Traits or Species – Space or Environment

How to understand the spatial structure of springtail community composition

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Abstract

How communities are structured and the processes shaping species composition are among the basic questions in ecology. Knowledge about these processes is essential to predict changes in community composition in response to changes in for example climate or land use practices. Soil communities are considered to be both remarkably species-rich and to have many generalist species with seemingly similar niche requirements. Soil fauna composition shows a large variation even at small spatial scales and both local environment and spatial configuration of habitats are regarded as important forces shaping the community composition. In this thesis, I examine the factors influencing small-scale community composition of springtails (Collembola) in two habitats, a variable and dynamic salt marsh and a more stable mature pine forest.

The functional traits of species determine both their responses to the environment and their effects on ecosystem processes. The current knowledge on environment - species - traits relationship is limited in spite of its potential importance for ecosystem function. I show that by combining perspectives from two closely linked theoretical frameworks – metacommunity ecology and community assembly theory – we get a better understanding of the important ecological factors operating in this system.

I found that the factors influencing community composition was context dependent, but in a predictable way. In the environmentally variable habitat, salt marsh, with spatial and temporal heterogeneity, there was evidence of strong environmental filtering. Small-scale topography was the strongest predictor of community composition, likely due to disturbances restricting where habitat-generalists can persist. In contrast, in the more stable habitat, mature pine forest, environmental filtering appeared weaker and biotic interactions seemed to have a stronger impact. Coexisting species were more similar in traits related to resource utilisation and sensory ability than expected, and variation in species composition was explained mainly by spatial factors like the distance between samples, i.e. each local community seemed to depend on the composition of the surrounding communities.

Keywords: Collembola, community assembly, diversity pattern, functional traits, soil fauna, environmental filter, species interaction, variance partitioning, disturbance regime

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Dedication

To all of you believing in me when I couldn’t myself,
this would never be without you

Diversity is a survival factor for the community itself
Daniel Quinn

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 Widenfalk L.A., Bengtsson J., Berggren Å., Zwiggelaar K., Spijkman E., Huyer-Brugman F., Berg M.P. Environmental filtering of soil fauna traits in a late successional salt marsh vegetation (submitted to *Oecologia*).

II Widenfalk L.A., Malmström A., Berg M.P., Bengtsson J. Small-scale Collembola community composition in a pine forest described by spatial configuration and functional traits (manuscript).

The contribution of Lina A. Widenfalk to the papers included in this thesis was as follows:

I Main author, data handling and analysis, idea and concept together with co-authors, design and identification by Matty P. Berg, Krista Zwiggelaar and Evelien Spijkman.

II Main author, data handling and analysis, practical work and identification together with Anna Malmström, Ola Bengtsson and Annhild Andersson, idea and design together with Jan Bengtsson, Matty P. Berg and Anna Malmström.

Abbreviations and symbols

CWM	Community-Weighted Mean trait value
ME	Mass Effect metacommunities
MS	Manuscript (not yet published studies)
NE	Neutral metacommunities
PD	Patch Dynamic metacommunities
RDA	Redundancy analysis
SS	Species Sorting metacommunities
α	alpha-diversity (local)
β	beta-diversity (turnover)
γ	gamma- diversity (regional)

1 Introduction

All ecosystems are heterogeneous at multiple spatial scales (Ettema & Wardle, 2002). In both environmental variables and community composition spatial structure is ubiquitous, and is caused by a variety of processes. Differences in species composition between communities are predominantly linked to processes such as species interactions, environmental constraints and the limited dispersal abilities of many species (Leibold *et al.*, 2004; Diamond, 1975). Identifying the most important factors behind community structuring is essential to predict changes in community composition, i.e. the species, genetic or trait composition of a community, in response to changes in for example climate or land use practices (Suding *et al.*, 2008; Bardgett *et al.*, 2005).

The environment and the spatial configuration of habitat patches are important factors shaping the community composition and diversity of species, the relative role of these factors are the main focus of this thesis. I include two studies with similar designs in two ecosystems, with many similarities but also important dissimilarities with regard to disturbance regimes, to examine the relative role of structuring forces under different conditions. The soil fauna community is considered species rich and has been called “the poor man’s tropical rainforest” (Giller, 1996). Its composition shows a large variation even at small spatial scales (Ettema & Wardle, 2002). It is therefore a suitable study system to investigate community assembly. Springtails (Collembola) are one of the most abundant soil arthropod groups and our ecological understanding is higher than for many other soil organisms. In this thesis I use field studies of Collembola communities in two ecosystems to understand the structuring mechanisms at small spatial scales.

1.1 Processes structuring ecological communities

An ecological community is defined as a group of individuals of different species living in the same area and that interact with each other in some way

(Morin, 1999). Often the term is used together with a taxonomic and a geographical restriction, for example 'the plant community of this forest' or 'the fish community in lake NN'. The identity and properties of the species included in a community, and their relative abundance, will determine its composition and how it will respond to changes in environmental conditions, and its effects on ecosystem processes (Lavorel & Garnier, 2002). Species interactions (like competition, predation and mutualism) structure communities and are modified by environmental conditions. Additionally, community composition may also be structured by stochastic disturbances, such as flooding, wind-throws or fire (Begon *et al.*, 2005).

In many ecological studies the results are context dependent, meaning that when and where you carry out the study influence the outcome. One reason for this is the different disturbance regimes that act upon the species in a community. Ecological disturbance is defined as a temporary change in the environmental conditions that causes a distinct change in an ecosystem (Pickett & White, 1985). These disturbances may be large scale, conspicuous events such as fires, wind-throws and flooding, but can also be less obvious to the human eye. Even smaller disturbances, like dry spells influencing soil conditions, can have severe impact on organism communities. Disturbances may have a strong impact on population and community dynamics (White, 1979). However the impact varies to a high degree, even between taxonomically similar communities, and results in that community composition is contingent on disturbance frequency and intensity. An example is fire where the severity of fire greatly affects the community composition during recovery (Malmstrom, 2012).

In heterogeneous environments (spatial and/or temporal), environmental conditions can set the boundaries for which species that will be able to colonise and persist in any given patch (Chase & Leibold, 2003; Hutchinson, 1951). Species adapted to a specific environment thus have an opportunity to dominate a community. This results in landscapes with a high diversity, as different species are found in patches with different conditions. In contrast, in landscapes with little variation in environmental variables between patches, all species are able to persist in suitable habitats and the composition of the communities is thereby mainly determined by biotic interactions (Hairston *et al.*, 1960). However, dispersal limitation can result in species, that otherwise could be very prevalent in an area, being absent from parts of the landscape that are too far away from source patches. On top of these deterministic processes, stochastic events can alter the community composition in an area, especially in small patches (Paine & Levin, 1981). Most structuring forces act on all systems at some level, but the most important mechanism may vary between different communities.

Another important context to consider when studying community composition is the spatial scale, as all ecosystems are heterogeneous at multiple scales (Ettema & Wardle, 2002). Examining the same system but at different scales give us a better perspective of the structuring mechanisms of communities, as they typically have a certain spatial scale on which they impact the organism community (Berg, 2012). Hence, it is important to select the scale of study that best answer the particular ecological questions of interest.

