Springtails in Space

Factors Structuring Collembola Populations and Communities, Revealed by Trait-based Analyses

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Springtails in Space. Structuring Factors for Collembola Populations and Communities, Revealed by Trait-based Analyses and Variation Partitioning

Abstract

The relative influence of environmental conditions, biotic interactions and dispersal limitation for community structure and diversity patterns is a reoccurring theme in community ecology. In studies of soil fauna communities, small-scale horizontal and vertical variations in environmental variables and biotic interactions have often been disregarded, despite these being key factors to understanding the diversity of soil fauna communities.

In this thesis I examined the spatial distribution patterns of springtail (Collembola) species and communities in three different ecosystems: a salt marsh, mature pine forests and a high Arctic tundra meadow. The different systems consisted of a, to the human eye, homogeneous habitat. Still, they had different disturbance regimes and small-scale heterogeneity in environmental variables. In the three first studies the focus was on species and trait composition and diversity, at scales from 10 cm to 300 km. In the fourth paper I question the use of species-level analyses of distribution patterns, as different age classes within a species might be structured by different factors.

I found that when habitat conditions were kept as similar as possible, the pine forest Collembola communities had similar functional diversity, although there was a high species turnover both between samples within study sites and between sites. The functional similarity between samples was lower in the salt marsh habitat, a habitat characterized by frequent inundation events. The small-scale variation in species and trait composition was best explained by spatial variables in the stable mature pine forest floor, while in the dynamic salt marsh environmental variation was most important.

Coexisting species showed a higher difference in traits than expected in the pine forest, while coexisting species were similar in traits in the salt marsh. This indicates that species interactions can have a large impact on the community composition of springtails at small spatial scales. Small-scale niche partitioning may be one explanation for the high local diversity observed in many soil communities.

I found that incorporating species-specific trait information in studies greatly helps our understanding of the mechanisms structuring communities, despite the finding that in some species of collembolans different age classes may use space differently. To improve our understanding of Collembola communities both these factors should be considered in future studies.

Keywords: age classes, biotic interactions, Collembola, dispersal limitation, environmental filtering, intraspecific interactions, soil fauna, spatial analyses, traits.

Sammanfattning

Hur miljöförhållanden, biotiska interaktioner och spridningsbegränsningar påverkar diversitet, artsammansättning och artegenskaper (funktionell mångfald) hos organismsamhällen är ett återkommande tema inom samhällsekologi. För markfauna inkluderas sällan småskalig variation i miljöfaktorer eller biotiska interaktioner vid analyser av dessa mönster. Detta trots att dessa faktorer kan vara nyckeln till att förstå den ovanligt höga mångfalden av arter i markfaunasystem.

I den här avhandlingen undersöker jag den rumsliga fördelningen hos arter och samhällen av hoppstjärtar (Collembola) i tre olika ekosystem; ett saltträsk, äldre tallskogar och en gräsmark i högarktisk tundra. Alla tre systemen består av habitat som uppfattas som homogena för det mänskliga ögat, men som skiljer sig åt när det gäller störningsdynamik och miljöfaktorers småskaliga variation. De tre första studierna fokuserar på samhällenas art- och egenskapssammansättning och på diversitetsmönster, på skalor från 10 cm till 300 km. I den fjärde studien ifrågasätter jag användningen av egenskaper mätta på art-nivå vid analyser av fördelningsmönster, eftersom olika åldersklasser inom en art kan påverkas på skilda sätt ekologiskt.

I mina studier såg jag att när habitatförhållandena hölls så likartade som möjligt så uppvisade hoppstjärtsamhällena en låg variation i funktionell diversitet, även när det var en stor variation i vilka arter som förekom i markprover inom och mellan lokaler. Den funktionella likheten mellan prover var lägre i saltträsket, ett habitat som karaktäriseras av regelbundna översvämningar. Den småskaliga variationen i art- och egenskapssammansättning förklarades bäst av den rumsliga strukturen hos proverna i det stabila skogshabitatet medan miljöfaktorer beskrev sammansättningen av arter och egenskaper bättre i det dynamiska saltträsket.

Arter som förekom tillsammans visade större skillnader i egenskaper än förväntat i tallskogen, medan samexisterande arter i saltträsket var mer lika varandra. Detta tyder på att artinteraktioner kopplade till resursutnyttjande kan ha en stor betydelse för den småskaliga samhällsstrukturen hos hoppstjärtar, om inte en stark påverkan av vissa miljöfaktorer bidrar till att utesluta arter som klarar dessa förhållanden dåligt. En småskalig skillnad i ekologiska nischer kan vara en förklaring till den höga lokala artrikedomen i många markfaunasamhällen.

Förståelsen för vilka mekanismer som strukturerar samhällen ökar genom att inkludera artspecifika egenskapsdata, men detta kompliceras av att olika åldersklasser inom en art kan påverkas av olika faktorer och ha olika utbredning. För att öka förståelsen av vad som påverkar artsammansättningen och diversitetsmönster i olika organismsamhällen bör båda dessa aspekter tas med i framtida studier.

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Dedication

To the collembolans, whom I've grown to love
      To my family, what would I be without you?

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. (2015). Spatially structured environmental filtering of collembolan traits in late successional salt marsh vegetation. *Oecologia* 179, 537-549

II **Widenfalk L.A.**, Malmström A., Berg M.P. & Bengtsson J. (2016). Small-scale Collembola community composition in a pine forest soil - Overdispersion in functional traits indicates the importance of species interactions. *Soil Biology & Biochemistry* 103, 52-62.

III **Widenfalk L.A.**, Malmström A., Berggren Å., Berg M.P., Leinaas H.P. & Bengtsson J. Regional patterns of species and traits distribution among Collembola in mature pine forests across south-central Sweden (manuscript).

IV **Widenfalk L.A.**, Leinaas H.P., Bengtsson J. & Birkemoe T. Does age and sociality of springtails (Collembola) determine their small-scale distribution? (submitted manuscript).

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

I   Main author, data handling and analyses, wrote much of the paper with contribution from MPB, JB and ÅB, idea and concept together with MPB, KZ, ES, JB and ÅB.

II   Main author, data handling and analyses, wrote much of the paper with contribution from JB and MPB, practical work together with AM, Ola Bengtsson, Ljudmila Skoglund and Annhild Andersson, sampling design, idea and concept together with JB, MPB and AM.

III Main author, data handling and analyses, wrote the paper with contribution from JB, practical work together with Ola Bengtsson, AM and Ljudmila Skoglund, sampling design, idea and concept together with JB, AM, ÅB, MPB and HPL

IV   Main author, data handling and analyses, idea and writing the paper together with TB, HPL and JB.

Abbreviations

CWM	Community-Weighted Mean (used for trait values)
MEM	Moran's Eigenvector Maps
PCNM	Principal coordinates of neighbour matrices
Rao	Raos's quadratic entropy (a functional diversity index)
RDA	Redundancy analysis
Simpson	The Simpson diversity index (expressed as 1-D)
α	alpha-diversity (local diversity)
β	beta-diversity (difference between local diversities)
γ	gamma-diversity (regional diversity)

1   Introduction

The importance of maintaining a high biodiversity has gained increased attention during the last decades, much due to the apprehension that human actions cause declines in biodiversity (Cincotta et al. 2000, Hector and Bagchi 2007, Luck 2007). Assessing the effect of different changes in e.g. land use or climatic conditions on measures of biological diversity are commonly used as part of conservation or research programmes (e.g. Secretariat of the Conservation on Biological Diversity 2014). However, there are still large gaps in our knowledge about diversity patterns at different scales, in different ecosystems and for many organisms groups. Additionally, we have a better understanding of factors influencing local diversity (alpha-diversity, α) than of how differences in diversity between local communities (species variation or turnover, beta-diversity, β) influence the diversity at larger scales (gamma-diversity, γ) (Anderson et al. 2011, Socolar et al. 2016).

All ecosystems are heterogeneous at multiple spatial scales (Ettema and Wardle 2002). In both environmental variables and community composition, spatial structure is ubiquitous, and is caused by a variety of processes acting at different scales. Differences in species composition between communities are predominantly linked to processes such as species interactions and environmental filtering (i.e. environmental constraints exclude species not adapted for those conditions), modified by the limited dispersal abilities of many species (Diamond 1975, Leibold et al. 2004). 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 (Bardgett et al. 2005, Suding et al. 2008). That is, we need to know the relative importance of biotic interactions or dispersal limitation compared to environmental factors, for the spatial structuring of species and communities.

Examining the same system but at different scales give us a better perspective of the structuring mechanisms of communities.

There is an increased awareness that other measures of biodiversity than species richness are needed to understand what drives diversity patterns. To analyse the functional traits (i.e. properties of species affecting their role in the ecosystem, hereafter referred to as traits) that each species possesses instead of their taxonomical identity may reduce context dependency and enable generalizations about the factors behind patterns in diversity and species composition across ecosystems (McGill et al. 2006). Using traits might also increase our mechanistic understanding of observed patterns (Eros et al. 2009).

Table 1. *Some key concepts used in the thesis, and how I have used them in my papers.*

Concept	Definition	Usage in my studies
Community	Individuals of different species living in the same area and that interact with each other[1,4]	All Collembola found within a site, also called site-based community
Assemblage	All members of a community that also belong to the same phylogenetic group[2]	Used interchangeable with community, as I focus only on Collembola communities
Local community	The community as above, within a restricted small area. Often used when referring to alpha-diversity.[3]	All Collembola found within a soil sample, local sample-community
Local area	A restricted part of a habitat with more or less homogenous conditions, referred to as a patch in meta-community literature[4]	Each soil sample, even though the boundaries are not natural as they come from a continuous habitat
Site	A study area, usually of a size recognised more or less as a habitat	Each study is conducted within one or several sites, in which an area of < 800 m^2 was sampled
Region	A larger area consisting of many habitats and landscapes[4]	An area of $\sim 10^4$ km^2 in the south-central part of Sweden (paper III), although only pine forest within
Environment	The conditions of a habitat that could affect species fitness or composition[5]	Included aspects are: soil properties, climate and micro-climate, vegetation
Space	The spatial configuration of patches/samples, used as a proxy for dispersal limitation and biotic interactions[5]	MEM-variables or trend surface polynomial variables are included as explanatory variables. Additionally, I analyse distance between samples and spatial autocorrelation.
Scale	The range of a process or a study, includes both extent (the furthest apart points) and grain (the resolution of data points[6]	Includes only spatial scale (could include time), and mostly refers to the extent of studies

Trait	A property of the species measured at individual level and that affect the species interaction with the environment and other species[7]	Literature-based species properties that describe the role of the species in the ecosystem
Functional diversity	An aspect of biodiversity incorporating what species do, instead of their taxonomic belonging[8]	Measured by Rao's index: The extent of dissimilarity in trait values among species
Overdispersion	In a certain trait, coexisting species are less similar than expected from random assembly, also called trait divergence[9]	Tested for five traits connected to dispersal and resource utilisation, interpreted as indicating biotic interactions
Underdispersion	In a certain trait coexisting species are more similar than expected from random assembly, also called trait convergence[9]	As above, interpreted as environmental filtering in contrast to biotic interactions
Species pool	All species that could potentially coexist in a given community[10]	The observed species of each study used as species pool for analyses

1 - (Morin 1999), 2 - (Fauth et al. 1996), 3 - (Hawkins and Compton 1992), 4 - (Leibold et al. 2004), 5 - (Cottenie 2005), 6 - (Levin 1992), 7 - (Lavorel and Garnier 2002), 8 - (Petchey and Gaston 2002), 9 - (Weiher and Keddy 1995), 10 - (Zobel 1997)

2 Thesis aims

The aims of this thesis are:

To determine the relative importance of biotic interactions or dispersal limitation compared to environmental factors for the spatial structure of springtail species or communities. I do this by examining:

➢ species and trait composition and diversity within sites (i.e. comparing local samples) (**Paper I-II**)
➢ species composition, species and trait diversity of communities at a regional scale with low environmental variation between sites (**Paper III**)
➢ spatial distribution of age classes in two species with different life history tactics (**Paper IV**)

In addition, I also examined at what spatial scales these patterns and possible mechanisms can be detected.

