Diversity patterns in coniferous forest springtail assemblages

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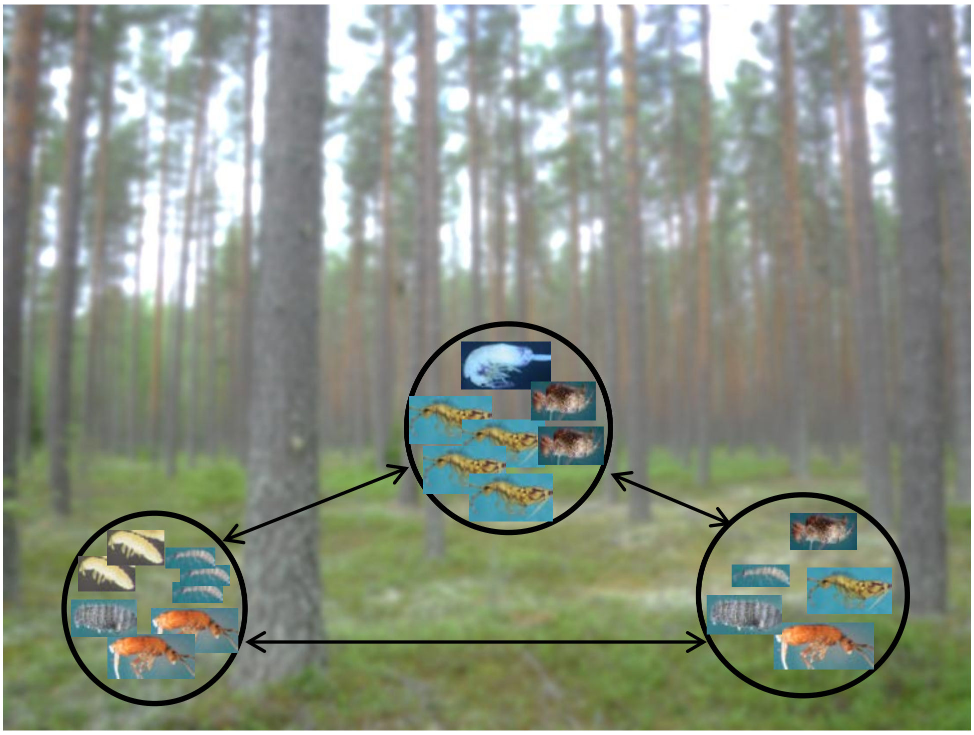

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Contents

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; Luck 2007) 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; Loreau *et al*. 2001; Hector & Bagchi 2007). When communities have reduced species richness they can become more vulnerable to disturbances such as for example invasions by alien species (Devin & Beisel 2008, Schmid *et al.* 2009). Retaining high species diversity can insure reliability in ecosystem functions and decrease the variability of communities (McGrady-Steed *et al.* 1997), as occasional species extinctions are buffered by remaining species (Naeem & Li 1997). To understand the interactions between biodiversity and other properties of ecosystems, it is necessary to get a full picture of the diversity patterns among different communities and assemblages. Depending on what system and which taxa are being under study the findings can be contrasting (Naeem *et al.* 1995; Filser 2002). It is therefore important to examine a wide range of communities to enable generalised conclusions.

Soil ecosystems are regarded to be species-rich and have been termed “the poor man’s rainforest” by e.g. Giller (1996). Soil organisms also play an important role for ecosystem functioning, predominantly for decomposition and nutrient cycling (Petersen & Luxton 1982; Verhoef & Brussaard 1990). Despite this, these diverse communities are relatively unknown, and the mechanisms for the supposedly high diversity are less well known than for many above-ground living animals, but see Nielsen *et al.* (2010) showing the importance of small-scale heterogeneity. One of the taxonomically and ecologically best known groups of soil animals are springtails (Collembola). Hence, this group is likely to be useful as a model community for studying diversity patterns in soil systems.

In this essay I will discuss biodiversity patterns among soil dwelling collembolan. After a brief description of ways to measure biodiversity and some general information about springtails I will present a literature review of studies from this area.

Biodiversity

Diversity can be measured in a number of ways and at several spatial and temporal scales. Species diversity, trait diversity and taxonomic distinctness are all measures describing biodiversity (Magurran 2004). Most diversity studies are done on a subset of all taxa within a location, when including organisms based on their taxonomical resemblance (within a restricted area in space and time) the subset is called an assemblage (Fauth *et al.* 1996). I will focus on the species diversity component of biodiversity and mainly include studies done on Collembola assemblages.