1.2 The importance of traits for community composition

The general understanding of spatial heterogeneity for species distributions (the absolute dimensions depending on the size and home range of the organism) is hampered by context dependencies such as the environmental conditions of the system studied and the exact identity of co-occurring species, even when the same taxa is studied (Berg, 2012). An increasing body of research has indicated that species functional traits (hereafter called traits) determine both species' responses to the environment, their effects on ecosystem functioning and ecosystem processes (Cadotte *et al.*, 2011; Lavorel *et al.*, 2011; de Bello *et al.*, 2010; McGill *et al.*, 2006; Lavorel & Garnier, 2002), and would thereby be a more appropriate measure than species identity in community ecology. Traits are properties of the species, assumed to describe the role of the species in the ecosystem (Chase & Leibold, 2003). Traits have been divided into r*esponse traits* - how species react to the environment or biotic interactions, and *effect traits* - the impacts species have on ecosystem processes such as nutrient turnover or environmental conditions such as micro-climate (Violle *et al.*, 2007). However, such information is missing for most species. Easily measured traits such as body size are therefore often used, and assumed to act as proxies of traits more closely linked to the processes of interest.

The concept of traits is old in ecology and goes back to the ideas of natural selection on variation in species properties (Darwin, 1859). Since then it has been used and phrased in different ways within community ecology (Zaret, 1980), life history theory (Stearns, 1992) and niche theory (Chase & Leibold, 2002; Hutchinson, 1951). Using traits instead of species when describing the responses of communities to environmental changes could provide a better understanding of the important factors behind spatio-temporal shifts in community composition (Dias *et al.*, 2013; McGill *et al.*, 2006). It may also decrease context dependency and increase the amount of variation explained when analysing organism-environment relationships, as it mirrors the species adaptions to different environments. Observations on trait distribution in natural communities have previously been rather anecdotal and the trait distribution among communities from different habitats remains to be examined, although an increasing number of studies of especially plants e.g. (Leps *et al.*, 2011; de Bello *et al.*, 2009) have adopted this approach and some studies of animal communities are also available e.g. (Astor *et al.*, 2014; Salmon *et al.*, 2014).

1.3 Theoretical frameworks

In the literature, two theoretical frameworks are commonly used to describe community composition and the mechanisms that structure those communities, *community assembly theory* and *metacommunity ecology*. In this thesis I use these theories as frameworks to interpret the patterns in community composition and diversity. Although I'm not directly applying the theories in my studies, the ideas and methods of analysing the data stem from them. Most often they have been used for separate analyses in different systems, but by doing so the explanatory power of combining the two frameworks is not utilised.

In the *community assembly theory* species community patterns are described by examining if co-existing species are more or less similar to each other (with regard to different traits) than by chance. These observations are assumed to reflect ecological processes structuring the communities (Weiher & Keddy, 1995; Diamond, 1975). If environmental conditions are important for local community composition, then species in local communities should be a particular subset of the species in the regional pool; i.e. they should be *under-dispersed* or *convergent* in certain traits. This is described as an 'environmental filter' selecting those species that are best adapted to given environmental conditions. If the environmental conditions of patches within an area are dissimilar this should result in a high turnover of traits among patches; i.e. a higher trait beta-diversity than expected by random assembly from the regional species pool (de Bello *et al.*, 2009). Conversely, if local interactions like competition for resources are important species are expected to be less similar in traits than if randomly assembled from the regional species pool. The species of a community should then show *over-dispersion* (*divergence*) in traits related to competition and resource use because species with similar traits cannot coexist, called 'biotic filter' (Cornwell *et al.*, 2006). Additionally, depending on which traits are examined, both under- and over-dispersion in trait composition can be expected.

The term *metacommunity* refers to a collection of local communities in more or less defined patches of potentially interacting species that are interconnected at the regional level by dispersal (Chase & Bengtsson, 2010; Gonzalez, 2009). Partitioning of community variation in environmental and spatial components (Cottenie, 2005) has been used to place real communities in defined types of metacommunities, types that in reality are overlapping: *patch dynamics (PD)*, *species sorting (SS)* and *mass effects (ME)* (dispersal-driven). According to theory, in SS metacommunities local community composition should to a large degree be affected by environmental conditions. The species best adapted to the conditions in each patch should inhabit the patch (Leibold *et al.*, 2004). Metacommunities following PD and ME should be more affected by spatial configuration of patches. The latter two may be distinguished by PD having a smaller effect of environmental conditions as patches are assumed equal in quality and spatial dynamics are dominated by dispersal and local extinctions (Cottenie, 2005). In ME the patterns in species composition depend on the degree of dispersal in the system. With high dispersal the strongest competitor will be able to colonise all patches while at lower dispersal environmental conditions at least partly determine species composition (Leibold *et al.*, 2004). Additionally, metacommunities can be *neutral* (NE), where species are ecologically equivalent and their long-term dynamic is related to stochastic events (Hubbell, 2001).

2 Study system

The composition of soil fauna communities shows a large variation even at small spatial scales (Ettema & Wardle, 2002). Variables affecting the aggregation of individuals of different species could be difference in soil pore size, root structure and soil depth as well as small-scale vegetation structure (Viketoft, 2013; Berg & Bengtsson, 2007). Soil communities are surprisingly species-rich and the reason for this observed high diversity are less well known than for many above-ground living animals (Wardle, 2006; Giller, 1996). Understanding mechanisms operating at fine spatial scales are important for understanding local diversity and composition of these communities. It might also be an important component in explaining biodiversity patterns at larger spatial scales.

The few spatially explicit studies on the small-scale distribution of soil organisms show an aggregated distribution of microbes (Acosta-Mercado & Lynn, 2002; Saetre, 1999) at spatial distances of a few meters, and nematodes (Liang *et al.*, 2005; Ettema *et al.*, 2000) and earthworms (Jimenez *et al.*, 2006) at spatial distances from a few up to 100 meters. The scale of ecological interest, when studying soil fauna in a local community context, is therefore much smaller than for, e.g., plants or larger animals (Astrom, 2011; Nielsen *et al.*, 2010). Environmental factors identified as having an important influence on the aggregation of soil fauna communities are soil structure and soil microclimate, vegetation composition and the amount of leaf litter (Berg, 2012). Environmentally structured variation in community composition is often attributed to niche differences in e.g. tolerance to abiotic conditions. In addition to these processes, aggregation can also occur because of dispersal limitation or species interactions such as competition (Gonzalez, 2009). For small organisms with limited active dispersal, this may occur on very small spatial scales (centimetre to metre) (Astrom, 2011).

2.1 Springtails

Collembola (springtails) are a diverse class of hexapods (Figure 1) that inhabit most ecosystems and habitats on earth (Rusek, 1998). The Collembolan taxonomy is still not resolved and each year several new species, and sometimes even new subfamilies (Hopkin, 1997), are discovered (Rusek, 1998). Most species live in the upper organic-dominated layers of the soil but some species inhabit the more mineral dominated horizons (Petersen & Luxton, 1982), while others can be found on the soil surface, in the vegetation or within almost any other habitat (Christiansen, 1964). They are often, together with mites (Acari), one of the most abundant arthropod groups in soils (Filser, 2002; Petersen & Luxton, 1982). Collembola community composition has a rather high temporal and spatial variability (Siira-Pietikainen & Haimi, 2009; Berg & Bengtsson, 2007; Chernova & Kuznetsova, 2000). However, species composition is considered predictable under stable environmental conditions (Chernova & Kuznetsova, 2000; Bengtsson, 1994).