3 Background

3.1 Diversity patterns, alpha, beta and gamma diversity

All ecosystems are heterogeneous at multiple spatial scales (Ettema and Wardle 2002), for this reason spatial patterns of species composition and diversity are also found and need to be managed at multiple spatial scales (Levin 2000, Bengtsson et al. 2002, Chust et al. 2003, Vanbergen et al. 2007, Nielsen et al. 2010, Krasnov et al. 2015, Martins da Silva et al. 2015, Ekroos et al. 2016). Examining the same system but at different scales give us a better perspective of the structuring mechanisms of communities. These mechanisms typically have a certain spatial scale on which they impact the community of focal organisms (Berg 2012). Hence, it is important to select the scale of study that best answer the particular ecological questions of interest. However, selecting this scale a priori is not always possible.

One important aspect of diversity patterns is whether the diversity at a regional level (gamma-diversity, γ) can be found in each of the included communities (alpha-diversity, α), or if a large proportion of the regional diversity is due to a change in species composition between sites (i.e. high beta-diversity, β) (Fig. 1). This is important because it tells us if we need to consider all parts of an area to determine the regional diversity, or if we only should focus on the most species rich local areas within the region. The literature on β-diversity is large, starting already with Whittaker's description of vegetation communities (Whittaker 1960). Many different ways of measuring and describing β-diversity have emerged since then, with some attempts to unify the concept and clarify the different benefits of them (Anderson et al. 2011, Socolar et al. 2016). When the variation between sites is of interest, beta-diversity is usually measured as the difference between γ-diversity and mean α-diversity (partitioning β-diversity, or *variation*) (Anderson et al. 2011), (Fig 1A). When local communities are sampled along a gradient it is more common to use pairwise-differences in species composition

between sites (pairwise β-diversity, or *turnover*), based on dissimilarity indices such as the Jaccard, Sörensen, Bray-Curtis indices (Anderson et al. 2011) or the Chao index (Chao et al. 2005) (Fig 1B), all with slightly different ways of treating rare species and false missing species. The empirical literature describing patterns of diversity at different scales remains scattered and patchy (but see e.g. Drakare et al. 2006, Soininen et al. 2007) and we know more about what generally determines local alpha-diversity than about what determines beta-diversity (Socolar et al. 2016).
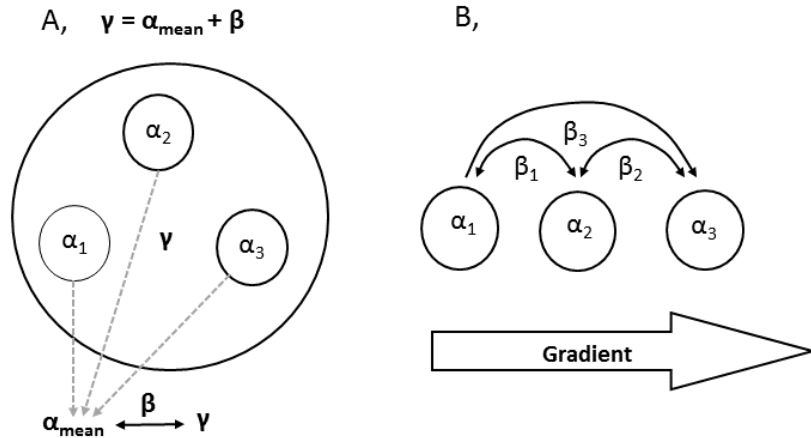

Figure 1. Two ways of measuring β-diversity often used in ecological work. **A,** *variation* in species between sites are calculated from the observed α- and γ-diversity, here by additive partitioning. Separating the part of regional diversity attributed to variation between sites from that of the average of local diversity. **B,** the *turnover* of species along any gradient (in space, time or environmental properties of sites). This is calculated based on pairwise dissimilarity is species composition between sites. Based on Anderson et al. (2011) after the definitions by **A,** Lande (1996) and **B,** Whittaker (1972).

As the appropriate scales at which to define the γ-diversity and α-diversity are not absolute and sometimes hard to determine, it can be useful to partition the regional diversity at several scales in a hierarchal view of the system (Crist et al. 2003) (Fig 2). The relative contribution of the diversity at the smallest spatial scale sampled, compared to the variation at each higher level in the design, will give information of at what spatial scale the largest changes in diversity are occurring.
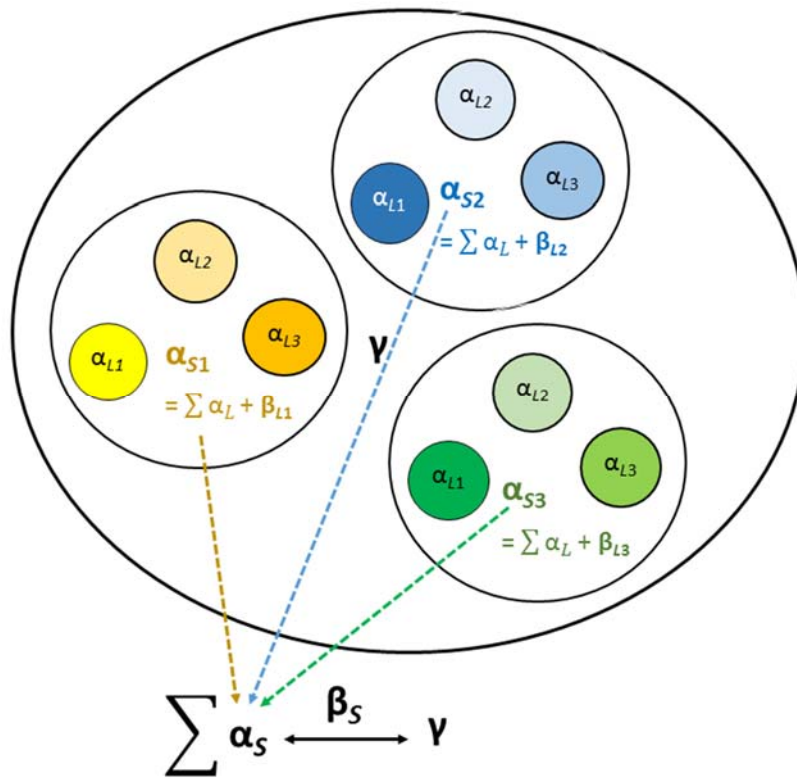
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Figure 2. In a hierarchal design, the local diversities at the lowest spatial scale (α_L) can be aggregated to determine the diversity at higher spatial scales (α_S) and the difference between these describe the between-sample variation (β_L). The regional diversity (γ) is then the sum of local-sample diversity, between samples variation and between sites variation (β_S). Based on the method described by Crist et al. (2003).

In **Paper I and II** the diversity found within each habitat (site-community, α_s regarded as γ in these studies) is partitioned into local-sample diversity (α_L) and between samples diversity (β_L), to determine if the diversity within each habitat is distributed homogenously or if we can detect substantial small-scale variation in community composition within the sites. In **Paper III,** the diversity found in the 16 mature pine forests sampled in the whole region of south-central Sweden, is considered as the γ-diversity. I partition this into the local-sample-diversity (α_L) and the site-diversity (α_S), and the corresponding variation between samples within sites (β_L) and between sites (β_S). This enables us to determine at which scale (sample or site scale) variation is most important for a high regional diversity. I also relate the species turnover, as measured by pairwise-dissimilarity (β turnover) to the distance between sites, to further

examine at which scale the largest differences in species composition are occurring.

3.2 Functional diversity and 'traits'

Functional traits are properties of the species, measured at individual level, that either determine how the species react to different stressors or environmental conditions (response traits) or how it influences ecosystem functioning (effect traits) (Lavorel and Garnier 2002). However, the term traits is often used for any property of a species considered as describing the species role in the community or ecosystem. In this thesis I do not specifically separate between response and effect traits. Most traits used are measured at species and not individual level and can be considered response traits, although some are likely both response and effect traits. Analysing the traits that each species possess instead of their taxonomical identity has been proposed to reduce context dependency and enable generalizations about the factors behind patterns in diversity and species composition across ecosystems (McGill et al. 2006). Using traits might also increase our mechanistic understanding of observed patterns (Eros et al. 2009). Species traits, rather than species identity, are considered to determine the responses of species to environmental changes (de Bello et al. 2010, Cadotte et al. 2011). Additionally, if the focus is on ecosystem functioning, or ecosystem services, functional diversity is thought to be a better predictor than species richness or species diversity (Elmqvist et al. 2003, Loreau et al. 2003).

Functional diversity can be measured in a number of different ways (Naeem et al. 2009). To be easily compared with measures of species diversity (i.e. Simpson 1-D), the Rao's quadratic entropy, hereafter referred to as Rao, is one of the most frequently used. The Rao index describes the community functional diversity as the extent of dissimilarity in trait values among species in a community (de Bello et al. 2009). If all species have the same value in the examined trait, Rao will be equal to the Simpson diversity index. Most studies find that the species beta-diversity is considerably higher than the functional beta-diversity (Ackerly and Cornwell 2007, de Bello et al. 2009). This can be interpreted as functional stability i.e. that across space species are replaced with other species possessing the same niche, and therefore, the same traits. Determining for which taxonomic groups and at what scale this is true is important as increasingly more effort is given to manage multifunctional landscapes (García-Martín et al. 2016). It is also important to understand what determines functional diversity when we are interested in how to manage ecosystem services (Elmqvist et al. 2003).

We have used trait information on all observed springtail species obtained from a database including mainly literature data from northern Europe (M.P. Berg, unpublished). We used this information to assess the functional diversity of the sites and samples based on five different traits in each of the three community-papers (**Paper I, II and III**). The questions posed were: (1) is the turnover in functional diversity equally high as the turnover in species diversity? And if so (2) is the functional composition, based on community weighted means (CWM), of each trait related to the same factors as the species composition? Additionally, we ask (3) is the communities overdispersed or underdispersed in any of the examined traits?

3.3   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). 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, as well as its effects on ecosystem processes (Lavorel and Garnier 2002). Species interactions (i.e. competition, predation and mutualism) structure communities (*biotic filtering*) and are modified by environmental conditions (*environmental filtering*) excluding some species from colonizing the community and reducing the competitive ability of others (HilleRisLambers et al. 2012). Historical factors, speciation and dispersal limitation will affect which species will be available for these 'filters' to act on (Zobel 1997, 2016). Additionally, community composition may also be structured by stochastic disturbances, such as flooding or wind-throws (Paine and Levin 1981, Begon et al. 2005). Often, environmental filtering and dispersal limitation are most important when communities are studied at large spatial scales (including many communities), while biological processes or biotic filtering (e.g. competition) are more important at smaller spatial scales (Götzenberger et al. 2012) (in this thesis mainly local sample-communities). This scale-dependent change in structuring factors might to some degree be caused by a higher probability of including a substantial gradient in environmental variables important for the community composition when increasing the spatial scale (Willis et al. 2010).

In heterogeneous environments (spatial and/or temporal), environmental conditions can set different boundaries for which species that will be able to colonise and persist in any given local area (Hutchinson 1951, Chase and Leibold 2003). Species adapted to a specific environment thus have an opportunity to dominate that community. Since different species are found in

local areas with different conditions, this results in sites, landscapes or regions (depending on spatial scale considered, hereafter called *areas*) with a high diversity. In contrast, in areas with little variation in environmental variables between local areas, all species tolerating these conditions are able to persist in every suitable habitat (local area) and the composition of the communities is thereby mainly determined by biotic interactions (Hairston et al. 1960). However, dispersal limitation or stochastic events can result in species being absent from parts of the area, although the conditions of the local areas and biotic interactions would not restrict its colonization. Most communities are structured by several different factors selecting species at different temporal and spatial scales (Vellend 2010), the relative strength of the different factors will vary with the disturbance regime of the system, spatial scale of study and taxonomic group in focus.

If environmental filtering is the main structuring factor, communities should consist of species similar in traits affecting how they respond to the environmental variables imposing the "filter" (Cornwell and Ackerly 2009). The communities are then considered to be *underdispersed* or *convergent* with respect to that trait, i.e. the community has a lower variation in that trait than if the community was randomly assembled from the regional species pool (Fig 3A). This should also be seen by environmental variables (those imposing the selection) explaining a larger part of the variation in species composition than does spatial variables (Borcard et al. 1992, Cottenie 2005).