Diversity indices

There is no consensus about which indices to use when describing diversity, since there are different drawbacks and advantages with all of them (Peet 1971; Magurran 2004). What type of index to choose depends on what aspect of the diversity you would like to describe and how the data is gathered. Community composition, species richness and evenness are all ways of describing the species diversity and structure of communities (Magurran 2004). Often more than one of these measures should be given to show a more complete picture of how the assemblage or community is composed. If only for example a heterogeneity index, such as the

Simpson's diversity index, is given, it is impossible to tell whether the value is high or low because of the species richness or the dominance component.

Several different types of heterogeneity indices are used to describe the local species diversity of habitats; the measure most commonly used is the Shannon index (for example in Bengtsson & Rundgren 1988; Cassagne *et al.* 2004; Kuznetsova 2006; Lindberg & Bengtsson 2006) while the Simpson index has recently become more popular. It is recommended by e.g. Magurran (2003) and used by Malmström *et al.* (2009). Some definitions of measures used and commonly used formulas for calculating these indices are shown in Box 1.

Box 1. Some indices of diversity. Where p_i = the proportion of individuals found in the *i*th species, n_i = the number of individuals in the *i*th species; and N = the total number of individuals.

Richness: estimations of the number of species in a community.

Species richness: Number of taxonomic units (e.g. species) per a specified number of individuals or per a specified collection unit

Estimated richness: There are a number of ways to estimate the species richness in a community, without sampling all individuals in it. One of the first indices used for this is Chao's estimator S_{Chao1}, estimating the absolute number of species in a sample based on the number of rare species in a sample. $\boxed{S_{Chao1} = S_{obs} + F_1^2/2F_2}$
Where S_{obs} = number of species in the sample, F_1 = number of observed species represented by a single individual and F_2 = number of number of observed species represented by two individuals.

Rarefied richness: The number of species expected in a sample when back-calculated to a specific number of individuals or specific sample size (smaller than the maximum). Assumes random distribution.

Dominance: indices describing the community based both on the species richness and the distribution of the individuals among those species, i.e. taking into account how common the species are.

Shannon index: $\boxed{H' = - \sum p_i \ln p_i}$
Can also be calculated with $\log_2$ and $\log_{10}$. Recalculated as $e^{H'}$ the value can be interpreted as the number of species expected if all species had been equally common.

Simpson indices: $\boxed{D = \sum p_i^2}$ or $\boxed{D = \sum (n_i [n_i - 1])/(N[N-1])}$
This form is called Simpson index of dominance (D) and is interpreted as the probability that two randomly chosen individuals from a community belongs to the same species. Usually a Simpson index of diversity, expressed as 1-D or 1/D, is used instead to enable increase of value with increasing richness. Highly influenced by the most abundant species and has low sensitivity to species richness, after it exceeds 10 species.

Evenness: describing the relationship between number of individuals of different species, not considering the richness of the community.

Shannon evenness: The ration between the observed diversity and the maximum diversity, expressed as: $\boxed{J' = H' / \ln S}$ where $\ln S = H_{max}$, the value of the diversity index if all species would be equally abundant.

Simpson evenness: Ranges from 0 to 1 and is not related to the richness of the community sampled. $\boxed{E_{1/D} = (1/D)/S}$

How to measure diversity

The smallest sample unit used (the sample grain) and the extent of the study, are fundamental features when comparing diversity patterns (Crist *et al.* 2006). At what scale the species samples are taken often affect the outcome of the analyses (Tylianakis *et al*. 2006). Investigating scale-dependent patterns of species richness has been a focus from several different theoretical perspectives, for example species-area relationships (Crist *et al.* 2006) and landscape/context dependent responses of communities (Chust *et al.* 2003, Hendrickx *et al.* 2007). In 1960 Whittaker pointed to the link between spatial scale and diversity by partitioning the regional diversity, called gamma-diversity (γ), into an alpha- (α) and a beta- (β) component (gamma = alpha * beta or $\gamma = \alpha * \beta$). When measuring the diversity within a local area or habitat it is often termed the α-diversity and for a region or landscape the expression γ-diversity is used (Figure 1). The turnover of species between local areas is described by the β-diversity; this can also be expressed as the amount of differences between areas that is not explained by the mean α-diversity. Recently a lot of attention has been given to using additive partitioning (first suggested by Lande (1996)) instead to describe the relationship between gamma diversity and the components of alpha diversity and beta diversity (Crist *et al*. 2003; Crist *et al.* 2006). The benefit of this approach is that it gives the same unit for all three diversities (Lande, 1996), making it easier to compare different studies and to use the result in applied contexts (Gering *et al.* 2003, Anderson *et al.* 2011). There are others arguing for continuing to use multiplicative partitioning as it makes the alpha- and beta-components independent of each other (Baselga 2010), with each part describing a different property of the overall gamma diversity (Tuomisto 2010).