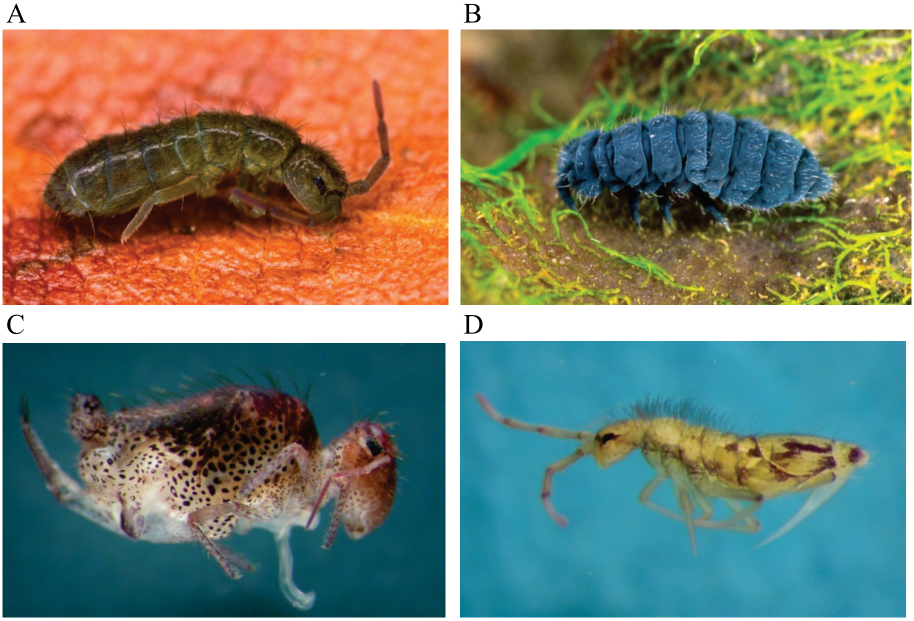

Figure 1. Springtail (Collembola) species, A. *Isotoma viridis* occurring in both study areas, B. *Anurida maritima*, C. *Allacma fusca* and D. *Entomobrya nivalis* also occurring in both study areas. Photo A and B Steven Hopkin, C and D Arne Fjellberg

Collembolans are known to be affected by soil moisture (Huhta & Ojala, 2006; Kaczmarek, 1975) and pH (van Dijk *et al.*, 2009; Hagvar, 1990), as well as temperature (Wolters, 1998; Christiansen, 1964), resource abundance (Takeda, 1987) and detritus quality (Rantalainen *et al.*, 2004; Teuben & Smidt, 1992). The role of biotic interactions in soil communities is debated. Some studies indicate that niche partitioning is more pronounced among soil animals than previously believed (Takeda, 1987; Kaczmarek, 1975), which has been explained by variation in habitat diversity on smaller scales (cm-scale) than usually considered (Nielsen *et al.*, 2010). Other studies that have highlighted the importance of species interactions in determining the Collembola community structure are Hågvar (1990) and Kuznetsova (2006). In a study comparing springtail communities in natural and cultivated forests (Cassagne *et al.*, 2004) the species populations increasing in cultivated stands were all widely distributed species, suggesting that these populations of generalist species were released from competition of more specialized species. Recent studies on Collembola community composition show however that environmental variables usually explain more of the community variation than spatial variables (Ponge & Salmon, 2013; Martins da Silva *et al.*, 2012) at scales ranging from landscape (km) to plot (m) level.

Many Collembola species have been found to have slow dispersal rates (Ojala & Huhta, 2001; Bengtsson *et al.*, 1994), especially species connected to forest habitats (Ponge *et al.* 2006; Auclerc *et al.* 2009). However, detailed data on dispersal abilities are sparse or completely lacking for most species. In an experimental study on effects of habitat fragmentation, dispersal limitation could not be detected for springtails at up to 3 meter distances (Astrom & Bengtsson, 2011). Studies of community assembly during primary succession on areas differing in isolation suggest that dispersal is not a limiting factor for community composition of Collembola, and found environmental constrains or biotic interactions to be equally probable structuring forces (Ingimarsdottir *et al.*, 2012). Experimental studies have shown that when the whole fauna is extinguished from a patch (defaunated) or the patch is allocated to another habitat, the species establishing in the patch is the ones that are most abundant in the immediate surroundings (Rantalainen *et al.* 2004; Ponge *et al.* 2008). These studies indicate that one of the crucial factors determining the species composition in any local area is the species pool present in the surrounding landscape.

3 Aims and predictions

In this thesis I include two studies with similar designs in two ecosystems with many similarities, but also important dissimilarities with regard to disturbance regimes. I wanted to estimate the relative role of the forces structuring soil communities under different conditions. To this aim, I examined the Collembola communities in a salt marsh (**paper I**) and in a mature pine forest (**paper II**). Both systems have to the human eye homogeneous environmental conditions but have a small-scale patchy vegetation mosaic of tussocks/lower vegetation (**paper I**) and lichens, bryophytes and dwarf shrubs (**paper II**). The salt marsh is influenced by regular flooding resulting in a stressful salt/inundation environment for the community. The pine forest has been left undisturbed for >200 years and the environmental conditions are likely stable and quite favourable for a springtail community.

My aim with the thesis is to use these habitats with small scale heterogeneity and different disturbance regimes to understand the important mechanisms that structure the community composition under different circumstances. I expected to find that the role of environmental and spatial parameters for small-scale variation in the springtail community composition would differ between the two studied systems, with environmental variables being of higher importance in the disturbance affected salt-marsh community of **paper I** than in the stable environment of a pine forest floor of **paper II**. By including functional traits in addition to species identity I expect to better understand the factors that create the observed patterns.

Based on the two theoretical frameworks used in the thesis, my predictions were:

In heterogeneous environments with frequent disturbance regimes, represented in **paper I** by a salt marsh regularly affected by salt-water inundation**,** local communities would be influenced mainly by environmental filtering. This means that they would consist of species more similar to each other in traits (connected to disturbance tolerance) than expected by chance and that trait turnover between local communities would be larger than expected by chance. On the other hand, in a stable and more homogeneous environment such as the pine forest floor of **paper II**, the communities would be structured by competition and other biotic interactions. Local communities are thus predicted to be *over-dispersed* in traits connected to resource utilisation and the trait turnover between local communities would be smaller than expected by chance.

When there is a strong environmental gradient present, as in the salt-marsh of **paper I,** I predicted that environmental variables affecting the distribution of species would be more important than spatial arrangement of communities for their composition, both when composition is based on species identity and to an even larger extent when examining the trait composition. We believe that the effect will be more pronounced when traits are examined since functional traits have a direct connection to how species respond to their surroundings. In the absence of strong environmental gradients and with stable conditions allowing all species to have time to disperse over the entire studied area (**paper II)**, biotic interactions like competition become more intense and this would cause a small-scale spatial variation in species composition not explained by environmental variables. The species in the immediate surroundings would hence have stronger effect on the community than the environmental conditions of each patch.

4 Methods

4.1 Study areas

The study area of **paper I** is located on a barrier island on the northern coast of The Netherlands (Figure 2). The island is continuously formed from sand deposition and therefore has a chronosequence of land formation and vegetation succession that spans over more than 100 years. The studied area is located in a salt marsh on one of the oldest parts in the middle of the island (Schrama *et al.*, 2012; Olff *et al.*, 1997). Frequent flooding with salt water, mainly from September to March, causes periods of high salinity and inundation stress for the organisms in the salt marsh. The area is left undisturbed by humans or cattle giving a late successional vegetation dominated by Sea couch (*Elytrigia atherica*), a halyphytic tall grass, and a sparse cover of Sea rush (*Juncus maritimus*) growing in tussocks (Figure 3).