On the other hand, if biotic filtering (limiting similarity by biotic interactions) is the most important structuring factor, communities should be *overdispersed* or *divergent* in certain traits (Fig. 3B). Species in a community would be different in traits connected to how they use the habitat and interact in the community, as species with too similar requirements would not be able to coexist (Hardin 1960). When examining variation in species composition, spatial variables would explain a larger part than environmental variables (Borcard et al. 1992, Cottenie 2005). Spatial variables describe the spatial configuration of samples used in the analysis (Borcard et al. 2011b). This can be included in different ways, I use trend surface analyses using polynomial of coordinates (**Paper III**), principal coordinates of neighbour matrices (PCNM) or Moran's Eigenvector maps (MEM) (**Paper I, II and IV**). In **Paper III** I also include a comparison of dissimilarity matrix with distance matrix. Spatial variables are considered as a proxy for dispersal limitation or biotic interactions. A large proportion of community variation explained by spatial variables, without evidence of overdispersion in traits indicating biotic filtering, would suggest that dispersal limitation is important for community composition (Cottenie 2005).
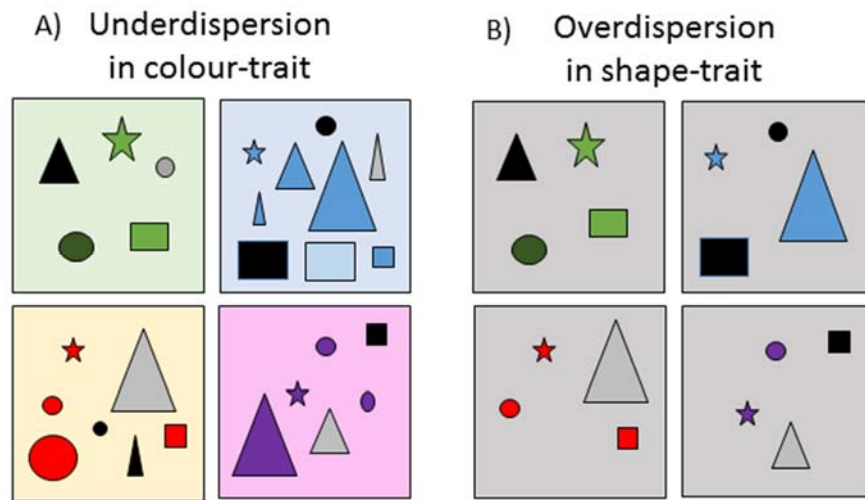
Figure 3. Species in each local area in **A,** are more similar to each other than if assembled by random regarding colour, as environmental constraints exclude species with certain colours from each habitat. Here the different colours of the boxes represent different environmental filters. Species interactions within each local area in **B,** exclude species too similar to others in shape. At this level the environmental differences is not driving the composition and therefor no colours are given for the boxes. Based on Cornwell and Ackerly (2009).

The variation in the environment, dispersal limitation and biotic interactions are important factors shaping community composition and diversity of species. The relative role of these factors are the main focus of this thesis (Fig. 5). As a proxy for dispersal limitation and biotic interactions, different variables describing space (spatial configuration) are included. This thesis includes two studies on the small-scale spatial structure of Collembola communities (**Paper I & II**). They have similar design but are conducted in very different ecosystems, with some similarities but also important dissimilarities with regard to disturbance regimes, vegetation and environmental conditions. This was done to examine the relative role of structuring forces under different conditions. **Paper III** examines structuring factors at a larger (regional) scale, including sites across south-central Sweden that are similar in vegetation and soil conditions, but with distances between sites ranging from 500 m to 260 km. This enables me to discuss the relative importance of structuring factors depending on spatial scale, and large-scale environmental gradients.
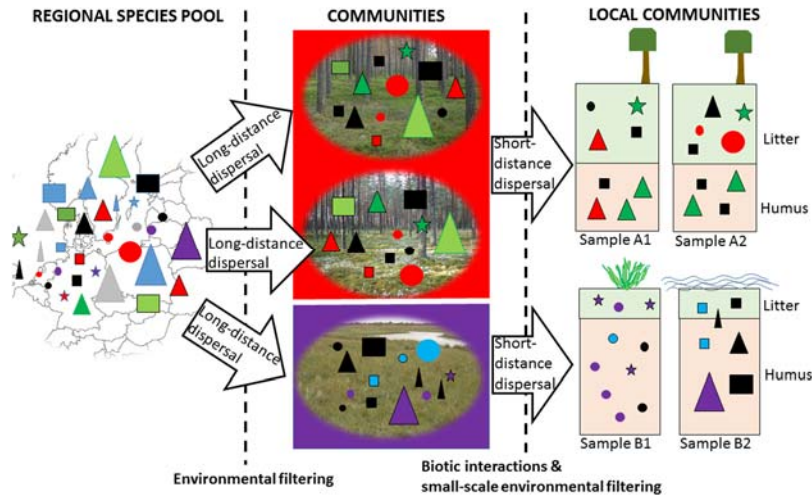
Figure 4. Community assembly processes act on several different scales. Environmental filtering and dispersal limitation exclude species from colonizing some habitats within a region, resulting in communities within habitats with different environmental conditions also having species with different traits. Comparing the "purple community" with one of the "red communities" at the community level, they both show underdispersion with regard to colour-traits, not seen when comparing the two red communities. Within each habitat, biotic interactions may exclude species too similar in some traits from coexisting. Large variation in small-scale environmental conditions between samples may result in local sample-communities with species even more similar in traits. The two local communities (sample A1 and A2) within the pine forest are overdispersed in shape-trait, while the two in the salt marsh (sample B1 and B2) are underdispersed in shape-trait.

Shapes and colours represent different traits, with colour-traits responding to a large scale variation separating the two habitat types and shape-traits affecting the response to local-scale variation in environmental conditions or to biotic interactions. Developed from ideas in Zobel 1997, Loreau et al. 2001, Cornwell and Ackerly 2009, Götzenberger et al. 2012, HilleRisLambers et al. 2012

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3.4 Intra-specific variation

Analyses of spatial species distribution patterns of communities commonly view all con-specifics as behaving similarly and as possessing the same traits (Astor et al. 2014, Krasnov et al. 2015, and **Paper I-III** of this thesis), a practice that has been criticized by Violle et al. (2012). Recent work by Rudolf and Rasmussen (2013) has emphasized the risk of missing important differences between life stages (i.e. age classes, Fig. 5) when using species-level traits. This risk is obvious in species where food or habitat requirements change dramatically between juveniles and adults, such as insects or amphibians with aquatic larval and terrestrial adult stages. However, also species that live in the same habitat throughout their lives might differ substantially in their spatial distribution as e.g. feeding preferences, drought or temperature tolerance, and the strength of interspecific interactions may vary with age (e.g. Gilbert et al. 1999, Amarasekare and Sifuentes 2012). If these effects are large, this may make interpretation of species-level patterns less reliable (Violle et al. 2012).

In **Paper IV** I question the assumption, in the first three papers, that all individuals within a species respond similarly to the structuring factors environmental filtering and biotic interactions (i.e. space). This is done by analysing data on spatial abundance distribution of age classes in two Collembola species with different level of social behaviour obtained in an unpublished study by Birkemoe & Leinaas.

Figure 5. Collembolans have direct development, i.e. the juveniles resemble the adults in appearance as soon as they hatch from the egg. In most species they undergo 5-8 instars (developmental stages) before they reach reproductive maturity. Photo: Arne Fjellberg (four instars of *Vertagopus arborea*).

4   The biology and ecology of Collembola

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 and Wardle 2002). Springtails (Collembola) are one of the most abundant soil arthropod groups and our ecological understanding is higher for this group than for many other soil organisms. It is therefore a suitable study system to investigate community assembly. In this thesis I use field studies of Collembola species and communities to understand the structuring mechanisms, both at small spatial scales and at regional scale. I do this in three different ecosystems, with different degrees of environmental variability and disturbance regimes.

Collembola (springtails) are a diverse class of hexapods (Fig. 6) that inhabit most ecosystems and habitats on earth (Rusek 1998). Most species live in the upper organic-dominated layers of the soil (these are called *hemiedaphic*) but some species inhabit the mineral soil horizons (*euedaphic*) (Petersen and Luxton 1982), while others can be found on the soil surface or in the vegetation (*epigeic*), or within almost any other habitat (Christiansen 1964). They are often, together with mites (Acari), the most abundant soil arthropods (Petersen and Luxton 1982, Filser 2002). Collembola have direct development, with juveniles resembling adults, and juvenile instars often occur in the same macro-habitat as the reproducing adults (Hopkin 1997), but see Jensen et al. (2006). As for most soil animals, behavioural studies are scarce (but see e.g. Christiansen 1964, Bengtsson et al. 1994, Chauvat et al. 2014). There is a range from social species - where pheromones dominate over environmental signals when it comes to the formation of coordinated colonies (Leinaas 1983) - to species where environmental variation explains most of the spatial distribution patterns at a local scale (Hertzberg et al. 1994).
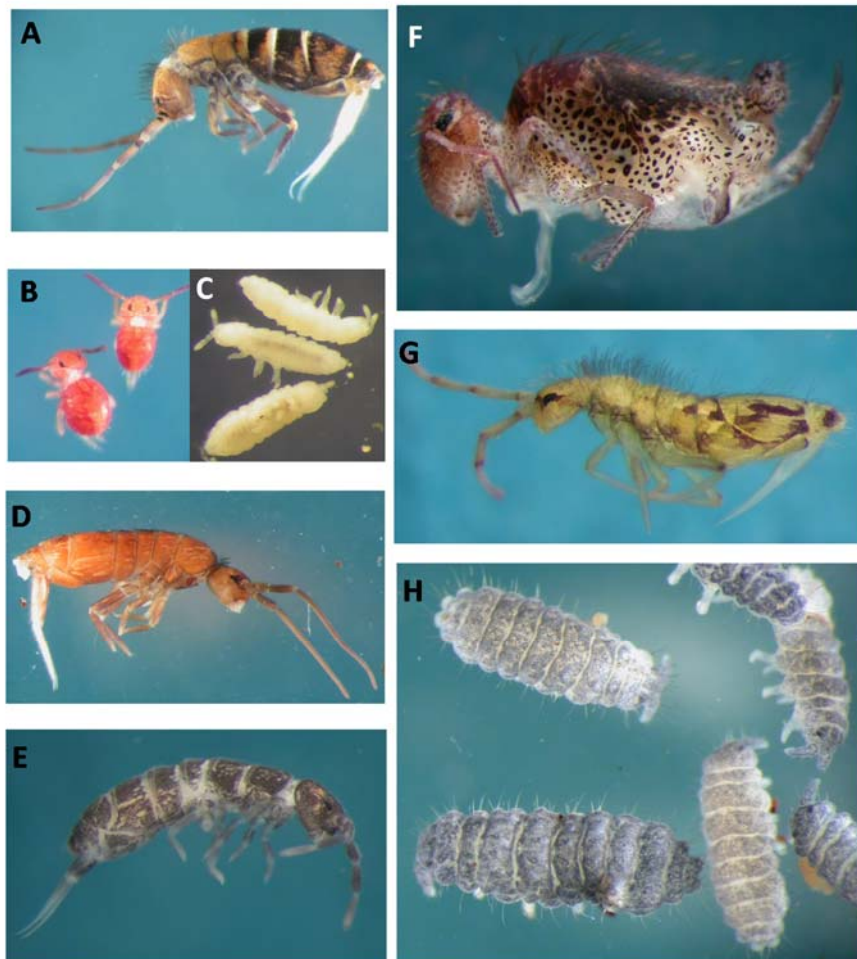
Figure 6. Collembolans can have different shapes, colours and sizes. Some examples of the species included in the pine forests of this thesis, with info about the life form and maximum body length given within brackets. **A,** *Orchesella bifasciata* (epigaeic, 2.5 mm) **B,** *Sphaeridia pumilis* (hemiedaphic, 0.5 mm) **C,** *Hymenaphorura polonica* (euedaphic, 1.8 mm) **D,** *Pogonognathellus flavescens* (hemi, 4.5 mm) **E,** *Parisotoma notabilis* (hemi, 1.0 mm) **F,** *Allacma fusca* (epi, 4.0 mm) **G,** *Entomobrya nivalis* (epi, 2.0 mm) **H,** *Neanura muscorum* (hemi, 3.5 mm). Photos: Arne Fjellberg.