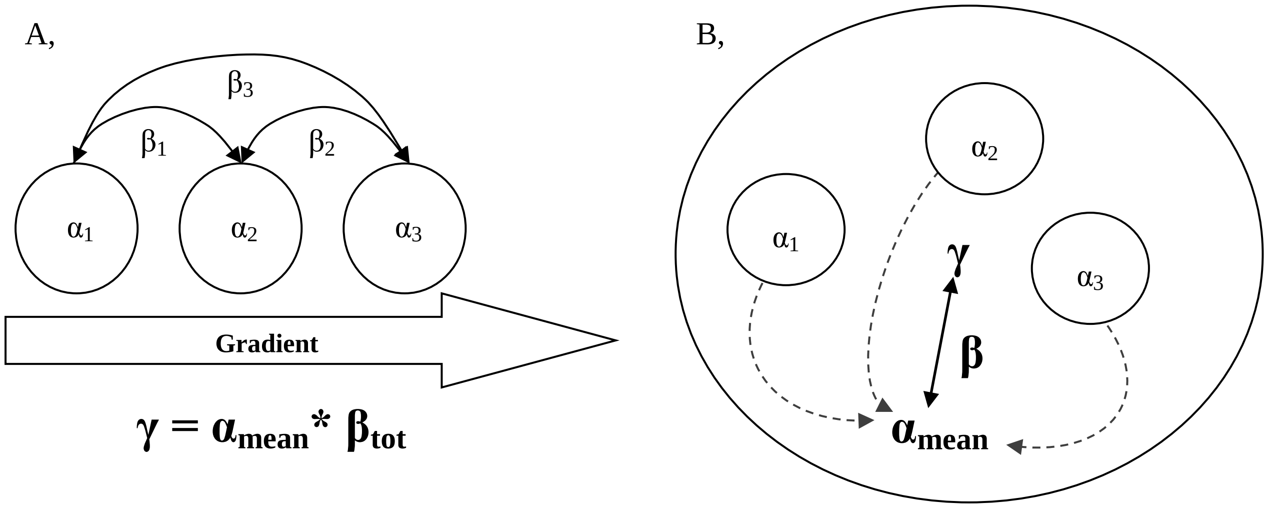

Figure 1. The relationship between α-, β- and γ-diversity, interpreted after the definition by A, Whittaker (1972) or B, Lande (1996).

Many aspects of the study design are important for the outcome of the observed diversity patterns. The species richness increases with the area sampled (Peet 1974), a phenomenon that most ecologists are aware of but not always acknowledges. Depending on the scale used for the study the result can vary considerably (Tylianakis *et al*. 2006). Also, the number of sampling occasions affects the richness observed with repetitive sampling of the same area leading to higher observed richness than including more sub samples at one occasion (Magurran 2004). Expanding the time period when samples are taken also increase the observed species richness as diurnal and seasonal variation will affect the species found (Magurran 2004).

Soil fauna and Collembola

Soil fauna and springtails are important for the nutrition turnover of soils (Verhoef & Brussaard 1990; Petersen 1994) and can also be used as indicators of environmental stress, as this often affect the species composition (Hågvar 1994; Rusek 1998). The importance of soil fauna for a number of ecosystem processes or functions (Persson *et al*. 1980; Petersen 1994) and the lack of knowledge about the structure and dynamics of soil communities has been brought to attention at a number of occasions (Bengtsson 1994; Giller 1996; Rusek 1998). Still, there are not much more general conclusions today than when these reviews were written. Research in soil ecology has increased and the knowledge about soil fauna communities improved, for example has the awareness of the importance of looking at several spatial scales increased (Ettema & Wardle, 2002). Still, there is much information about soil biota lacking (Coleman 2008). Collembola is generally considered indirectly affecting nutrient cycling through their effect on soil microbes (Hättenschwiler *et al*. 2005), but there are contrasting findings, and the specialisation and function of different Collembola species is not clear today (Filser 2002).