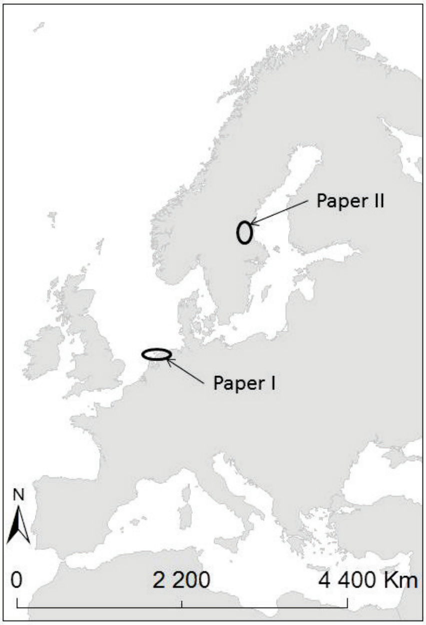

Figure 2. Europe map showing the location of both study areas, on the north coast of the Netherlands (**paper I**) and in the north middle of Sweden (**paper II**).

For the study in **paper II** we selected a >200 year old pine forest on the east of North Middle Sweden (Figure 2). The area has a flat topography and the soil is formed by glacifluvial sand. The homogenous vegetation cover is of the Cladonia-Pinetum type, but with a small-scale patchy distribution of bryophytes, lichens and dwarf shrubs (Figure 4). Dominating within the sampled plot was a feather moss (*Pleurozium schreberi*) linked to acidic soils and reindeer lichen (*Cladonia rangiferina*). The forest stand has been used for long-term ecological experiments, with the area used in this study as a control plot not receiving any treatments over the years. More details of the study area, soil properties and soil fauna can be found in Persson *et al.* (1980).

Figure 3. The late successional vegetation stage of the salt marsh used as study area in **paper I.** The vegetation, dominated by the halophytic grass Sea couch, looks homogeneous to the human eye but variation in soil moisture content and topography were detected. Photo: M.P. Berg

Figure 4. The forest floor of the mature pine forest used as study area in **paper II**, with a small scale mosaic of lichens, bryophytes and dwarf shrubs. Photo: L.A. Widenfalk

4.2 Study design

To establish the spatial distribution of Collembola species we used spatially explicit sampling designs. The sampling schemes where designed to include a high number of sample-pairs at close distances while still covering a spatial distance that would allow us to detect the spatial structuring of the Collembola communities. In the salt marsh (**paper I**) we created a plot, 35 m by 25 m, with a grid of 12 basal nodes and additional sampling points at fixed distances from each other (Figure 5), giving 172 samples at distances of 0 to 30 meters from each other. In the pine forest (**paper II**) we created a plot of an irregular grid, 5 m by 20 m, from which 100 samples were collected at distances 0 to 20 m (Figure 6). Each sample in these designs represented a patch with the species found in each patch representing a community.

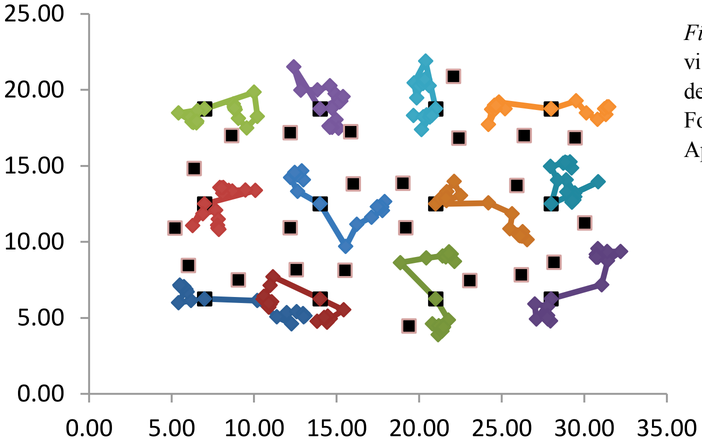

Figure 5. Schematic view of the sampling design from **paper I**. For more details see Appendix, paper I.

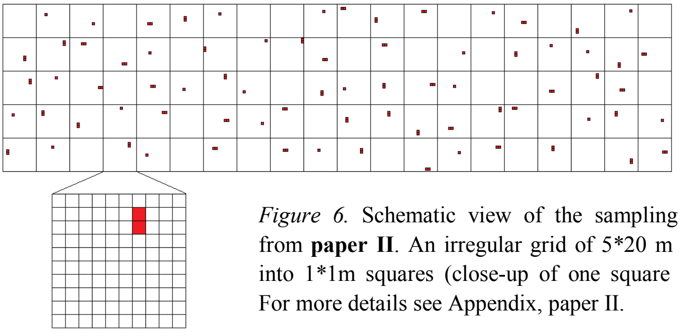

Figure 6. Schematic view of the sampling design from **paper II**. An irregular grid of 5*20 m divided into 1*1m squares (close-up of one square below). For more details see Appendix, paper II.

4.3 Sampling

We sampled soil cores, transported them to the research facility and extracted animals from the soil by drought treatment, to obtain soil fauna samples of all communities. Fauna samples were stored in alcohol for later identification.

Paper I: Soil cores (diameter 10 cm, height 5 cm) were taken using a soil corer and carefully placed in plastic containers. Collembola were extracted with modified Tullgren extraction (following van Straalen and Rijninks (1982)) during three weeks, and the weight of samples was measured before and after extraction. Collembola were identified to species using the identification keys of Fjellberg (Fjellberg, 2007; 1998) and Hopkin (2007), and counted.

Paper II: A soil corer (square 10×10 cm, height 10 cm, Figure 7) was used to extract the litter layer and vegetation (Figure 8) which was removed by hand before the humus layer was sampled with an auger (6 cm diameter) pushed down to the beginning of the mineral soil. Collembola were extracted in Tullgren funnels for three to four days. Collembola were identified to species using the identification keys of Fjellberg (Fjellberg, 2007; 1998), and counted.

Figure 7. Soil corer used for extraction of litter layer in the pine forest (**paper II**). Photo: L.A. Widenfalk

Figure 8. Difference in litter quality and structure between the studied system, lower complexity and thinner in the salt marsh (**paper I**) than in the pine forest (**paper II**). Photo: M.P. Berg and L.A. Widenfalk

The extraction method used with the salt-marsh samples (**paper I**) increase the likelihood that all specimens are included, as the slower extraction is less harmful for the soil fauna. As some of the small deep-living animals can take some time to move out from the sample (> 4 days) they could be missing from the forest samples. However, we know from experience (A. Malmström, unpublished data) that the number of individuals extracted after day three is extremely low in the type of funnels used for **paper II**. The samples from the forest (**paper II**) are also dominated by the species that are extracted slowest. Thus, another extraction method would not have given any differences in the results. Both studies were considered thoroughly sampled based on visual inspection of Coleman-rarefaction curves, confirming that most species had been found. More than 90% of the total species richness was found after approximately 50% (86 samples) for the salt-marsh data (**paper I**) whereas for the pine forest data (**paper II**) this happened already after 25% of the in total 99 samples.