Collembola community composition often shows rather high temporal and spatial variability (Wolters 1998, Chernova and Kuznetsova 2000, Berg and Bengtsson 2007, Siira-Pietikäinen and Haimi 2009). However, species composition is considered predictable under stable environmental conditions (Bengtsson 1994, Chernova and Kuznetsova 2000). Collembolans are known to be affected by soil moisture (Kaczmarek 1975, Huhta and Ojala 2006) and

pH (Hågvar 1990, van Dijk et al. 2009), as well as temperature (Christiansen 1964, Wolters 1998), resource abundance (Takeda 1987) and detritus quality (Teuben and Smidt 1992, Rantalainen et al. 2004). 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 (Kaczmarek 1975, Takeda 1987), which has been explained by variation in habitat diversity on smaller scales (cm-scale) than usually considered in ecological studies (Nielsen et al. 2010). Other studies have highlighted the importance of species interactions in determining the Collembola community structure (Hågvar 1990, Kuznetsova 2006). In a study comparing springtail communities in natural and cultivated forests (Cassagne et al. 2004) the species increasing in cultivated stands were all widely distributed species, suggesting that these populations of generalist species were released from competition of more specialized species. However, recent studies on Collembola community composition show however that environmental variables usually explain more of the community variation than spatial variables (Martins da Silva et al. 2012, Ponge and Salmon 2013, Chen et al. 2014) at scales ranging from landscape (km) to site (m) level.

It has been shown that the dispersal ability differs between species of Collembola and that this affects their ability to recover after disturbance (Dunger et al. 2002, Lindberg and Bengtsson 2006, Ponge et al. 2006, Åström and Bengtsson 2011, Malmström 2012). Many species have been found to have slow dispersal rates (Bengtsson et al. 1994, Ojala and Huhta 2001), especially species connected to forest habitats (Ponge et al. 2006, Auclerc et al. 2009). Others are able to disperse long distances through passive dispersal (Dunger et al. 2002, Moore 2002, Hawes et al. 2007, Hawes et al. 2008). 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 (Åström and 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 (Ingimarsdóttir et al. 2012). This study found environmental constraints or biotic interactions to be equally probable structuring forces. 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 are the ones that are most abundant in the immediate surroundings (Rantalainen et al. 2004, Ponge et al. 2006). 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.

5 Methods

Datasets from three regions and three ecosystems were used to examine the spatial patterns of Collembola species and communities (Table 2). All studies are based on observational data, in un-replicated sites or regions and analysed with multivariate statistics, spatial analyses and trait-based null models.

Table 2. *Properties of study sites included in the thesis.*

|	Ecosystem	Region	Main spatial scale	Ecological scale	Traits
Paper I	Salt marsh	Holland	Local	Community	5 from litterature
Paper II	Mature pine forest floor	Sweden	Local	Community	5 from litterature
Paper III	Mature pine forest floor	Sweden	Regional	Community	5 from litterature
Paper IV	High Arctic meadow	Svalbard	Local	Species & age class	Body length measured

5.1 Study areas and sampling design

To establish the spatial distribution of Collembola species at different scales we used spatially explicit sampling designs, using different schemes for each of the four studies. The sampling schemes were 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 (Fig 7). The collembolans found in each sample in these designs are regarded to represent a local community (measuring the sample-based diversity, α_L), and the individuals found in a site represent the site-community (α_S), this is used as the "gamma" in **paper I and II** as only the small-scale variation within one habitat is studied. In the regional study (**paper III**) diversity is measured both for local communities (α_L), site based communities (α_S) and for the whole region of south-central Sweden (γ). The small-scale spatial variation in abundance of species or of age classes within species are examined in **paper IV** as the variation between samples. Details about the spatial extent of sampling areas and number of samples are given in Table 3.

Table 3. *For each paper the sampling design are described by, the distances between samples (**paper I, II & IV**) or sites (**paper III**), the extent of the study area, size (area, not volume) of each soil fauna sample and the number of samples included.*

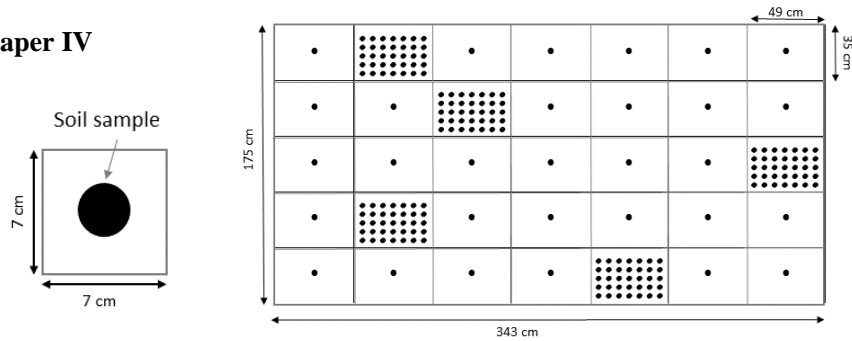|	Distances	Extent	Sample size	No of samples
Paper I	0 cm - 30 m	25*35 m	10 cm diameter	172
Paper II	0 cm - 20 m	5*20 m	10 cm * 10 cm	99
Paper III	500 m – 260 km	120*260 km	10 cm * 10 cm	320 (20/site)
Paper IV	3.5 cm – 3.5 m	2*3.5 m	10 cm diameter	205

Paper I
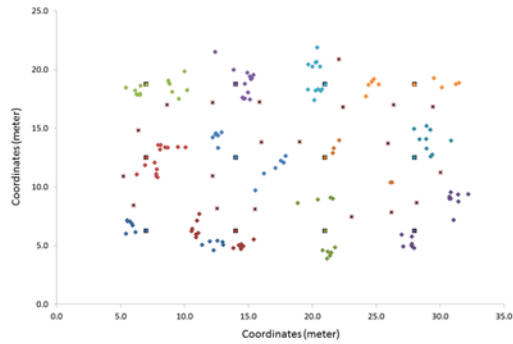
Paper II
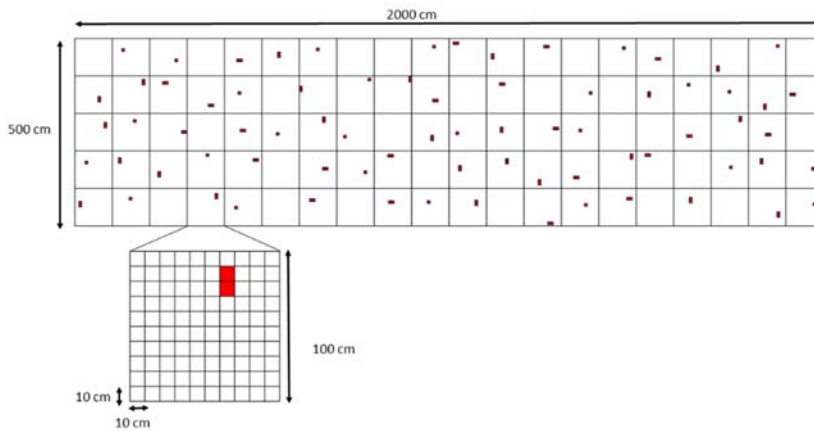
Paper IV

Figure 7. Schematic view of the sampling designs of all papers. In **Paper I** with each dot representing a soil core (sample), colours indicate samples in the same "series". **Paper II** with each red square representing a sample, in total 100 samples within 5 m * 20 m. Below are a close-up of one 1 m * 1m square from which two adjacent samples are taken. In **Paper III** a similar design as in **Paper II** was used, although only 20 samples were taken. **Paper IV** with each dot representing sample (soil core) taken in the centre of a 7 cm * 7 cm square, to the left a close-up of one of these are shown. See text and Appendix of each paper for more details.

5.1.1 A late successional salt marsh in Holland – **Paper I**

The study area is located on a barrier island on the northern coast of The Netherlands (Fig. 8A & D). The island is continuously formed by 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 of the island (Olff et al. 1997, Schrama 2012). 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 has a late successional vegetation dominated by Sea couch (*Elytrigia atherica*), a halophytic tall grass, and a sparse cover of Sea rush (*Juncus maritimus*) growing in tussocks (Fig. 9A). In this area 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 (Fig. 7A), giving 172 samples at distances of 0 to 30 meters from each other.
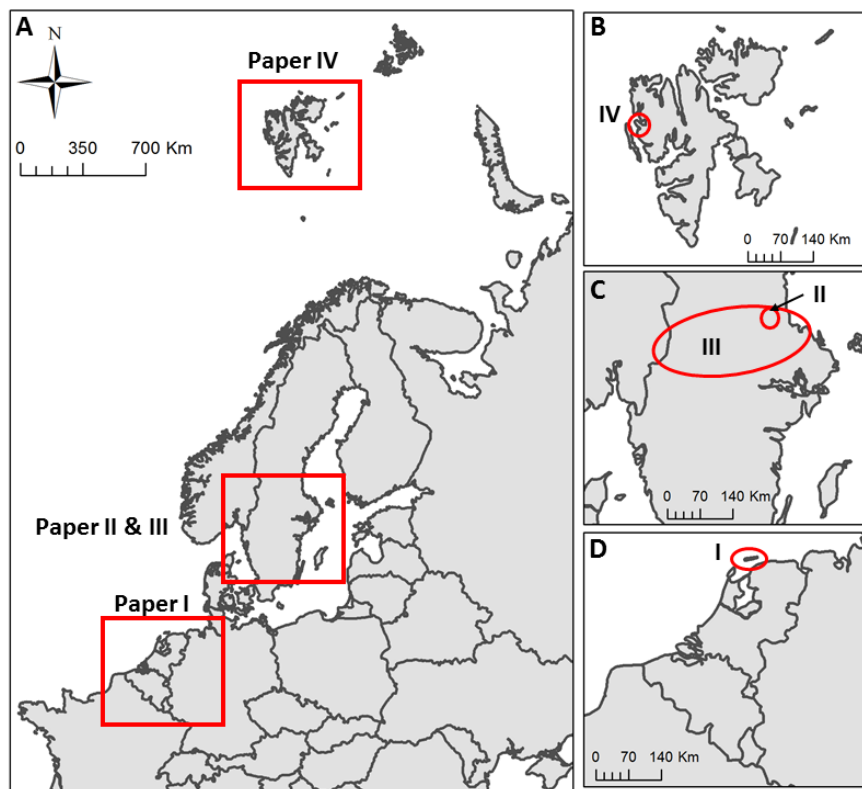

Figure 8. The four studies were conducted in different parts of northern Europe (**A**), furthest north **B,** is Svalbard where the study of **Paper IV** was conducted. **C, Paper II and III** was sampled in pine forest in south-central Sweden and **D, Paper I** was conducted on an island on the northern coast of the Netherlands.