Collembolans

The Collembolan taxonomy is still not untangled and each year several new species, and sometimes even new subfamilies (Hopkin 1997), are discovered (Rusek 1998). The number of described species globally is today around 8000 (Bellinger *et al*. 2011), with an estimated total species richness close to 15000 (Coleman 2008); from the Nordic countries just over 400 species are reported (Fjellberg 2007). Most species live in the upper organic-dominated layers of the soil but some species inhabit the more mineral dominated horizons (Petersen & Luxton 1982), others can be found on the soil surface, in the vegetation or within several other more specialized habitats (Christiansen 1964). Collembolans can be found almost everywhere on earth and in the most extreme environments, from deserts to arctic tundra (Rusek 1998). They are often one of the most abundant arthropod groups in soils, rarely exceeded by others except the Acari (Petersen & Luxton 1982; Filser 2002). Much of the known Collembola biology and ecology is presented in the book “Biology of the Springtails” by Hopkin (1997).

The species richness of Collembola communities has been shown to vary considerably with time (Chernova & Kuznetsova 2000). Also the species composition of Collembola communities has been considered to have rather high temporal and also spatial variability (Berg & Bengtsson 2007; Siira-Pietikäinen & Haimi 2009). However, under stable environmental conditions the species composition can be considered predictable (Bengtsson 1994; Chernova & Kuznetsova 2000).

Variables affecting Collembolans

Collembolans are known to be affected by the moisture (Kaczmarek 1975; Huhta & Ojala 2006) and pH (Hågvar 1990; van Dijk *et al*. 2009) of soils, as well as temperature (Christiansen 1964; Wolters 1998), resource abundance (Takeda 1987) and detritus quality (Teuben & Smidt 1992; Rantalainen *et al*. 2004). Some studies indicate that niche partitioning is more pronounced among soil animals than previously believed (Kaczmarek 1975; Takeda 1987) which could be explained by variations in habitat-diversity on smaller scales (cm-scale) than usually considered (Nielsen *et al.* 2010). Other studies have found that species interactions could be important in determining the Collembola community structure (Hågvar 1990; Kuznetsova 2006). In a study comparing springtail communities in beech forests and spruce stands (Cassagne *et al.* 2004) the species with increased populations within the cultivated spruce stand were all widely distributed species, suggesting that these populations of generalistic species were released from competition of more specialized species.

Studies examining ecosystem functionality often consider springtails as pure fungivores (Hättenschwiler *et al*. 2005; van Dijk *et al.* 2009), although other studies have pointed out that most Collembola are opportunistic omnivores (Christiansen 1964; Filser 2002) with a considerable part of their diet potentially consisting of bacteria (Christiansen 1964; Petersen & Luxton 1982) or detritus (Petersen & Luxton 1982; Rusek 1998). They can even be predators and regulate the populations of other organisms (Gilmore & Potter 1993; Rusek 1998). Bödvarsson (1970) found that between 12% and 71% of specimens with gut content did not contain any fungal hyphae. The simplification of considering Collembola as solely consuming fungi can result in misinterpretations of their position in the soil food web and their importance for ecosystem functions of the soil system.

Studies focusing on the dispersal rate has found that of many Collembola species to be rather low (Ojala & Huhta 2001), especially for species connected to forest habitats (Ponge *et al*. 2006; Auclerc *et al.* 2009). Nevertheless, little is still known about the dispersal abilities of most species and there is a risk of underestimation when measuring migration on short time scales. Whether most disturbances affecting the species composition of human altered systems are operating at larger scales than re-colonization can compensate for, or not, is not known today. When all fauna is extinguished from a patch (defaunated) or the patch is allocated to another habitat, the species that are most abundant in the immediate surroundings will dominate, after enough time for colonization to take place (Rantalainen *et al*. 2004; Ponge *et al.* 2008). These studies indicate that one of the crucial factors determining the species composition in any local area is the species pool present in the surrounding landscape, the importance of a diverse species pool for the maintenance of functional groups have been argued previously when considering Collembola communities recovering after drought (Lindberg & Bengtsson 2005). A study looking at soil fauna responses to landscape heterogeneity found that the landscape variables within 48 ha around the site predicted the species similarity of Collembola communities more than the variables in the immediate surrounding and when using larger areas, up to a maximum of 5670 ha (Chust *et al.* 2003).

