits).

In the first two studies focusing on trait responses, I examined which factors determine land snail community assembly, linking the observed pattern to potential mechanisms, such as environmental filtering and niche partitioning (Paper I), and I tested the relative importance of environmental and spatial factors in determining community composition (Paper II). In the third and fourth study, focusing on trait effects, I measured traits of snails that potentially influence leaf litter decomposition (Paper III) and applied these findings to real community data to examine if impacts of soil calcium on community wide consumption rates (the snail communities' potential effect on leaf litter decomposition) are mediated by traits (Paper IV). In the following I discuss the most important findings of my thesis in the context of current research development.

5.1 Trait responses

Studies using trait-based approaches to disentangle the relative importance of different filters involved in community assembly usually find little evidence for overdispersion. In a recent meta-analysis (Götzenberger *et al.*, 2012), only 12 % of the considered studies found trait overdispersion (with 18 % of the studies significantly deviating from the null model). In contrast, Freschet et al. (2011) found a general prevalence of underdispersion in plant communities across spatial scales (local to global) and ecosystems, including most major biomes of the earth (Freschet *et al.*, 2011). The findings of my first article are in agreement with this study. From twelve tested traits, only two showed overdispersion and eight showed underdispersion. Overdispersion in shell shape was the only hint for a possible niche partitioning related to limiting similarity. This may support the general view that competition is not particularly strong in terrestrial snails (Cook, 2008; Solem, 1985). In contrast, I found clear evidence for environmental filtering for traits related to moisture conditions (survival of dry period, humidity preference). The other traits that showed underdispersion (maximum shell size, age at maturity, number of offspring, reproduction mode, ecosystem occurrence, and microhabitat occurrence) were more difficult to interpret and might be linked to both dispersal- and environmental filtering. In a study on the assembly of snail communities in fens, Schamp et al. (2010) also reported underdispersion in shell size which was associated with environmental conditions (habitat pH). Studying earthworm communities using morphological and ecological traits, Decaëns et al. (2008) found evidence for environmental filtering, despite earthworms are known to exhibit strong competitive interactions (Lavelle & Spain, 2001).

It is, however, difficult to compare results of assembly analyses among studies and organisms. For example, the outcome of an assembly test is highly dependent on the scale of the study with trait overdispersion more likely to be detected on small scales (Götzenberger *et al.*, 2012). In general, it is challenging to identify the appropriate scale at which certain organisms truly interact.

I interpreted trait underdispersion as environmental filtering, because certain traits, especially tolerance traits, showed a clear link to environmental variables. However, for traits where the relation to the environment is not as clear, I cannot fully exclude alternative explanations for the observed underdispersion, such as predation (Abrams & Chen, 2002; Chase *et al.*, 2002; Zaret, 1980), natural enemies such as pathogens (Mitchell & Power, 2003), and competitive exclusion in the presence of a common limiting factor (Mayfield & Levine, 2010). Contemporary coexistence theory highlights two outcomes of competitive interactions (HilleRisLambers *et al.*, 2012; Chesson, 2000). First, taxa which are too functionally similar can be eliminated. This is the case when trait differences function as stabilizing niche differences. Alternatively, all taxa that do not possess the near optimal trait can be eliminated. This is the case when trait differences translate into relative fitness differences. Beyond that, both processes can be influenced by abiotic and biotic factors. Thus, although trait-based studies of community composition capture the cumulative effect of relative fitness differences and stabilizing niche differences, it remains difficult to infer the relative importance of environmental versus biotic (competitive) filters from the observed pattern of underdispersion or overdispersion, unless a clear mechanistic link between a trait and an environmental factor can be determined, or a trait that is clearly (and mainly) involved in competition is identified. This is particularly challenging since traits can be involved in both processes simultaneously. Combining trait based (and phylogenetic) approaches with experiments and demographic models testing for relative fitness differences and stabilizing niche differences, would therefore be a major step forward to improve the understanding of processes governing community assembly and the traits that are involved (Adler *et al.*, 2013; HilleRisLambers *et al.*, 2012).

Recent studies showed that certain traits in soil invertebrates vary consistently with environmental conditions (Dias *et al.*, 2013b; Makkonen *et al.*, 2011) and across eco-regions (Dias *et al.*, 2013b). For instance, Dias *et al.* (2013) successfully used traits underlying desiccation resistance to explain species distribution pattern of terrestrial isopods in relation to water availability across Hungary. Makkonen *et al.* (2011) experimentally studying the effect of climate warming on arctic collembolan communities, showed that traits determining the vertical structuring of communities (drought tolerance, number of ocelli, body size, and body pigmentation intensity) respond to changes in temperature. Vandewalle *et al.* (2010), discussing the usefulness of functional traits as indicators of land use change across ecosystems and organisms, suggested that the response of functional diversity indices to habitat composition and landscape heterogeneity is consistent across geographical regions (Vandewalle *et al.*, 2010).