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5.1.2 A mature pine-forest floor in Sweden – **Paper II**

We selected a >200 year old pine forest (Jädraås) in the east of south-central Sweden (Fig. 8A & C). The area has a flat topography and the soil is formed by glacifluvial sand (Fig. 9B). The homogenous vegetation cover is of the *Cladonia-Pinetum* type, but with a small-scale patchy distribution of bryophytes, lichens and dwarf shrubs (Fig. 9C). Dominating within the sampled plot was a feather moss (*Pleurozium schreberi*) linked to acidic soils and reindeer lichen (*Cladonia rangiferina*). More details of the study area, soil properties and soil fauna can be found in Persson et al. (1980). We created a plot of 5 m by 20 m, from which 100 samples were collected (separating the litter and humus layer) at distances 0 to 20 m in an irregular grid (Fig. 7B).
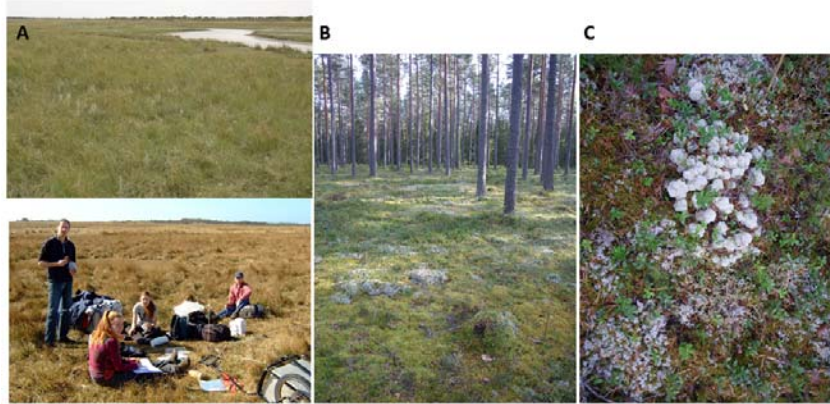

Figure 9. The salt marsh of **Paper I** (**A**) was dominated by Sea couch, with a sparse cover of Sea rush tussocks. Frequent inundation events with salt water creates a regular disturbance regime for the soil fauna community. The mature pine forest of **Paper II** (**B**) had a flat topography and a small scale mosaic of lichens, bryophytes and dwarf shrubs covered the ground (**C**). Photos: **A,** Matty Berg, **B & C** Lina A. Widenfalk.

5.1.3 Mature pine forests across south-central Sweden – **Paper III**

This study includes 16 sites within mature pine forests along latitude 60° in south-central Sweden, from the east coast to the border of Norway (Fig. 8A & C and Fig 10). All sites resemble the site from **Paper II** in terms of topography, forest structure and history, being situated on top of glacifluvial sand and having similar soil chemistry properties (Fig. 10B-E). The ground vegetation was more or less the same, with more bilberries (*Vaccinium myrtillus*) in some of the sites but most often dominated by lichens, bryophytes, cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*). Within each site I selected a homogenous area, minimizing the variation between sites, and created a plot of 5 m by 20 m, in a similar manner as for **Paper II** (Fig 7B). From this 20 samples were collected (separating humus from litter) in an irregular grid.
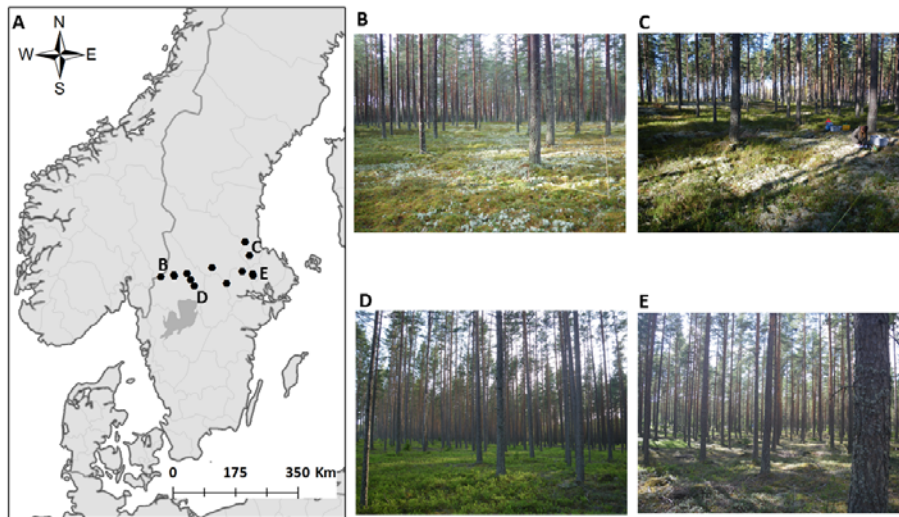

Figure 10. The 16 sites of Paper III was **A,** located across south-central Sweden, shown as dots in the map. They were all located in mature pine forests, four examples shown in **B-E** with location indicated in the map, with flat topography and low variation in most environmental variables. Photos: Lina A Widenfalk.

5.1.4 A high Arctic meadow on Svalbard – **Paper IV**

The study area of **Paper IV** was located in a high Arctic meadow situated approximately 2 km south east of Ny-Ålesund, Svalbard (Fig. 8A & B). This meadow was characterized by a *Cassiope tetragona-Dryas octopetala* vegetation type with 50-100% coverage (Brattbakk 1981) (Fig. 11). The selected area of the study had a continuous cover of the dwarf-shrub *C. tetragona* (Arctic bell-heather). The organic layer (0.5 and 6 cm thick) was

situated on top of coarse stones and silt. In this area we created a plot, 3.5 m by 2 m, which was divided into 35 squares. Five squares were randomly chosen for intensive sampling to study small-scale aggregation (including 35 samples, Fig 11) and from the rest of the squares only one sample was taken (Fig. 7C). This gave 205 samples at distances of 2 cm to 3.5 m from each other. The data were collected in 1995 by co-authors Birkemoe and Leinaas (unpublished data), and were analysed for this thesis to examine the assumption that species-level traits can be used in community studies.
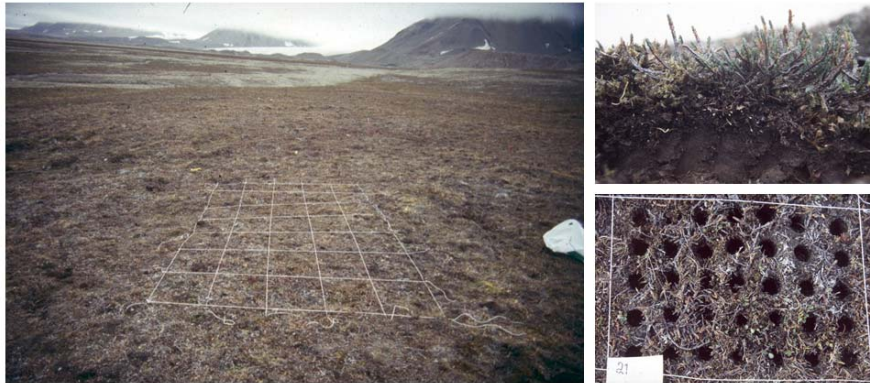

Figure 11. The sampling area of **Paper IV** located in a high Arctic tundra meadow with a continuous cover of the Arctic bell-heather (top right) and a small scale mosaic of additional dwarf shrubs, bryophytes and lichens. The area was divided into 35 squares by thin white threads, in five of the squares 35 soil core samples were taken (bottom right) while in the remaining 30 samples only one sample was taken in the centre. Photos: Tone Birkemoe

5.2   Soil fauna sampling and measures of body length

For all four studies, soil samples were collected including the full organic layer profile and in **Paper IV** also the upper part of the mineral soil. From these samples soil fauna was extracted using different versions of Tullgren funnels, placing the organic material on nets and creating a drought gradient in the sample forcing the animals to move downwards into a collection funnel leading to a preserving liquid. All collected Collembola were then determined to species level and counted, giving abundance data of each species in each sample. For the pine forest soils (**Paper II & III**) the litter layer and the humus layer were counted separately and then pooled or analysed separately. Also for the Arctic meadow (**Paper IV**) two layers (humus and mineral soil) were counted separately although few individuals were found in the mineral soil.

The collected samples of **Paper IV** included < 10 species of which five were determined to species level and two found to dominate all samples, *Folsomia quadrioculata* and *Hupogastrura tullbergi*. The body length (from tip of head to abdomen) of these two species was measured for all individuals, using a stereo-microscope with 16 × magnification. As body length is strongly correlated with age in these species (Birkemoe and Sømme 1998, Birkemoe and Leinaas 1999, Sømme and Birkemoe 1999) and we had data of the size distribution of different life stages (i.e. hatchlings, juveniles and reproducing adults) from populations in similar conditions (Birkemoe and Sømme 1998) we categorized the individuals into these three age classes.

5.3 Environmental variables explaining Collembola community structure

To examine the relative influence of environmental filtering on the community composition or the abundance distribution, compared to that of biotic interactions or dispersal limitation, we measured environmental variables known to affect Collembola. For further details about how these were measured and treated in the analysis, see the individual papers. A broad summary of all variables included in the different papers and at what scale they were measured are given in table 4.

In the salt marsh of **Paper I**, the major environmental gradient is imposed by frequent flooding of salt water, there is a small-scale variation in topography affecting the influence of these inundation periods for different parts of the sampled area. The included measures of environmental conditions were *small-scale topography*, *soil moisture content*, *thickness of the leaf litter layer*, *vegetation height* and *number of J. maritimus stems* (Fig. 12). The vegetation height affects the micro-climatic conditions in each sample, and the number of stems are a proxy for the size of tussocks that give shelter to the collembolans.

Figure 12. In **Paper I** the number of *Juncus* stems within a soil core (top left) and the thickness of litter layer (bottom left) were included as environmental variables. In the pine forest of **Paper II and III** the soil samples were taken with a steel frame (bottom centre) and stored in cooling boxes until extraction (bottom right). The vegetation composition differed slightly between sites in **Paper III** (top centre and right) but had no effect in the analyses. Photos: M Berg & L Widenfalk.

Table 4. *The environmental variables included in the analyses of each paper*

	Variable	Scale of measure	Paper
Soil properties	pH	Sample (**II**) / Site (**III**)	**II, III**
	Soil moisture	Sample / Site(**III**)	**I, II, III, IV**
	Litter thickness	Sample	**I, II, III**
	Humus depth	Sample	**II, III, IV**
	Prop organic matter	Sample	**II, IV**
"Food"	C:N ratio	Site	**III**
	Microbial activity	Sample	**IV**
	Active hypha	Sample	**IV**
Micro-climatic	Topography	Sample	**I**
	Ground veg. cover	Sample	**II, III**
	Vegetation height	Sample	**I**
Climate	Temperature	Site	**III**
	Cold-period	Site	**III**
	Growing degree days	Site	**III**
	Precipitation	Site-cluster	**III**
	Snow cover	Site-cluster	**III**
Vegetation composition	Species p/a	Sample	**I, IV**
	Species frequency	Sample	**III**
Other	Tussock size (shelter)	Sample	**I**

The mature pine forest floor in **Paper II** was selected to be as homogenous in environmental conditions as possible with regard to factors known to affect springtails (i.e. topography, moisture, and vegetation cover), to enable detection of biotic interactions in the absence of strong environmental filtering. However, small scale variation could still be present and we measured the *thickness of litter* and *depth of humus* layer, the *proportion organic material* in the humus, the *pH* of the humus and the proportion of *vegetation cover* as it affects the micro-climatic conditions. There was a small scale mosaic in ground vegetation within the samples area, consisting of bryophytes, fruticose (bush-like) lichens and dwarf-shrubs (Fig. 9 and 12) Therefore the *vegetation composition* (measured in presence/absence of all species) was included as a separate (biotic) component in the analysis and paper. In this thesis the variation explained by this component is added together with the proportion explained by the other environmental variables (see below).

In **Paper III** 16 sites were selected based on being similar in forest stand age, forestry history, soil type (glacifluvial sand) and having areas with flat topography. We included three different sets of environmental variables. Climatic variables were included based on information from available climate-station data from as close by as possible for snow cover and precipitation, therefore some sites had the same values for some of the measures (denoted site-cluster in Table 4). For the temperature data we instead used extrapolated measures combined with correction for topography from Meineri and Hylander (2016). Included measures were *annual precipitation*, annual *temperature* and mean temperature of annual *cold-periods*, number of *growing degree days* (GDD) and thickness of *snow cover*. The local environmental variables was either soil properties measured in five samples per site (*pH*, *C:N ratio*, *soil moisture*, *thickness of litter* and *humus depth*) or vegetation variables connected to micro-climatic conditions measured for each soil fauna sample (*tree cover* and *ground vegetation cover*). The vegetation composition was described based on the presence/absence of each species in every soil fauna sample, and included as the frequency per species based on these 20 samples. (Fig. 12).