Species richness at a regional scale has been shown to decrease with increased latitude within temperate areas (Ulrich & Fiera 2009) as a consequence of climatic differences; especially the length of winter period seems to be responsible. This pattern is commonly seen among many other taxonomical groups as well, e.g. gammarids (Devin & Beisel 2008) and birds (Peet 1974). Landscape fragmentation and type of land-use have also been shown to affect both Collembola abundance and species richness at a landscape level (Ponge *et al*. 2003; Sousa *et al.* 2006), although the patterns differed to some extent between the countries studied.

Diversity studies of Collembola

What has been done so far?

Many of the studies including Collembola during the 1980's and 1990's were investigating nutrient cycling and metabolism of soil systems, with springtails as one of the functional groups of soil fauna (Persson *et al.* 1980; Petersen & Luxton 1982; Petersen 1994; Rusek 1998). Studies containing information about diversity patterns or species numbers of Collembolan assemblages have often a focus on how one or several environmental factors affect soil communities (e.g. Takeda 1987; Hågvar 1994). I will summarize some of the knowledge so far about species diversity of springtails in coniferous forests, with focus on Scandinavia but including studies from northern Europe and North-West Russia.

Research questions that have a high representation in the literature are how the species composition and abundance of Collembolans are affected by different types of pollution (Bengtsson & Rundgren 1988; Hågvar 1994; Lock *et al*. 2003; Kuznetsova 2009). Other commonly investigated areas concern their community response to forestry related disturbances; with harvest intensity (Ponge *et al.* 2003; Siira-Pietikäinen & Haimi 2009) clear-cut burning (Malmström *et al*. 2009) and fertilization (Haimi *et al*. 2000) as some focus areas. Acidification and liming has been shown to have strong effects on species composition of forest Collembolans in several studies, some of these findings are summarized in (Rusek 1998). With increased awareness of climate changes and the effect it can have on species extinction rates, studies incorporating climate variables such as draught (Lindberg *et al*. 2002; Lindberg & Bengtsson 2006) has gained interest.

A problem when preparing this review is that many studies do not considered the species identity, instead all Collembola are lumped together as one functional group and only the total abundance or biomass is given (for example Andrén & Lagerlöf 1983; Haimi *et al*. 2000; Wikars & Schimmel 2001; Atlegrim & Sjöberg 2003; Haimi *et al.* 2005). Other studies focus on the change in species composition of only the most abundant species in the community after a disturbance (Kuznetsova 2003; Haimi *et al.* 2005), disregarding the less common species. Since species richness is the focus of this essay, studies like these cannot be included.

Summarizing findings from comparable studies

I have analysed 26 data sets (from 16 papers) more explicitly (see Appendix A for more information), with regard to the total species richness of springtails as well as some diversity indices. The factors that can explain the difference in these measures are considered, and some general patterns are discussed. To be included in this synthesis a study had to fulfil several criteria: (1) **geography/location**, only studies conducted in the northern parts of Europe with a boreal-temperate climate were included and studies from islands were excluded (2) **sampling method**, the individuals should be soil dwelling, collected by extraction from soil cores (3) **habitat**, samples taken from undisturbed coniferous forest to minimize variations caused by environmental factors (4) **information given**, enough to determine the number of species and approximate sampling effort (5) **natural systems**, no microcosms or litter bag experiments were included.

Most studies were conducted in Sweden, Finland or Russia and the dominating habitat types were Scots pine forest or Norway spruce forest, although there were some examples from other countries and habitats as well (See Appendix A). The age of the forests studied varied from young stands of 20-50 years (Bååth *et al*. 1980; Huhta *et al*. 1986; Lindberg & Bengtsson 2006) to old growth forests with 100-300 year old trees (Ingelög *et al*. 1977; Chernova & Kuznetsova 2000; Malmström *et al*. 2008). Sampling occasion varied between studies, with late spring (May) and autumn (August-November) being most common. Whether the samples were taken the same month, once or twice a year (Bengtsson & Rundgren 1988; Chernova & Kuznetsova 2000; Kuznetsova 2009); only at one occasion (Ingelög *et al*. 1977; Bååth *et al.* 1980; Ponge *et al.* 2003) or monthly during a longer time period (Persson *et al.* 1980; Huhta *et al.* 1986), also varied considerably.

Results – comparable studies

The observed species richness reported ranged from 15 to 54 species, including all studies giving a value of total number of species. When only the local species richness (alpha diversity) was considered, the maximum value was 41 and the mean value from these studies was 27.4 (Table 1). This also includes values from studies summing all species observed from several sampling occasions. There was a tendency for studies conducted in Sweden

(Bengtsson & Rundgren 1988; Malmström *et al*. 2009) to report fewer species than studies from Russia and continental Europe (Ponge *et al.* 2003; Kuznetsova 2006) (Table 2).