4.4 Environmental variables

The study area in **paper I** was selected because of the dynamic environmental conditions and heterogeneity in factors that affect Collembola, i.e. topography (determining the effect of flooding events), thickness of a litter layer (resources) (Figure 8) and vegetation height (shelter from harsh climatological conditions, especially heat and drought). These variables were measured in each sample point except for topography, which was measured 1 cm to the North of the extracted sample. Additionally, presence and size of *Juncus* tussocks (assumed to provide shelter) was measured by counting the number of roots visible in each sample (Figure 9). The amount of soil & litter (proxy for habitat size) and the percentage of moisture in each sample (areas highly affected by inundation should hold a higher moisture content) was measured by weighing the samples before and after soil fauna extraction.

In contrast, the study area in **paper II** was selected because of the stable environmental conditions and homogeneity in factors affecting the springtails, i.e. topography moisture, and vegetation cover. However, some variables had a small scale variation that could affect the community and were therefore measured. Thickness of litter and of humus layer describe the habitat size for the communities (Figure 8), and the proportion of the soil consisting of organic material (measured by burning the humus samples giving the % of carbon) is a closer measure of actual resource availability. The pH of the soil affects the habitat quality for Collembola. All these variables were measured in each samples used for fauna extraction, except for pH which was measured on a sample taken adjacent (to the north-west of the sample) to the extracted fauna sample. Additionally, we determined the vegetation cover of each sample point as a proxy of the microclimatic conditions (especially moisture) of each sample. In this area the moisture content at any given sampling moment was judged not representative of the long term moisture of that point. As the area had a small-scale patchiness of the species composition in the ground floor vegetation (Figures 4, 7, 8) all plant species present in each sample was noted and used to describe the effect of vegetation composition on the springtail community.

Figure 9. Juncus maritimus tussocks give shelter to the springtails, by counting the roots from the underside of a soil core their impact on the community can be interpreted (**paper I**). Photo: M.P. Berg

4.5 Springtail traits data

To understand changes in Collembola abundance and spatial distribution of species, a number of traits were selected. These have previously explained shifts in Collembola species composition across time, space and experimental treatments (Van Dooremalen *et al.*, 2013; Bokhorst *et al.*, 2012; Malmstrom, 2012; Martins da Silva *et al.*, 2012; Makkonen *et al.*, 2011; Krab *et al.*, 2010). The traits used in both papers were body length, antenna/body ratio (describing sensory ability), life form (i.e. vertical stratification), moisture preference and macro-habitat width (see Table 1 for definitions and ecological significance, and **paper I** for more details on the calculations of the traits). Trait values were obtained from a large Collembola trait database (M.P. Berg, unpublished data), mainly based on literature data.

Table 1. *Definition, ecological significance and value ranges (within* ***paper I*** *and* ***paper II*** *separately) of the five examined traits.*

Trait	Definition	Ecological significance	Range or Categories	Ref
Body length	Length (in mm) measured from head to tip of abdomen	Connected to dispersal ability, life form, ecophysiological variables	0.5-5.4 mm (**paper I**) 0.4-4.5 mm (**paper II**)	1, 2, 3
Antenna/body ratio	The ratio between antennal length and body length	Linked to active dispersal because the need to detect surrounding faster	0.1-0.7 (**paper I**) 0.1-1.25 (**paper II**)	1, 3, 4
Life form	In which part of the soil (vertical stratification) the species is mostly encountered	Species living on the surface are often more mobile, with higher sensory ability and more pigmentation	Euedaphic Hemiedaphic Epigaeic	5
Moisture preference	Soil moisture conditions that the species is mostly connected to	Reflects ability to tolerate high or low soil moisture content	Xerophile Xero-meso Mesophile Meso-hygro Hygrophile	1, 2, 4, 6, 7
Habitat width*	Number of habitat types where the species has been found	Generalists are able to live in a broader range of habitat types than specialists	1-9 (**paper I**) 1-7 (**paper II**)	1, 3, 4, 6, 7, 8, 9

[1](Fjellberg, 1998); [2](Hopkin, 2007); [3](Fjellberg, 2007); [4](Potapov, 2001); [5](Gisin, 1953); [6](Bretfeld, 1999); [7](Kuznetsova, 2003); [8](Thibaud *et al.*, 2004); [9](Zimdars & Dunger, 1995); [10](Kuznetsova, 2002)

[*]For species stated to live in many habitats we added 1 score to the sum of given habitats in **paper I**, while in **paper II** all species stated to live in many habitats where categorised into the highest category (seven habitats)

Body size is a general predictor of physiological processes, such as ingestion, respiration, growth, and defecation (Calder, 1996; Peters, 1986) and is correlated with many life history traits, such as age at maturity, reproductive output, generation time and longevity (Ellers & Jervis, 2003; Sokolovska *et al.*, 2000; Honek, 1993), as well as resistance to environmental stressors (Dias *et al.*, 2013; Peters, 1986). It is therefore a good trait to use when interested in resource utilisation and disturbance tolerance.

Life form is a proxy for vertical stratification and was assigned after Gisin (1953) who classified species into three categories, epigaeic (surface/vegetation-dwelling), hemiedaphic (litter-dwelling) and euedaphic species (soil-dwelling). It is also linked to body size. Larger species tend to be surface-dwelling and have high dispersal ability, while smaller species tend to be soil-dwelling and have low dispersal ability (Martins da Silva *et al.*, 2012; Ponge *et al.*, 2006; Berg *et al.*, 1998).

We assumed that the trait *antennal to body length ratio* (called antenna/body ratio) is a proxy for *sensory ability* and is linked to dispersal ability, as fast-moving species need spatial information more quickly than slow moving species.

Soil moisture is a key factor for the survival of Collembola (Makkonen *et al.*, 2011). On salt marshes with frequent flooding, the ability to tolerate high soil moisture contents is of importance for the competition between the species, but it could also be of importance in the pine forest as different vegetation cover holds different amounts of moisture. *Moisture preference* is a categorical trait with five levels, from drought tolerant (xerophilic) to inundation tolerant (hydrophilic).

Species that occur in a large number of habitats might be more tolerant against fluctuations in environmental conditions than species that are more specialised, occurring in a small number or a specific habitat. The trait *habitat width* was defined as the number of macro-habitat types in which species are commonly found (based on literature data, Table 1). For species stated in literature sources to 'live in many habitat types', we only increased the categorical value by one in **paper I**. For **paper II** we included all those species in the highest category, considering them as habitat generalists. This trait is also assumed to describe resource utilisation and disturbance tolerance.

4.6 Data Analysis

Basically the same set of statistical tests was used in the two studies; any major differences in the analyses are mentioned in the sections below. For more detailed descriptions of the data handling, underlying assumptions of the analyses and exact procedures are given in each paper.

4.6.1 Partitioning of species and traits diversity

To examine if there was a higher species turnover than traits turnover between the samples in our ecosystem we performed additive partitioning of species and traits diversity measures, as suggested by de Bello et al (2010; 2009). This assesses the proportion of *within community (alpha)* diversity (α) and *among community (beta* = turnover) diversity (β), to *total regional (gamma)* diversity (γ). We used the Simpson diversity index to describe species diversity and Rao's quadratic entropy to describe the community functional diversity (de Bello *et al.*, 2009).

4.6.2 Spatial and environmental variables structuring species and trait composition

To test if more of the variation in community composition was explained by traits than by species identity we performed variance partitioning in two separate analyses. Multivariate analyses were conducted using spatial or environmental variables, with the latter being additionally separated into abiotic and vegetation variables in **paper II**, in order to detect which set of explanatory variables explained most of the variation in species or trait composition. We also calculated the CWM (community weighted mean) of trait values for each of the five traits using the method of Garnier *et al.* (2004), weighing the species trait values in each sample by the relative abundance of the species. Datasets of forward-selected environmental and spatial variables and any combinations were constructed to perform separate RDA's from which the variance explanation of each part could be calculated using the sum of all canonical eigenvalues, according to the method by Borcard *et al.* (1992).