In the context of my thesis, some snail life-history traits (shell size, number of offspring, reproduction mode) as well as microhabitat occurrence played an important role in all three observational studies (Paper I, II, and IV), and tolerance traits (survival of dry period and humidity preference) were important in the two studies where information on moisture was directly or indirectly included in the set of environmental variables (Paper I, and II). The most important environmental factors emerging from these three studies are local habitat conditions including moisture conditions, vegetation structure and soil pH (which is related to soil calcium content). These findings are in agreement with studies emphasizing the importance of local habitat conditions, such as soil humidity, pH, as well as composition and diversity of plants, for the occurrence of snails (Dvořáková & Horsák, 2012; Martin & Sommer, 2004; von Proschwitz, 2004; Barker & Mayhill, 1999; Gärdenfors *et al.*, 1995). This could build a starting point for more systematic analyses of each trait-environment relationship.

Meta-community theory (Leibold *et al.*, 2004) suggests that local environmental conditions, in combination with spatial heterogeneity in biotic conditions are important in explaining the distribution of species and community composition across time and space (Ettema and Wardle 2002). In order to understand local community composition in habitat patches, neighbouring patches must be taken into account, as dispersal between patches can prevent local extinction under less favourable conditions (Leibold *et al.*, 2004). Thus, in addition to environmental factors, spatial configuration of the sampling sites should be considered in studies determining factors affecting community structure.

Numerous studies report the importance of both environmental and spatial components for species composition in a variety of organisms (Viketoft, 2013; Hájek *et al.*, 2011; Benefer *et al.*, 2010; Heino *et al.*, 2010; Tuomisto *et al.*, 2003; Labaune & Magnin, 2001). If intrinsic processes, e.g. dispersal limitation, are important, variation partitioning into spatial and environmental components should result in a high amount of variation explained by the pure spatial component. This has been shown, for instance, in a study comparing organisms with different dispersal abilities in fen ecosystems (Hájek *et al.*, 2011). Plants and snails having lower dispersal ability than bryophytes and diatoms, exhibited a stronger spatial structuring. In contrast, a multi-scale study on collembolan communities, a group of soil invertebrates that is also regarded to be dispersal limited, found no evidence for the importance of spatial variables, and thus emphasized the role of environmental variables for explaining collembolan community variation (Martins da Silva *et al.*, 2012). Interestingly, microalgae and diatoms, which have been believed to have almost infinite dispersal abilities due to their microscopic size and large population sizes (implying that they are mainly structured by environmental factors), have recently been shown to exhibit spatial structuring (Heino *et al.*, 2010; Verleyen *et al.*, 2009), which is likely related to dispersal limitation.

Although snails are generally assumed to be dispersal limited (Schilthuizen & Lombaerts, 1994; Baur & Baur, 1993; Day & Dowdeswell, 1968), I found that environmental components were more important than spatial components in explaining the variation in community trait composition across a wide range of different habitats spanning a regional scale (Paper II). This finding agrees with Martins da Silva et al. (2012) who also found evidence for the importance of environmental factors for structuring communities of supposedly dispersal limited soil invertebrates. However, the spatial component in our study was still significant, and omitting it would have led to a loss of information, making it impossible to detect spatial pattern that are independent from environmental variation. To summarize, the findings of Paper II indicate that snails may not be as dispersal limited as previously thought. Indeed, a few studies report the capacity of snails for passive long-distance dispersal through assisted dispersal by birds (Kawakami *et al.*, 2008; Gittenberger *et al.*, 2006). This emphasizes the need to further study the role of passive or assisted dispersal in taxa that are assumed to be poor active dispersers, and identify traits that are involved in this process.

5.2 Trait effects

Similar to response traits, it is necessary to identify sets of easily measurable effect traits and establish standard protocols to measure them, in order to make reliable predictions of the influence of biotic communities on ecosystem processes and services. This has been extensively done for plants (Cornelissen *et al.*, 2003), but comparable standard procedures are still greatly lacking for soil fauna and many other organism groups (Pey *et al.*, 2014; de Bello *et al.*, 2010).

Candidates for soil invertebrate functional traits that serve as effect traits comprise body size, feeding habit (Faber, 1991), feeding rate and assimilation rate (Kadamannaya & Sridhar, 2009; Dudgeon *et al.*, 1990). Recently, it has been shown that both plant litter and macro-detritivore identity jointly affect decomposition (Vos *et al.*, 2011), emphasizing the need for a better understanding on which traits are driving such interactions. Nevertheless, there are only a few studies to date which attempt to systematically measure traits that may affect decomposition using a large number of soil invertebrate species (Hedde *et al.*, 2007; Dangerfield, 1994).