Table 1. The mean values of diversity indices and abundance of the Collembola communities included in the literature review.

	Mean (±SE)	N
SR (total)	27.43 (1.80)	21
SR (mean)	18.49 (1.04)	10
H	2.08 (0.06)	13
1/D	5.79 (0.41)	13
Abundance	48237 (6343)	26

The arithmetic mean value (± standard error) is calculated from the given values in the literature according to appendix A, with 7-26 datasets included depending on availability (N = number of datasets used). SR (total) = the total number of species found within a habitat, SR (mean) = species richness of a habitat calculated as the mean for each sampling occasion / sample area, H = Shannon index, 1/D = the reciprocal of the Simpson's index and Abundance = the number of individuals per m^2.

Table. 2 Species richness (SR,) and abundance (individuals m^{-2}) of Collembola communities from three different regions, given as mean values for each region with standard error within brackets. N are the number of studies used to calculate each mean value.

	SWEDEN		RUSSIA & FINLAND		GERMANY & FRANCE	
	Mean (±SE)	**N**	**Mean (±SE)**	**N**	**Mean (±SE)**	**N**
SR (total)	22.4 (1.88)	12	36.1 (3.13)	8	38.0 (2.00)	3
Abundance	39863 (7596.9)	12	43334 (6631.4)	11	99711 (27804.6)	3

Among the studies included here, we can see a weak logarithmic relationship between abundance and species richness (Figure 2). The total Collembola abundance showed a range of 5000-85000 individuals m^{-2} for all but one study, in a French spruce forest an as high density as 154000 collembolans m^{-2} were recorded (Pflug & Wolters 2002). The mean value of close to 50000 individuals m^{-2} (Table 1) is in line with values given by most studies from coniferous forests (Petersen & Luxton 1982; Teuben & Smidt 1992).

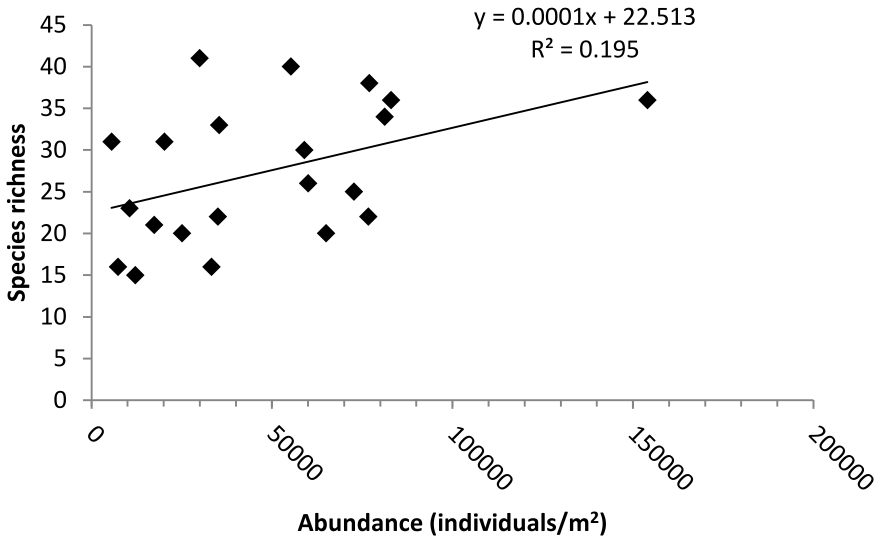

Figure 2. Fitted linear relation between total species richness (number of species) and abundance (number of individuals per square metre), with R^2adj = 0.153 (N = 21, P = 0.045).

It is probably more meaningful to look at the species richness as estimated by the mean value for the samples collected, since the effect of variation in sampling effort is minimized when repetitive sampling is standardized to a mean value. However, this measure was not commonly presented and therefore only values from 10 different data sets could be included. The range of the mean species richness per sample was 13-23 with an average of 18 (Table 1). When comparing the mean species richness with the total abundance of individuals within the area, no relationship could be detected (Figure 3).