4.6.3 Variables affecting the community weighted mean of traits

To examine if spatial or environmental variables could best predict the CWM of each trait, we included both sets as predictor variables in multiple linear regressions with CWM as response variable. The amount of variability explained by each set of predictor variables was assessed based on Sum of Squares decomposition, and compared with the residual from each regression.

4.6.4 Under- vs over-dispersion of traits

To detect assembly patterns, i.e., to test if local communities consisted of species more similar or dissimilar to each other than expected by chance and if trait turnover between local communities was larger than expected by chance, we compared observed values of functional diversity (Rao) with expected values of randomly assembled communities. Null models were created by keeping the abundance distribution of species within each community as observed, i.e. the number of species per sample and the total species occurrence frequency, but randomizing the trait values assigned to each species (Mason *et al.*, 2012; de Bello *et al.*, 2009). If the observed α-Rao value is significantly lower than expected it is interpreted as trait under-dispersion, i.e. that trait values are more similar than expected by chance, while a significantly higher value represents trait over-dispersion. An observed β-Rao value lower than expected indicates low turnover of traits in the system (de Bello *et al.*, 2009).

4.6.5 Distance of spatial autocorrelation and visualising spatial patterns

To determine the distance at which the environmental variables are autocorrelated we created semi-variograms for **paper I** (Klironomos *et al.*, 1999). This method fits a curve to the variables, describing the way the variable changes with distance. The model can then be used to create visual images of the pattern called kriging maps, by extrapolating values in between sampled points with a smoothing function.

Because we had too few samples for semi-variograms to be fitted successfully in **paper II**, we instead constructed correlograms using Moran’s I statistics. This method also finds the distance of spatial autocorrelation in a variable but it does not fit a curve to the values and no map can therefore be created.

5 Results and discussion

Understanding the relationship between species- and functional diversity and what affects this in different communities is a key question in ecology. My results suggest that on small spatial scales (0-30 m), factors structuring the composition of the springtail community are context dependent, but in a predictable way. In a dynamic environment with spatial and temporal heterogeneity in variables affecting the species, there was evidence of strong environmental filtering, with species being more similar (under-dispersed) in each local sample (community) and environmental variables contributing to the largest part of explained variation in species and trait composition. In contrast, in stable and more homogenous habitats, environmental filtering appeared weaker and biotic interactions seemed to have a stronger impact. Coexisting species had less similar traits than by chance (over-dispersion) and variation in both species and trait composition was explained mainly by spatial factors like the distance between samples, i.e. each local community seemed to depend on the composition of the surrounding communities. In the present study, trait composition was also to a high degree explained by the spatial configuration of both vegetation and abiotic variables.

The results support the “new” focus on functional traits in ecology. Using the properties of species instead of species identity results in a larger proportion of the total variation in community composition being explained, giving more information about the possible structuring mechanisms that cause the observed patterns.

5.1 Diversity patterns

Although the total species richness was higher in the Swedish pine forest (**paper II**) compared with the salt marsh in the Netherlands (**paper I**), the Simpson index showed a higher regional γ-diversity for the salt marsh (Table

2). The pine forest community was heavily dominated by one species-complex (*Willemia anophthalma*, *Mesaphorura yosii* and *Karlstejnia norvegica*, all small, deep-living, unpigmented and blind species) resulting in lower values of the diversity index due to unevenness.

Table 2. *Regional Collembola species and trait diversity in the two studied systems. Species diversity measured by Jost-corrected Simpson (1-D) index and all traits diversities measured by Jost-corrected Rao Q-values.*

	Salt marsh	Pine forest
Species richness (no)	22	28
Species diversity (Simpson)	5.80	3.90
Multi-trait diversity (Rao)	1.87	1.22
Body length (Rao)	1.26	1.07
Antenna/body ratio (Rao)	1.26	1.05
Life form (Rao)	1.55	1.27
Moisture preference (Rao)	1.44	1.17
Habitat width (Rao)	1.35	1.30

Put together, the two studies of this thesis suggest that there is *ecological redundancy*, or *functional compensation*, in the soil-dwelling springtail communities at a small spatial scale, even in dynamic environmental conditions. This means that several coexisting species possessed the same traits, suggesting that if one of these species is lost there would be little change in ecosystem functioning. High species diversity but with apparent low resource specialisation is a general patterns seen in many soil communities (Digel *et al.*, 2014; Maraun *et al.*, 2003; Anderson, 1975). Ecological redundancy is considered important for resilience in the system, i.e. for the ecosystem to not be altered when, e.g., climatic conditions are changed (Diaz & Cabido, 2001). In the present studies, ecological redundancy could be interpreted from the higher regional species diversity (Simpson index) than the trait diversity in both systems. The turnover between points within each study plot was also higher for species than for traits (Figure 10). Higher turnover for species than for traits has been shown previously for plant and land snail communities at landscape scales (Astor *et al.*, 2014; de Bello *et al.*, 2009; Ackerly & Cornwell, 2007), indicating that species are replaced by species with similar trait values retaining the overall function in the system. This suggest that on the scale of present studies, the communities have similar properties and observed changes in species identity do not change the role the community has in an ecosystem context, e.g., nutrient cycling or decomposition.

The turnover in the communities between sample points was overall low, except for the species turnover in the saltmarsh that contributed to 50% of the regional diversity in that system. In the stable forest system, there was almost no turnover in trait diversity, with local community diversity accounting for 97-100% of the regional diversity (Figure 10). This suggests that there is little spatial variation in ecosystem functioning within this system. The finding of low species turnover across space in the forest system in **paper II** is in line with previous findings of stable environmental conditions leading to predictable species composition of Collembola communities in time in similar forest ecosystems (Chernova & Kuznetsova, 2000; Bengtsson, 1994), while xeric (dry) or hygric (wet) habitats was shown to fluctuate more (Chernova & Kuznetsova, 2000), consistent with the result from **paper I**.