We included three different explanatory components in **Paper IV**, describing different aspects of the habitat conditions for Collembola. Soil properties include food quality and available life space, in the humus surrounding each soil core we measured the *thickness of humus layer*, *soil moisture*, relative amount of *soil organic matter*, *microbial activity* and amount of *active fungal hypha*. The vegetation composition was based on the presence/absence of all observed species or vegetation types (i.e. bryophytes, lichens or grasses) within each square surrounding a soil fauna sample. The

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abundance of <u>other Collembola</u> species than the focal species was included, to determine if competitive exclusion was important, but more likely reflecting environmental variations not captured by the measured variables.

5.4 Collembola trait data

Trait values for all observed springtail species in these studies were obtained from a database maintained by M.P. Berg (Vrije Universiteit, Amsterdam, The Netherlands). It includes mainly literature data from northern Europe, consisting of over 350 species (unpublished data). We used a number of traits that have previously explained shifts in Collembola species composition across time, space and experimental treatments (Krab et al. 2010, Makkonen et al. 2011, Bokhorst et al. 2012, Malmström 2012, Martins da Silva et al. 2016). Traits used in all community-papers (**Paper I, II and III**) were *body length*, *life form* (indicating vertical stratification), *moisture tolerance* and *macro-habitat width* (Table 5). For **Paper I and II** the *antenna/body length ratio* (i.e. active dispersal) was also included. In **Paper III** we include *regional distribution*, as a proxy for the potential of colonizing all parts of the region. These can all be considered as response traits, even though e.g. body length also can be considered an effect trait. In this thesis I aim to explain how communities are structured and what factors are effecting this, therefor the focus is on response traits rather than effect traits as I do not aim to describe the effect the species composition has on the functionality of the community.

Table 5. Definition, ecological significance and value ranges of the six examined traits.

Trait	Definition	Ecological significance	Range or Categories	Ref
Body length	Maximum length from head to tip of abdomen (mm)	Connected to ecophysiology, dispersal ability and life form	0.5-5.4 mm (**Paper I**) 0.4-4.5 mm (**Paper II**) 0.4-5.0 mm (**Paper III**)	1, 2, 3
Antenna/body ratio	The ratio between antennal length and body length	Assumed to be linked to sensory ability and active dispersal	0.1-0.7 (**Paper I**) 0.1-1.25 (**Paper II**)	1, 3, 4
Life form	Trait complex including: number of ommatidia, length of body, furca development and intensity of coloration	Proxy for vertical stratification, ecophysiology and dispersal ability	Euedaphic Hemiedaphic Epigaeic	5
Moisture tolerence	Level of soil moisture content the species is mostly associated with	Proxy for the 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**) 1-8 (**Paper III**)	1, 3, 4, 6, 7, 8, 9
Regional distribution	No of provinces in Scandinavia in which the species has been found	Proxy for climatic sensitivity and potential to colonize all parts of the region	6-58 (**Paper III**)	1, 3

1 - (Fjellberg 1998), 2 - (Hopkin 2007), 3 - (Fjellberg 2007), 4 - (Potapov 2001); 5 - (Gisin 1943), 6 - (Bretfeld 1999), 7 - (Kuznetsova 2003), 8 - (Thibaud et al. 2004), 9 - (Zimdars and Dunger 1995), 10 - (Kuznetsova 2002)

5.5 Analyses

In this thesis I use two main analysis methods. In **Paper I, II and III** I used ordination techniques (primarily RDA) together with variation partitioning to determine the relative contribution of explanatory components to the variation in species composition (Borcard et al. 2011b). In **Paper I and II** also the trait composition, based on the community weighted mean (CWM) of each trait in each sample, is examined in the same manner. I also performed variation partitioning of multiple linear-regressions, to determine the relative contribution of explanatory components to the variation CWM of single traits (**Paper I and II**) or abundance of species and age classes within species (**Paper IV**) (Legendre and Legendre 1998a). The selection process

determining which spatial and environmental variables to include in each analyses differed slightly between papers, this can be found in the method description of each paper. In the first three papers (**I, II, III**) I also performed null model analyses of the trait diversity, to determine if the communities (or local sample-communities) were overdispersed or underdispersed in the analysed traits (de Bello et al. 2009, de Bello et al. 2010). The null models are constructed by keeping the species richness and abundance distribution of each sample but randomly assign the trait values to each species. By comparing observed trait diversity values (alpha and beta Rao-values) with those obtained from null models I could determine if coexisting species are more or less similar to each other in the analysed trait, than if communities where assembled at random. For details about all analyses, such as data treatment, included variables etc. these are described in each paper and their appendices.

5.5.1 Alpha, beta and gamma diversity

The main focus of the first three papers (**I, II, III**) are on the distribution patterns of diversity, comparing local sample-diversity with diversity found within a site (habitat) or within a whole region (**Paper III**), although restricted to one habitat. This comparison was done mainly by partitioning (dividing) the regional diversity between the mean diversity within each local area and the difference between local diversities (Whittaker 1960). I used additive partitioning, so that the alpha and beta diversities are expressed in the same unit (Lande 1996). The comparison was made between measures of species richness, species diversity (Simpson diversity, 1-D) and functional diversity calculated by the Rao's quadratic entropy (hereafter referred to Rao). If all species in a community have the exact same trait values the Rao index equals the Simpson diversity (Botta-Dukat 2005).

For **Paper III**, the regional diversity based on the pooled data from all 16 sites was partitioned into local sample-diversity, site-diversity and the variation between units at each level, according to:

(1) $\quad \gamma = \alpha_S - \beta_S$

(2) $\quad \alpha_S = \alpha_L - \beta_L$

Where γ = regional diversity based on all observations,
α_S = average diversity within sites (N = 16),
β_S = average difference between sites,
α_L = average diversity within samples, i.e. local communities (N = 320) and
β_L = average difference between samples.

In **Paper III** β-diversity was also calculated as the pairwise site-dissimilarity in species composition, calculated by the Jaccard index using either binary or abundance data (Oksanen et al. 2016) or the Chao index (Chao et al. 2005).

5.5.2 Spatial analyses

The spatial configuration of samples in the three small-scale papers (**I, II and IV**) was described by distance based Moran's eigenvector maps (dbMEM), a method based on computing the principal coordinates of a matrix of geographic neighbours (Dray et al. 2006, Borcard et al. 2011a, Legendre et al. 2012, Legendre and Legendre 2012). MEM analyses are considered robust and suitable for discriminating between spatial and environmental effects on community composition (Griffith and Peres-Neto 2006). Each dbMEM-variable represents a spatial pattern at a given scale, from single maxima or minima within the study area to very small-scale variation with many maxima and minima (see papers and Appendixes of them for examples).

For the spatial variables of **Paper III** I instead performed trend surface analysis (Legendre and Legendre 1998b) as the low number of sites makes MEM-analyses difficult. The trend surface was constructed with a second order polynomial from the geographical coordinates of each site. This gives six spatial variables that describe either spatial gradients (N-S, E-W or diagonally across the area based on N-S × E-W) or non-linear relationships with either a minima or maxima (N-S^2 and E-W^2). How the selected spatial variables can be viewed in this study can be seen in **Paper III** - Fig. 7.

In **Paper I** the spatial scale of autocorrelation for environmental variables as well as the RDA-scores was determined based on semivariograms (Klironomos et al. 1999), and kriging maps were constructed to compare the spatial structure of small-scale topography with either of the community composition descriptors (species composition or CWM trait composition). In **Paper II and IV** the spatial scale of autocorrelation was examined based on correlograms (Giraudoux 2015). In **Paper III** the dissimilarity-indices (β-diversity measure) were correlated with a distance matrix based on geographical distance between sites and tested using Mantel statistics (Legendre and Legendre 2012), to detect if there was species turnover along a spatial distance gradient.

6 Results and Discussion

This thesis is based on four studies, all focusing on spatial distribution patterns of Collembola and the relative contribution of structuring factors for these patterns. However, this is examined at different spatial scales and for different levels of biological organisation – from age classes and populations to communities.

We found that the relative contribution of structuring factors was, as always, context dependent. When there was a larger variation in environmental variables between samples, this imposed a strong environmental filtering, structuring the communities even at a very small spatial scale (**Paper I**). However, in the absence of such gradients, biotic interactions were more likely to be important for the spatial structuring (**Paper II**). This also seemed to be true to some extent even at large spatial scales, often considered to show more evidence of environmental filtering (Götzenberger et al. 2012), when keeping the environmental variation as low as possible (**Paper III**). In the regional study we found some evidence for biotic interactions structuring the communities, even though they also seemed to be affected by some environmental filtering. In addition, different age classes within the same species may show different spatial structuring and be affected to different degrees by environmental filtering and biotic interactions; the level of difference between age classes is suggested to depend on the level of social behaviour that the species display (**Paper IV**).

6.1 Diversity patterns at different scales

When comparing the three studies examining species diversity patterns (**Paper I-III**), about the same proportion of the site-diversity was found in each local community (sample-diversity) in all studies when considering species richness (46-59% beta, Table 6). However, for the Simpson diversity the range is larger,

with sample-diversity contributing 50-83% of the site-diversity (Table 6). The dominance in individual numbers of a few species in the pine forests, more pronounced in some of the sites of **Paper III** than in the site of **Paper II**, makes the variation between samples less important when including the abundance distribution (Simpson diversity) compared to when only using presence/absence data (species richness). This pattern is in line with previous studies of Collembola communities finding different patterns for richness and abundance based composition (Chen et al. 2014). Some of the smallest species of Collembola, euedaphic species without coloration or furca, often occur in very high abundances in the deeper part of the organic layers. These dominate many of our samples in number, but would not be as dominant if instead considering biomass. If the question of interest is with regard the Collembola communities' function as decomposers, the biomass could be of larger importance as it correlates more directly to the amount of detritus/fungi they consume (Petersen and Luxton 1982). However, as we were more interested in the interaction between individuals and resource utilisation (that could be linked to biomass but that not always are so), the number of individuals is considered a more appropriate estimate of the species influence in the community.

Table 6. *Species richness (SR), Simpson diversity (1-D), and Rao Q (multi-trait diversity) found at the site-scale of a few m^2 in the first three studies, and the proportional contribution of between sample beta-diversity (% beta). The Simpson index and Rao index are calculated with Jost-correction.*

	Species richness		Simpson diversity index		Rao functional diversity index	
	SR	% beta	1-D	% beta	Rao	% beta
Paper I	22	59	5.80	50	1.87	16
Paper II	29	51	5.87	34	1.25	2
Paper III	25	46	5.91	17	-	-

For Paper III the values given is the average from the 16 sites included, SR range from 23 to 31. The functional diversity was not calculated for each sample in this study (only site-level) and are therefore not available.

For both species richness and species diversity, and regardless of habitat, we found a considerable variation in species composition between samples at this small spatial scale, showing that to estimate the diversity of a Collembola community a large number of samples are needed (Fig. 13). As these studies only include a single habitat (i.e. organic layer of either salt marsh or pine forest floor) this indicates that if we are to determine the species diversity of a larger unit (i.e. a forest stand, including also the trees, mires etc.) the number of samples needed would be even larger. Many studies of Collembola in boreal

coniferous forests include 2-20 samples of similar size as the ones in our studies (see e.g. (Bååth et al. 1980, Persson et al. 1980, Huhta et al. 1986, Bengtsson and Rundgren 1988, Chernova and Kuznetsova 2000, Pflug and Wolters 2002, Ponge et al. 2003, Kuznetsova 2006, Malmström 2008, Siira-Pietikäinen and Haimi 2009). My results suggest that a large part of the total diversity may not be detected by such a small number of samples. For example, if considering the SR of the 100 samples in **Paper II** to be the full diversity of the forest floor in that area, at that time, sampling with the intensity of the regional study, i.e. 20 samples, would give 79-89% (24.4 ± 1.45) of the actual species richness. If we instead had taken only 5 samples 58-70% of species richness would have been observed, and to include 90% of the species richness, 32 samples would be needed.