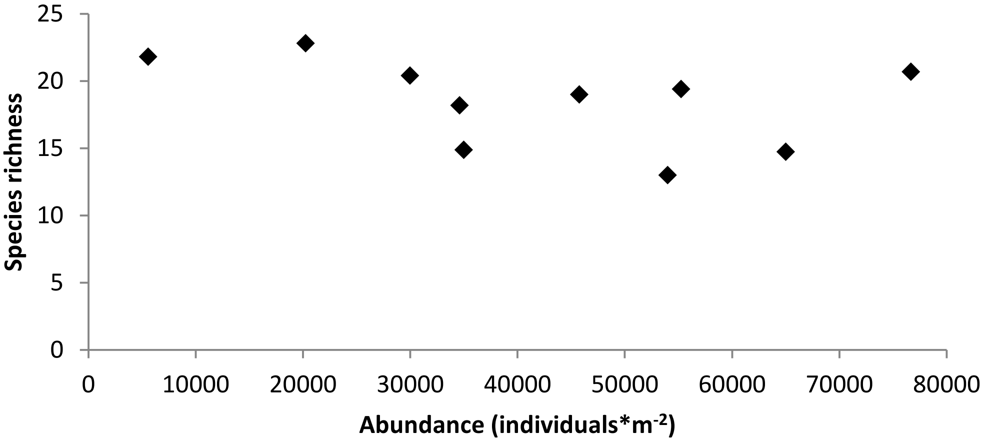

Figure 3. Species richness, as mean number of species found per sample, compared to estimated abundance of individuals from all samples included. No correlation was found (linear function gave R^2adj = -0.07, N=10, P=0.54).

In five of the studies included (eight data sets) the Shannon diversity index was given (Bengtsson & Rundgren 1988; Siira-Pietikäinen *et al.* 2001a; Siira-Pietikäinen *et al.* 2001b; Kuznetsova 2006; Lindberg & Bengtsson 2006) while only three papers gave the Simpson's index (Lindberg & Bengtsson 2006; Malmström *et al.* 2008; Malmström *et al.* 2009). Enough data to enable calculation of these two indices were however given in a number of papers, so the final summary includes 13 data sets for each index (Table 1 and Appendix A). Both indices showed some variability between studies, Shannon index ranging from 1.77 to 2.59 and the Simpson's index from 3.59 to 8.88.The highest values were reported from a young mixed coniferous stand in France (Ponge *et al.* 2003), lowest values were calculated from a slightly older mixed coniferous forest in southern Sweden (the *Vaccinum myrtillus* biotope of site VI in Bengtsson & Rundgren (1988)).

Discussion

Collembola communities has been studied in many systems and for a wide range of questions, still there is many unknown properties of their taxonomy, biology and ecology. Using several different studies to draw general conclusions can be useful when trying to get a broad picture of how this system is organised. The values of observed species richness from the studies analysed here, ranging from 15 to 54, showed similarities with the ones reported from other reviews. From several studies in forest soils, summarised in an article by Takeda (1987) there was also a rather limited range of observed species richness, neither exceeding 60 nor falling below 10 and most frequently falling within 20-35 species. This indicates that the studies used for my summary are representative for studies of Collembolans in forest systems.

There was some variability in the observed species richness between the studies, even if it was relatively small. Many factors can cause this variability and it is hard to determine which makes the greatest contribution. In a comparison of the total number of species reported from European countries (Ulrich & Fiera 2009), all Scandinavian countries (Norway, Iceland, Finland and Sweden) were found to have fewer species than expected from correlation with area and latitude, the reason behind this could not be determined. Some studies have found a gradient of both increasing species richness and abundance of Collembola from northern to southern latitudes, within temperate areas (Ulrich & Fiera 2009) and this can to some extent also be seen in this review, but inconclusive results have also been reported (Pflug & Wolters 2002).

Depending on the area sampled and number of repetitions in time, the observed species richness can differ substantially between studies (Crist *et al.* 2006) even when all other variables are being equal. Other aspects potentially influencing the results are differences in extraction method (Petersen & Luxton 1982; Huhta *et al.* 1986), habitat heterogeneity (Takeda 1987) and environmental variables (Chernova & Kuznetsova, 2000). Different studies, all claiming to investigate the habitat or alpha-diversity of an assemblage, can be collecting samples from a large range of area sizes, even when the organisms of interest are the same. The scale selected is depending on what the scientists designing the study see as the habitat or home range of the organisms.