In Paper III, I measured consumption rates, faeces production and assimilation rates of ten terrestrial litter feeding snail species. These traits were previously only assessed for a very limited number of snail species (often only one single species) and litter types (De Oliveira *et al.*, 2010; Mason, 1970a). I also assessed the influence of litter quality on consumption rates and found that the average consumption rates of the four tested species increased in the same order for both litter types. Together with the observed positive relationship between consumption rates and shell size, this might be a first indication that relative consumption rates are comparable among litter types and could potentially be predicted by shell size and litter quality. Although these findings are limited due to the limited number of species and litter types tested, they might have important implications for the assessment of the potential influence of soil invertebrate communities on leaf litter decomposition. In Paper IV, I exemplified how such data can be used in the context of the response-and-effect trait framework to identify traits that respond to environmental variation and traits that mediate communities' influence on ecosystem functioning. My findings suggest that a relatively small number of traits (shell size, calcium affinity, and degree of self-fertilization) may be useful to predict responses of snail communities to environmental changes (i.e. acid rain and Ca depletion in northern European soils), and their potential influence on ecosystem functioning (i.e. leaf litter decomposition).

There is growing agreement that the effects of community composition on ecosystem processes and services are mediated by the identity, variation and relative abundance of functional traits in a community (Díaz *et al.*, 2007a; Díaz & Cabido, 2001), with the two main components of community trait composition being the community weighted mean trait value (CWM) and functional diversity (functional richness, evenness, and divergence). Within plant ecology there seems to be stronger support for the importance of the CWM than for functional diversity (Díaz *et al.*, 2007a). Also, a recent study on isopods emphasized the major role of dominant trait values (CWM) in driving decomposition, compared to functional diversity which only exerted a subordinate role (Bílá *et al.*, 2014). My findings in Paper IV, that the CWMs of three traits (shell size, calcium affinity, and percentage self-fertilization) and one functional diversity measure (functional richness) explained community wide consumption rates, might also indicate a larger importance of CWM compared to functional diversity. However, the fact that CWM and functional diversity are not mathematically independent from each other (Moretti *et al.*, 2009) complicates the interpretation of the relative importance of these two components in observational studies. Recently, an experimental framework was introduced to disentangle the role of CWM and functional diversity, by constructing communities in such a way that these two components become independent (Dias *et al.*, 2013a).

A general problem in trait-based approaches, when little is known about species responses to the environment or their effects on ecosystem processes, is the question which traits should be included in the analysis, especially when they are inter-correlated. Recently, screening methods have been proposed to select the ideal number of traits related to the respective environmental variables (Pakeman, 2011a; Bernhardt-Römermann *et al.*, 2008) or ecosystem processes (Pakeman, 2011b). For soil invertebrates there is still a lack of available data on traits, although some databases exist by now. Even if such information is available, it is often compiled from different literature sources. Ideally, traits should be measured at the same study sites, since traits that are good proxies of species responses to environmental variation across large scales might not be as informative on local scales. Therefore, a better understanding of how and which traits are linked to the performance of organisms is needed and it is important to link traits to local environmental drivers and the species' physiological capability to cope with these local conditions (Rosado *et al.*, 2013). This is especially important for groups of organism of which knowledge on key traits, and the availability of trait information is still limited.

6 Conclusions and Future Perspectives

Trait-based approaches can bring new insights into how communities respond to their environment, and how they influence ecosystem processes. In this thesis I examined how trait-based approaches can be applied to terrestrial snail communities, representing a group of soil macro-detritivores, to achieve a better understanding of the processes determining community composition and communities' impact on ecosystem functions. Despite their known contribution to a variety of ecosystem functions, terrestrial snails have, to my knowledge, not been studied previously in this context.

I identified traits that responded to major environmental gradients. Several of these traits (especially tolerance traits) showed a consistent response in the observational studies and I suggest that their relationship to environmental factors should be investigated in systematic ways. Furthermore, shell size, reproduction mode, and calcium affinity responded to environmental variation (Paper I and IV), and were the most important traits that influenced the snails' potential effect on leaf litter decomposition (Paper IV), and thus qualify as response- and effect traits.

Although snails are not the major determinants of litter decomposition in many ecosystems, they are suitable as model organisms, and the trait-based methods used in this thesis can likewise be applied to other soil invertebrates playing a key role in decomposition processes.

My thesis exemplifies that trait-based approaches are useful to improve the understanding of how species and communities respond to the environment and how they influence ecosystem processes. This knowledge can build the basis for future studies testing specific mechanisms, and studies adding more complexity by including multiple trophic levels or multiple ecosystem processes, and integrating trait-based, phylogenetic, and demographic approaches. This type of studies is needed to predict and possibly mitigate consequences of global change for ecosystems.

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