However, the functional diversity (Rao) showed a lower variability in both habitat types (Table 6), with only 2% of the site-diversity depending on variation between sites in the mature pine forest and a little higher (16%) in the salt marsh with a higher variation in environmental conditions. This shows a high ecological redundancy in the local sample-communities, with species being exchanged between samples but replaced with other species possessing similar traits. This was especially true within the pine forest and could also be seen at the larger scale when comparing communities between sites (**Paper III**). The multi-trait Rao was 1.41 at the regional level and variation between sites (β-Rao) contributed to only 2% of the total diversity. If the functionality of the community is of main interest, that aspect of biodiversity might actually be captured by only a few samples in each site.
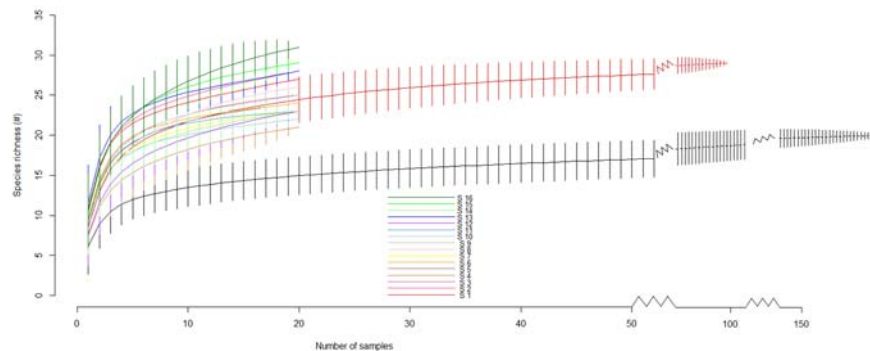

Figure 13. Coleman rarefaction curves of the sites in **Paper I** (black), **II** (red) and **III** (including only 20 samples/site). Some of the sites in **Paper III** seem to be close to an asymptote, while others are still increasing. It is obvious that 5 samples within one site would not capture the total species richness (at that moment) of a site adequately.

The most appropriate scale to study Collembola community composition on is hard to define, as it depends on which question and process we are interested in. Moreover, even when we know that we are interested in for example biotic interactions, it is still not determined at what scale most Collembola species interact. We detected spatial-autocorrelation in Collembola abundance at a meter-scale in all three systems studied (see **Paper I, II and IV**), indicating that the species and communities are spatially structured at that scale. Concerning environmental effects, it has been shown that responses to micro-climatic shifts mainly take place at a centimetre to decimetre scale for corticolous (living on bark) Collembola (Prinzing 2005). Collembola as a taxon are not restricted by isolation of a few kilometres to colonize pristine soils (Ingimarsdóttir et al. 2012), indicating that distance is not a major constraint for Collembola as a group. There still seems to be large differences between species, some limited to disperse actively with a high variability in this ability (Ponge et al. 2006, Auclerc et al. 2009, Malmström 2012), while others can take advantage of wind or water currents (Dunger et al. 2002, Hawes et al. 2007, Hawes et al. 2008). Therefore the species composition should be more influenced by distance than a simple measure of Collembola total abundance is. However, the total abundance of Collembola showed spatial autocorrelation at distances of < 5 meter (**Paper I-II**), indicating that within that scale we should define an interacting community. It might be that our samples are too small to be regarded as independent communities and our sites might include several interacting local communities. However, both scales are likely to capture interactions between some of the species and to be appropriate to detect effects of certain environmental constrains, as all communities are structured at multiple scales.

How decreased biodiversity affects natural systems has been studied from the perspectives of community stability (Macarthur 1955, Johnson et al. 1996) and ecosystem functioning (Lawton 1994, Hooper et al. 2005, Hector and Bagchi 2007). The process of lost diversity at regional or even global scale due to increased similarity between communities, i.e. decreased beta-diversity, has been called biotic homogenisation and is highlighted as a potential threat to some species groups and ecosystem services (Olden and Rooney 2006). Our regional study (**Paper III**) indicate that in Collembola communities there is a high redundancy in functional diversity and a large part of the regional diversity (measured by Simpson diversity or Rao diversity) is found within each local site (Simpson: 91% and Rao, 98-100% depending on trait considered). Still, the species richness depends largely on variation between local samples within sites. As we selected sites with a low variation in environmental variables between sites, we interpret our findings as a sign of

ecological redundancy. Hence, the lost species are replaced with other species with the same traits, and thereby keeping the functionality of the communities stable. However, this holds only true as long as the environmental variables remain quite constant. The effect of habitat fragmentation or changed climatic conditions could alter these findings. The patterns observed in this study could be used as a comparison for studies of e.g. homogenisation processes, indicating the "natural variation" within one habitat over a large geographical area.

6.2 Structuring factors of soil fauna communities

Soil ecosystems are species-rich and the surprisingly high species diversity despite an assumed low niche specialisation (low functional diversity) has been an enigma for soil ecologists for decades (Anderson 1975, Giller 1996, Maraun et al. 2003, Wardle 2006, Nielsen et al. 2010, Digel et al. 2014). In this thesis, I show that local communities of soil-dwelling Collembola probably are structured to a higher degree by niche partitioning than sometimes recognized. When minimizing environmental variation, examining stable mature pine forest communities, small-scale spatial variation in species and functional composition was best explained by spatial variables (**Paper II,** Fig 14) and each local-community (sample) included a larger diversity in measured traits than expected by random assembly (Fig 15B). This indicates that species interactions are structuring these Collembola communities at scales of a few meters. Competition as a structuring factor for soil fauna communities has been indicated in other recent studies (Caruso et al. 2013, Leinaas et al. 2015). In our study, coexisting species differentiated in *body length*, *sensory ability/active dispersal*, *soil moisture tolerance*, and *macro-habitat generality*. Soil-moisture tolerance and macro-habitat width are connected to the ability of the species to cope with different environmental conditions. Overdispersion in these traits at this small spatial scale suggests that strong competitors might exclude others based on resource utilisation. Previous studies have also found some support for larger differences among species in feeding preference and feeding guilds than often recognized (Jørgensen et al. 2003, Berg et al. 2004). A possible explanation for observed overdispersion is small-scale niche separation, due to competition in the past leading to divergent strategies (Connell 1980). Species with different traits could then co-exist in the same sample and soil layer, as they use different parts of the soil.

Examining factors structuring communities at the larger regional scale, when including communities from 16 mature pine forests across south-central Sweden (**Paper III**), indicates that at this scale, site-based communities are

structured both by environmental filtering and either dispersal limitation or biotic interactions (indicated by a large spatial effect) (Fig 14). However, the Collembola communities may mainly be structured on a smaller scale, making the structuring patterns weaker at this large scale. This is supported by the finding of similar amount of beta diversity between samples (β_L) as between sites (β_S) (about 50% of the diversity of either level when measured by SR). Most studies done for Collembola at this large scale examine changes across strong environmental gradients and find that this gradient is driving the community structure (Martins da Silva et al. 2012, Salmon and Ponge 2012, Martins da Silva et al. 2015). In contrast, by minimizing the variation in environmental variables we sought to examine the effect that dispersal limitation may have for these communities, and found that it is probably not a major driver. Many collembolan species are able to disperse long distances through passive dispersal, and dispersal limitation might act mainly at shorter distances among species with limited dispersal. Comparing the number of observed species in this study with the potential from a regional species pool showed that almost half of the total potential species richness was observed (50 out of 113 species, based on distribution maps by Fjellberg (1998, 2007). However, this includes all species and is not restricted to those that are likely to be found in similar forests. To get a better understanding of the processes determining the species composition at the regional scale, one way forward could be to determine the habitat-specific species pool (Zobel 2016) and compare observed functional diversity with expected from this larger species pool (rather than from the observed species pool of included sites). Data on the habitat specificity of all species within the area does exist but would need further verification before considered reliable. This approach would give information about species missing from our dataset, species that might have certain traits differing from the once observed in the sampled species. This potential difference between observed and excluded species would give further clues to what determines the coexistence of species.
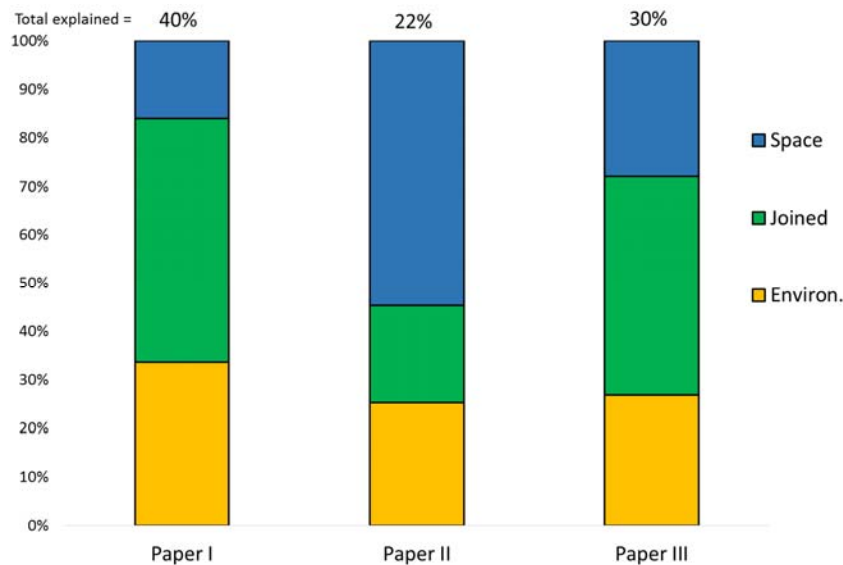
Figure 14. The spatially structured environment explained most of the variation in species composition in the salt marsh with a strong gradient in inundation (**Paper I**), while the pure spatial effect is large in the pine forest with homogeneous conditions (**Paper II**). Although the variation in local environment and climatic variables was kept at a minimum in the regional scale study (**Paper III**), almost equal amount of variation was explained by spatial and environmental factors. Percentages shown in the graph are the proportion of the explained variation that each part stands for, the proportion unexplained variation is given on top of each bar. The original analyses separated the environmental component into abiotic and biotic variables (**Paper II**) or local environmental and climate variables (**Paper III**). In this figure the proportion of explained variation has only been added together from the different fractions in respectively paper. This lead to a higher number of variables being included in the environmental component compared to the spatial component for **Paper II** and **III**, the relative contribution could therefore be skewed towards environmentally filtering.

However, there was some evidence for limiting similarity structuring also within these site-based communities, as they showed overdispersion in macro-habitat width (see **Paper III**). The ecological meaning of the identified 'limiting similarity filtering' at local and to some degree regional scale, needs further studies. For example, one could perform microcosm experiments with known composition of species with different traits and evaluate if they do compete for resources, as predicted.

When there is a large gradient in environmental conditions within the studied area, environmental filtering seem to be more important than the effect of species interactions (**Paper I**, Fig 15A). This has also been shown for mite communities at small spatial scales (Maass et al. 2015). In oribatid mite communities along a gradient of litter complexity structuring processes shifted from limiting similarity in simple sites to habitat filtering in sites with a higher

diversity in litter structure (Mori et al. 2015). The effect of environmental filtering can also vary in time, as influences of disturbances on the species composition are most pronounced shortly after the disturbance event, and then levels off as the disturbed sites are recolonized with species more sensitive to the disturbance but with different traits and competitive ability than the early colonizers (Bengtsson 2002, Russell and Griegel 2006). In a similar way as for testing the biotic filter, one could perform microcosm studies with communities exposed to different levels of the environmental variable proposed to be causing the difference in observed community trait diversities, to examine if species with certain traits react in the predicted way.
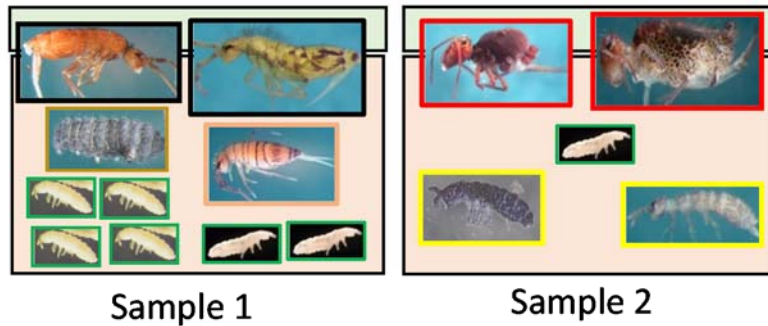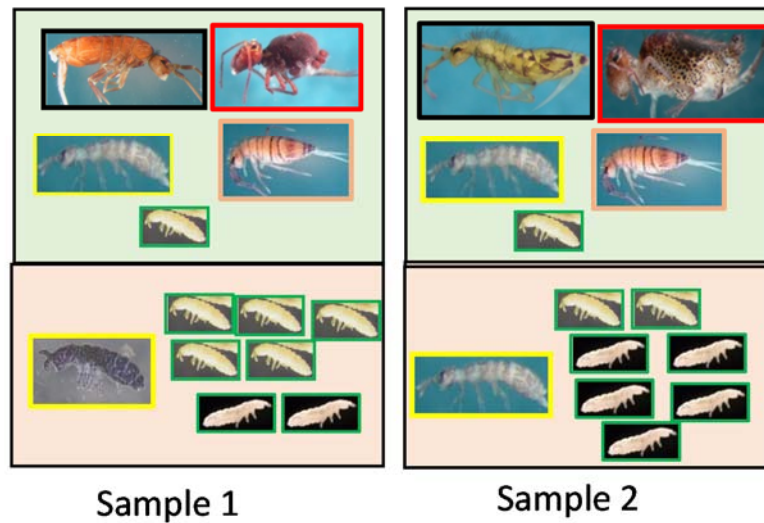
Figure 15. The local communities in **A,** the salt-marsh of **Paper I** are <u>underdispersed</u> in most traits, i.e. each sample include species with similar traits. The local communities of **B,** the mature pine forest in **Paper II** are <u>overdispersed</u> in several traits, i.e. coexisting species of each sample have more different trait values than expected. The green box represents the litter and the brown box the humus, of each sample. Communities within the sites of the regional study, including mature pine forests across south-central Sweden, show no strong structuring but are overdispersed in macro-habitat width and have a larger turnover in the trait regional distribution.