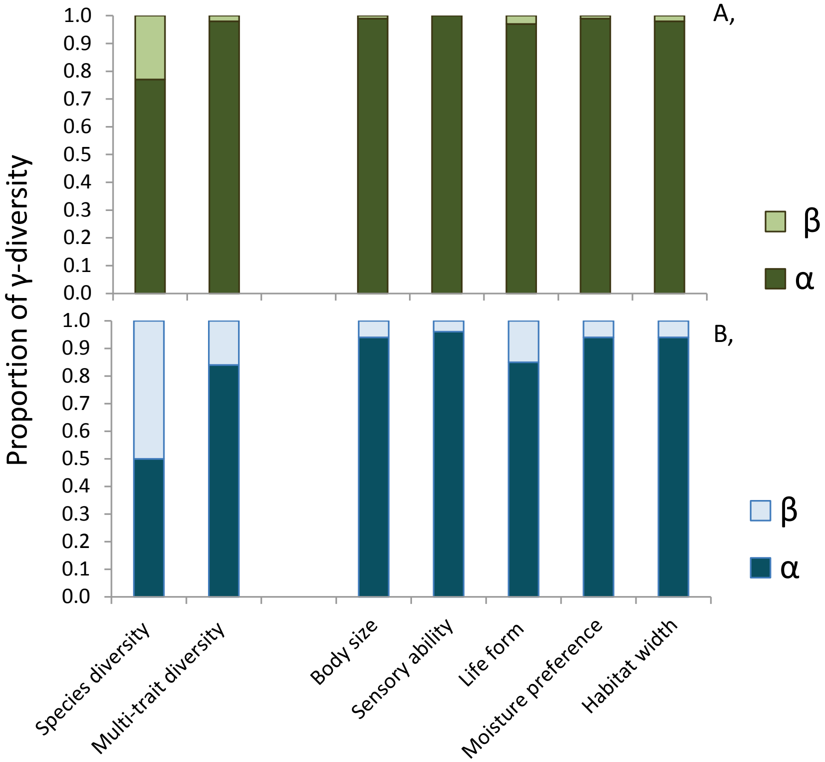

Figure 10. Proportion of regional (γ) diversity accounted for by local α-diversity and between samples turnover β-diversity in the A, pine forest (**paper II**) and B, salt marsh (**paper I**). Diversity is measured by Simpson species-diversity or Rao-trait diversity, the later for multi-trait Rao and for each individual trait.

5.2 Structuring forces of community composition

One way to identify factors structuring community composition is to compare the observed pattern with patterns from null models describing how the community would look if all species were randomly assembled in each community regardless of the traits they possess. I compare two systems that are homogenous at the spatial scale used in most community studies, i.e. what we see as a salt marsh habitat and a pine forest habitat. These habitats have however to different degree small-scale spatial heterogeneity in environmental variables previously shown to affect springtail communities. By comparing the two communities, which differ in the degree of temporal environmental variability, I hoped to shed some light on how environmental heterogeneity affects community structure.

Under spatially and temporally dynamic conditions, environmental filtering selecting those species able to tolerate extreme conditions is expected to be stronger than structuring forces of biotic interactions (Mason *et al.*, 2013). This was confirmed in **paper I** where local communities consisted of species with traits more similar to each other than by chance when averaging over all traits as multi-trait diversity, and especially in the trait 'habitat width' connected to resource utilisation (Figure 11A). This can be seen as in agreement with my prediction of under-dispersion in traits connected to disturbance tolerance, assuming species with a narrower habitat niche are more specialised to the conditions in the areas most affected by flooding. In contrast, in the stable environment of the forest floor (**paper II)** there was over-dispersion in the same traits and in antenna/body ratio, connected to sensory ability (Figure 11B). This supports the hypothesis that communities in stable environments are structured by biotic interactions, in this case possibly by competition between species with similar ways of utilising resources resulting in a minimal overlap in habitat width and sensory ability among co-occurring species. However, the link between the patterns observed of community trait-diversity and the actual processes leading to this would need to be confirmed by experimental studies.

The results from the variance partitioning support the difference in structuring forces operating in the two systems shown by the null model analyses. In the salt marsh (**paper I**) the largest part of explained variation in both species and trait composition could be attributed to the environmental variables (Figure 12, first and third bar). In the pine forest (**paper II**) the spatial components described more of species and trait composition than the abiotic or vegetation variables (Figure 12, second and fourth bar). Although, for CWM trait composition the joint effect of the three sets of variables explained 20% of the variation (discussed in more detail in **paper II)**. The larger part of pure spatial component is consistent with communities structured by biotic interactions, where dispersal and competition are determining observed patterns. The small spatial scale of the study and previous findings of springtails showing little dispersal limitations (Ingimarsdottir *et al.*, 2012; Astrom & Bengtsson, 2011) suggest that this should not be the primary structuring mechanism, wherefore I assume that biotic interactions such as competition is probably a strong driving force in this system. The difference between the two systems in this thesis can be perceived as a difference in the disturbance frequency and thus in the opportunity for biotic interactions to occur. When all species have the possibility to colonise and persist in all patches, the species ending up in any given patch can have a strong influence on the co-occurring species and spatial structures' in species composition can occur because species exclude each other from the patches they colonise.

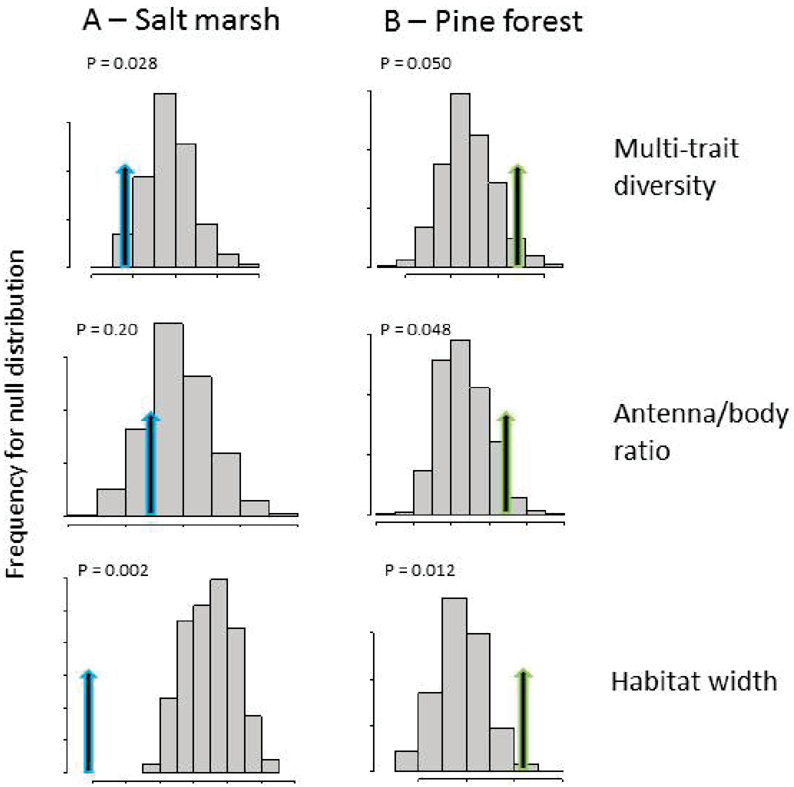

Figure 11. Contrasting results from the two studied systems of A, salt marsh and B, pine forest of observed α-diversity (arrows) compared with expected distribution (grey bars) from null models. Results for the multi-trait Rao index combining all traits and for two of the single traits analysed are shown (p-values given in the figures are based on one-sided Monte Carlo test with 499 permutations)

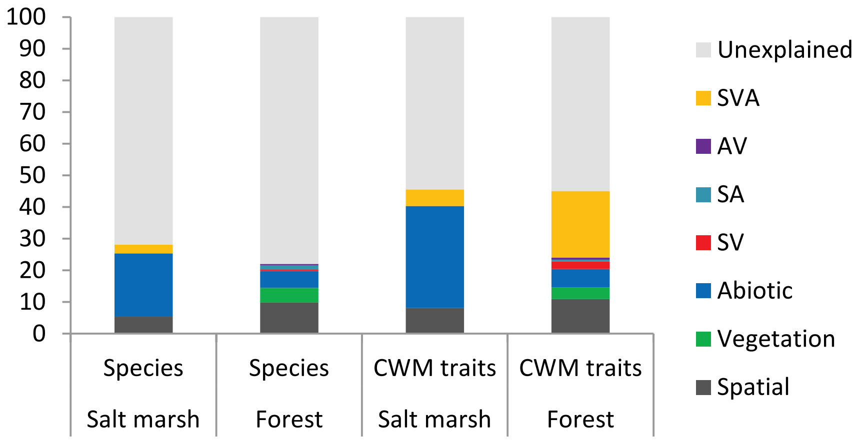

Figure 12. Partitioning of the explained variation in Collembola species and trait composition, into pure spatial and pure environmental components, and into the joint variation of the components. The environmental component is divided into abiotic and vegetation for the forest data (**paper II**), the environmental component of the salt marsh (**paper I**) is here called Abiotic. Abbreviations stands for shared contribution of the different sets of variables, i.e. the variation explained by the correlation of predicting variables; AV – vegetation and abiotic environment, SV – spatially structured vegetation, SA – spatially structured abiotic, SVA – the joint effect of all three (or two for **paper I**) components