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In three of the papers (**II, III & IV**), vegetation composition was included in the analyses as one part of the environmental filtering. Vegetation (either species richness or composition) has previously been shown to structure Collembola communities in arctic conditions (Ingimarsdóttir et al. 2012, Bokhorst et al. 2014) and to differing degree also of other soil animals in temperate areas (Nielsen et al. 2012, Viketoft 2013). However, in our studies the vegetation composition (measured as p/a of species or species groups or as frequency of them) had none or only a minor influence compared to the other examined variables. The pine forests and the Arctic meadows in our studies were selected to have homogeneous ground vegetation, which likely influenced the low importance of the observed variations in vegetation. For vegetation composition to influence the Collembola community, larger differences between samples in the plants quality for the animals are needed (Wardle 2006, Leinaas et al. 2015).

6.3 Intra-specific variation – are age classes structured by the same factors?

Between different groups within a species, e.g. age classes or sexes, there might be larger differences in the importance of different structuring factors than considered in most community studies (Rudolf and Rasmussen 2013). In this thesis, I show that there can be substantial differences between age classes of springtail species in the spatial structuring at small spatial scales of < 5 m (**Paper IV**). Two coexisting species with clear aggregation patterns greatly differed in how much the environment contributes to affecting the species' spatial structure. In *Hypogastrura tullbergi*, a species with more pronounced social interactions (e.g. synchronized molting when kept in cultivation, (Birkemoe and Leinaas 2000) displayed more or less the same structuring pattern for all three age classes, spatial factors explained most of the variation in abundance (Fig. 16, left). A high level of variation explained by spatial factors and not linked to any of the other measured explanatory factors were interpreted as confirming the assumed high level of self-organized behaviour in this species. For *Folsomia qudrioculata*, known to show moderately aggregated distribution linked to patchy vegetation cover, the different age classes differed in structuring factors (Fig 16, right). We suggest that for some species, the common practice within community ecology to assume all individuals within a species responding similarly can be problematic (cf. Violle et al. 2012).
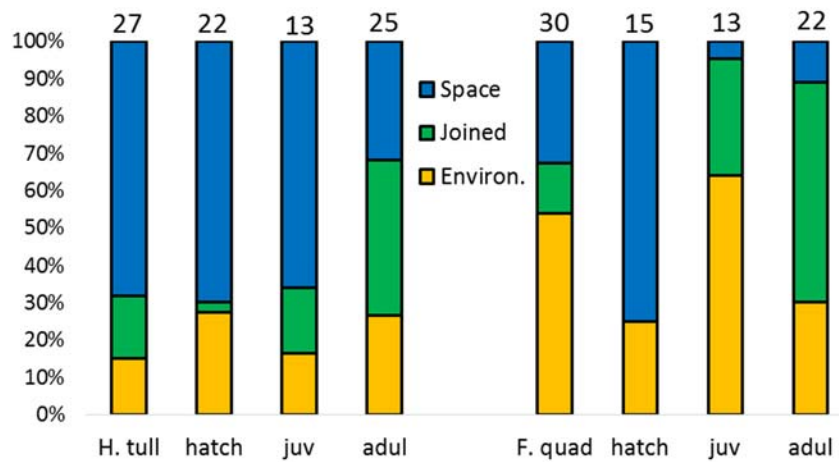
Figure 16. The proportion of explained variation in abundance of each species, or each age class of either species, are given on top of each bar. The bar show the relative contribution of either environmental variables (soil properties, vegetation composition and other Collembola), spatial variables, or the joint contribution of the two, i.e. spatially structured environment or covariation not possible to separate. The number of variables included in the environmental component is higher than the number of spatial variables, possibly skewing these results towards a larger influence of environment. A similar pattern is shown in **Paper IV** where the three components are shown separately.

6.4   Spatial patterns – in the context of biodiversity conservation

A long-standing debate in the conservation-literature has concerned SLOSS (single large or several small) and ways to design reserve systems and management to preserve the highest level of biodiversity (starting with Simberloff and Abele 1976). The answer to this question depends on how the biodiversity of concern is structured spatially. If most of the diversity at a regional level (gamma diversity, γ) can be found in each of the included communities (alpha diversity, α), i.e. if mean α ≈ γ, we could focus management on selected sites with the highest diversity or that are the least costly to preserve. However, if a large proportion of the regional diversity is due to a change in community composition between sites or turnover of species (i.e. a high beta diversity, β) we rather need to maintain the distribution of different habitats and site conditions across the whole region. In our study (**paper III**) we only observed approximately about 50% of the species richness in any one of our sites (Fig. 17). Compared to the known possible species pool for the whole region (not limited to pine forest species) of 113 species (Fjellberg 1998, 2007) we found about half of the species when pooling all sites. Considering the high proportion of rare species, it is likely that the full set of species for the habitat (mature pine forest) of the region (south-central

Sweden) was not captured by our study. Then, the actual proportion found in any site of the true regional SR, might be even lower. Even when only considering the species richness within a single habitat, within this very restricted habitat selection minimizing environmental variation, we need quite many sites to preserve the full species richness of the region. Increasing the number of habitats considered would probably add to the importance of beta-diversity. The result of this thesis suggest that also for small soil living animals such as Collembola, a large variation and number of sites are necessary for preserving the full species richness.
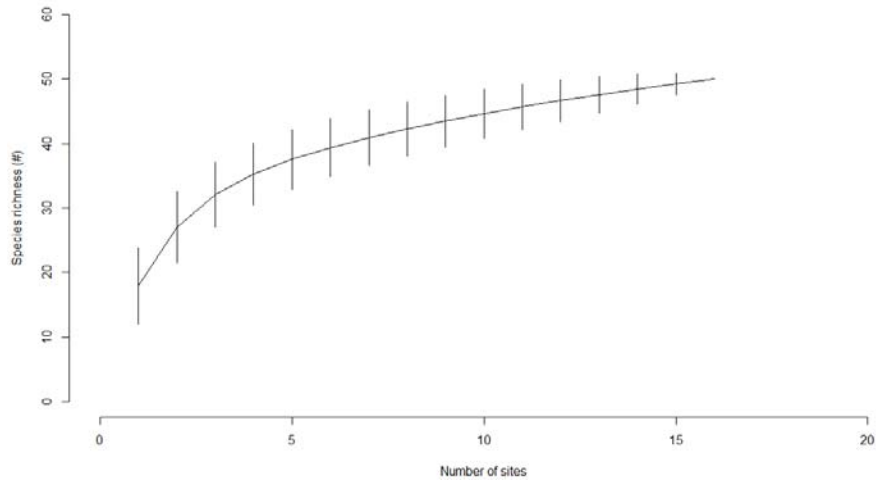
Figure 17. Coleman rarefaction curve of the number of observed species based on number of sites, from the regional study in pine forests across south-central Sweden (**Paper III**). The curve show that it has not reached an asymptote yet and the regional species richness is probably underestimated.

7 Conclusions

I studied two habitats with different disturbance regimes and with different variation in environmental variables of importance for the studied communities, a salt marsh with frequent flooding and a stable mature pine forest floor. I found that the relative contribution of spatial factors, indicating biotic interactions or dispersal limitation, for explaining small-scale species composition varied with the length of the environmental gradient. In the habitat that varied little in habitat quality or environmental variables (**Paper II**), the community appeared functionally homogeneous across the study site, indicated by a low turnover in functional diversity. In addition, local samples included species with a higher variation in traits than expected, i.e. local sample-communities showed overdispersion. In contrast, in the habitat with high environmental variability (disturbance frequency) (**Paper I**) I found larger variation in trait composition between samples, and that coexisting species possessed similar traits, i.e. local sample-communities showed underdispersion in traits. Further, when comparing several sites with similar environmental conditions (**Paper III**), site-based communities were very similar in functionality and diversity, although they differed in species composition. I therefore conclude that the length of the environmental gradient between samples or sites is of a higher importance than the length of spatial distance between the sites. This has been shown previously for plant communities (Willis et al. 2010) but is now also shown for the patterns of Collembola community structure.

A strong environmental gradient will probably always give evidence of underdispersion in traits and any biotic interactions also taking place will then not be considered as important, as they are not structuring the community as strongly. To enable biotic interactions to be detected by assembly null model methods, the environmental variation needs to be sufficiently small for limiting similarity processes to dominate. In **Papers II** and **III** we suggest that small-scale niche differentiations enables species to coexist within a small area, in

accordance with the results of experimental studies on increased small-scale heterogeneity of soils (Nielsen et al. 2010). The studies in this thesis, especially **Papers I and II**, highlight the benefit of trait-based analyses for reaching a higher mechanistic understanding of the factors creating observed diversity and composition patterns. Additionally, the predictability of functional diversity and composition is higher than for the species equivalent.

An assumption of the community studies in this thesis (**Paper I-III**), and of many similar trait-based studies today (see e.g. McGill et al. 2006, Weiher et al. 2011, Astor et al. 2014, Krasnov et al. 2015) is that we can use species-specific traits to describe the functional diversity of observed communities. This assumption is questioned in the last paper (**Paper IV**), where we found that each age class in one of the two examined species was structured in a different way (scale of spatial aggregation) and by different factors. This highlights the need for consideration of intra-specific variation in traits, as pointed out by Violle et al. (2012), but in this thesis also shown empirically for a group of animals in which all developmental stages have similar appearance and utilise the same macro-habitat.

Much of the nature conservation efforts of today are aimed at preserving ecological functions across large geographical areas (e.g. UNEP). For landscapes to maintain a high multifunctionallity (i.e. each area unit should deliver several functions) a higher biodiversity is needed than if only focusing on one function (Hector and Bagchi 2007, Gamfeldt et al. 2008). For this, we need to make estimations and decisions based on observed changes in, e.g., alpha- and beta-diversity. Depending on the specific system, the scale that these changes will take place will differ. To be able to manage both pests and threatened species in efficient ways, we need to understand which factors that are structuring populations and communities at different scales in many different kinds of systems. This thesis show that for collembolans there is not one factor that structures populations or communities, even when the scale are kept constant. Depending on the species specific properties and the gradient length of environmental variation the relative importance of spatial factors compared to environmental constrains differ.

In this thesis I show that using species-specific trait data can provide a better understanding of the mechanisms structuring community composition, although I also point out that it may give incorrect or less conclusive answers if age classes differ in structuring processes or trait values. To go further in studies of community composition mechanisms I suggest we need to focus both on small-scale variation in examined habitats to detect patterns of niche differentiation and to include variation in trait values between individuals and age classes.

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