That the same trait (habitat width) showed under-dispersion in one system and over-dispersion in the other indicates that it is important for, or good at describing, structuring of Collembola communities. Habitat generalists are likely to be able to colonise most patches but also be weaker competitors than species specialised to the particular environmental conditions of any patch. In **paper I** we saw that low-elevation points in the area have communities that consist of more habitat specialists. As locations with a low elevation are likely to be more affected by flooding with salt water, these communities experience higher salinity and longer periods of waterlogging, conditions which are stressful for most species and would select for species adapted for these particular conditions. In the stable conditions of the forest floor in **paper II,** habitat generalists and specialists, as well as species with high and low sensory ability, co-occurred to a high degree, indicating that there were some level of niche partitioning based on resource utilisation.

Within a single ecosystem, there can be a combination of structuring forces shaping the community. The influence of any structuring factor might vary both with time and between groups of species within the community (Vanschoenwinkel *et al.*, 2010). For example, in the salt marsh of **paper I** there are probably some species well adapted to high salinity and inundation that persist in the areas most affected by the flooding, while others disappear and have to recolonise the patch after the disturbance event. Directly after the disturbance the communities will be mostly affected by environmental filtering. With time, species recolonise the patches and community composition will then be more affected by biotic interactions. This has previously to been shown for Collembola communities in flooded systems (Russell & Griegel, 2006). Species with higher dispersal ability can be assumed to first recolonise and slower dispersers might show a stronger environmental dependency even at late stages of the succession. The result from any study examining community composition could thus be depending on the time since last disturbance event.

5.3 Distance of spatial autocorrelation

In both systems I could detect a small scale spatial patterning in some of the measured environmental variables, spatial autocorrelation occurring at distances of one to a few meters. The variables describing the Collembola community also showed small scale patterning, in the salt marsh (**paper I**) with patch sizes (indicated by range of spatial autocorrelation) of 6-8 meter for species and trait RDA-scores and in the pine forest (**paper II**) patch sizes around one meter for CWM of all traits. The smaller patch sizes in the stable habitat are consistent with the view of biotic interactions structuring these communities.

5.4 Trait based studies – closer to mechanistic understanding

There is an increasing use of functional traits to understand soil fauna communities (see Pey *et al.* (2014) for an review). For organism groups with poorly known or less resolved taxonomy, traits might be a better way to describe the diversity of a community than species *per se*. However, there have been suggestions that in these situations, using higher level taxa might reflect the species composition more closely than using traits (Ramsay *et al.*, 2006), if that is the main goal.

Nevertheless, a larger proportion of variation in community composition was explained when using traits instead of species as descriptor (traits 45% vs species 28% in the salt marsh and 45% vs 22% in the pine forest, Table 2). This shows that although it can be hard to explain exactly which species will be present given spatial and environmental information, it is possible to predict with a higher likelihood what traits we will find. This has also been shown in a recent study on land snails (Astor et al, MS) and could be support for the basic idea behind trait-based studies (McGill *et al.*, 2006). In many cases it is not necessary to know exactly which species you find in an area, e.g. when the goal is to preserve certain ecological functions. The conclusion is not surprising, since traits express adaptation to local conditions while species composition also includes a more random recruitment from a larger species pool affected by stochastic events. Additionally, there are only five traits included in both my studies, which inheritably give less variation of the trait composition than the species composition of 22-28 species. As more basic properties of different taxa are measured, a larger set of traits could be included in similar studies and this would show if these results hold also for larger trait-datasets. However, the results in this thesis suggest that using traits in the analyses often give a better understanding of the system. Especially when combining different analysing methods, examining both variations in composition and CWM, and comparing observed diversity patterns with null models. I believe that if the goal is not to describe the exact species composition, but rather to understand the system and the consequences of changed conditions, a trait-based approach will be very useful.

6 General remarks and ways forward

Although the two studies of this thesis are not replicated either in space or in time, I argue that they are useful for increasing the knowledge of community composition patterns for soil animals. When setting up a study there is always a trade-off between replication and thorough sampling within each replicate. To understand the small-scale pattern of these systems I needed to take many samples within each plot, to ensure enough pair-wise samples at each distance to allow for spatial analyses (semi-variograms or correlograms). Additionally, the number of individuals of each sampled community was rather high (**paper I**: 190 and **paper II**: 240 ind/sample) and in these studies exploring the species vs. trait approach, it was considered valuable to make sure to determine all individuals correctly to the species level.

For the understanding of mechanisms structuring communities and to examine how changes in community composition may affect the functioning of that community, I argue that traits can be a better way of describing the community than species identity. When interested in organism groups that are not as well-known (contrary to most studies of mammal and plant communities) it can also be much easier and more accurate to measure the traits of the organism than to determine them into species. This could for some ambiguous groups make the data collection much faster, as you do not need to make sure it is the right species, only collect some measurements of important aspects of its morphology. However, sometimes it could be as time consuming as species determination, but the trait approach gives better understanding of the function of the community, when the biology of each species is not well known.

From these results I predict that if we sample other Collembola communities in stressful or heterogeneous and dynamic environments, community composition will be best explained by environmental variables. Also, there would be shifts in the community weighted mean of traits between the extremes of environmental gradients. However, in Collembola communities in stable environments community composition would be better explained based on spatial variables. In each community the species will be over-dispersed in traits related to resource use and dispersal, indicating that in the absence of a strong environmental filter, there is opportunity for niche partitioning and small scale-structuring based on biotic interactions.

Although I haven't examined effects of shifts in species composition on ecosystem functioning, my results suggest that variation in many important soil processes is smaller than the turnover of species in these systems, indicating some functional redundancy in soil animal communities which should be the focus of further studies. A fruitful avenue for future research would be to combine explorative field studies in more (perhaps even more extreme) systems, or increasing the spatial or temporal scale of the studies, with experimental studies that test the suggested mechanisms. In this thesis I propose that the observed pattern in **paper II (**with spatial variables describing more than abiotic variables of species and trait composition) is caused by biotic interactions rather than dispersal limitations. To firmly draw the conclusion that biotic interactions actually do occur, one would need to perform microcosm experiments with known composition of species with different traits and evaluate if they do compete for resources, as predicted. To determine if the pattern observed in **paper I** (with local communities under-dispersed in certain traits) could be caused by environmental constraints on the species, microcosm communities should be exposed to different levels of the proposed variable to examine if species with certain traits react in the predicted way.

Another interesting extension of these studies would be to link the functional traits examined to the ecosystem processes we assume are affected, such as decomposition. I believe that forming Collembola communities, designed to be either *under-dispersed* or *over-dispersed* in e.g. life form or habitat width and measure the difference in the rate of decomposition would be a good start. This would give information about how observed differences in pattern between different systems translate into differences in the functioning of the system.

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