Standardized methods needed

Most strikingly during this attempt to summarize and analyse the data on Collembola diversity was the lack of standardized methods of collecting, measuring and presenting data. It is essential that data from a large number of studies can be compared for general conclusion to be drawn, and for scientific theories to be validated. Giving information about the sampling effort is one of the fundamental points to making this possible. For the diversity patterns among Collembola, I have found a number of areas where I think standardized procedures would benefit the research area:

- Using a consistent area sampled for each extraction, even better would be to use a consistent volume of soil collected for each extraction but this is often hard to achieve.
- If possible, use a standardised soil depth (in many studies 10 cm is used, but in some areas this is not convenient). If not, the depth of each sample taken should be clearly stated.
- It is preferable to calculate the number of individuals per amount of organic material instead of only per sampled area (as this is the “niche space” used by the individuals).
- The diversity values should be given for each sampling occasion or alternatively as a mean value over several occasions, never as an accumulated value. Repetitive sampling will always give higher species richness (Magurran 2004) and the effect of time is then hard to distinguish from other factors.
- If possible the “raw data” as number of individuals found for each species in each sample (or block) should be given in an appendix. This would enable later studies to use this data more efficient and meta-analyses to be conducted.

Often there is no possibility of determining standardized methods since the focal questions of different studies need different study designs. It is then important that the paper gives clear description of what has been done, for later studies to be able to use the data.

- State if diversity indices given are standardized by individuals collected or by area sampled.
- Information about what scale has been under study, i.e. the extent of the area used for each diversity index (alfa-diversity, gamma-diversity etc.).
- The extraction method and classification system used.
- As the density distribution of springtail communities often has a seasonal variation (Kaczmarek 1975) the sampling period should be as constant as possible for each study. It is essential that the time of year and duration of the samplings is stated.

For comparisons of species richness or diversity indices to be meaningful it is essential that the measurement is standardized by either the number of individuals counted or by the sampling effort (Crist *et al.* 2003; Magurran 2004). Most studies I have encountered have done this by including the same number of samples (and most often the same volume of soil in each sample) taken from each area under investigation or from each treatment. This enables the authors to compare their different areas or treatments as the sampling effort is the same for all, but since the sampling effort (e.g. the number of samples, the volume and years sampled) is not constant when comparing between different studies, recalculations of the diversity measures are needed. When data is presented for each sample, or at least each plot and each sampling occasion, this is possible to do. Unfortunately most studies only present one mean value or even a single total estimate. Because of this it is hard to draw any clear conclusions from this literature survey.

Most studies report the sampling effort by stating the number of occasions sampling took place, number of sub-samples collected and the volume taken for each sub-sample, some also state the extraction method used and the amount of time for each extraction. Still there are several studies lacking this type of information. Even when the information is present it can be hard to determine if two studies have been done with comparable sampling effort. If the species richness or diversity index given is a mean value from all the samples, the number of samples used is not as relevant. However, when the absolute value (e.g. total number of species at a site, diversity index calculated from data collected over a long time) is used, as often is the case; the number of samples taken is crucial. Comparing a study using 10 samples from one area and occasion with a study using 50 samples from two areas and five years is not useful, we cannot tell if the higher number in the second study is because of higher sampling effort or if the area actually included more species. When comparing the species richness of different areas without knowing the raw-data of the study it is hard to interpret the results, the apparent difference in SR could be because of differences in sampling effort or different abundance distribution of the species (so that the species-sampling curve will not have the same slope) instead (Gotelli & Colewell 2001).

Findings

I found a weak correlation between the abundance (individual density) of Collembolans and the total species richness. When using the mean species richness this pattern could not be supported. It is not surprising that mean values are less dependent on density than are the total values, as using mean values buffer all extreme values that can otherwise be seen.

Data compiled from studies using more efficient extraction methods or that use a larger part of the soil (increased volume but the same area) will show a higher abundance of individuals, and have a higher probability of including rare species that are only present in a few of the samples. When summarizing all samples to a total species richness value, these rare species will increase the observed species richness substantially if different species are found in the different samples. When instead calculating a mean value of observed species number, rare species will only have a minor influence by increasing each sample value slightly.

The diversity indices used were the Shannon index (H´) and the reciprocal Simpson’s index (1/D), both showed rather stable values with ranges normally reported from many other Collembola communities (e.g. Takeda 1987, Chauvat *et al.* 2011). The study by Takeda (1987) presented the diversity as the Shannon index calculated with $\log_2$, so the values stated there are consistently a bit higher than they would be if calculated with the natural logarithm. The lowest values for both indices were found in a mixed coniferous forest in the south-west of Sweden (Bengtsson & Rundgren 1988); however, this study did not include the litter layer of the soil, which most other studies have done. Including the whole soil profile would probably increase the species richness of the samples, as the species composition show a high variability when comparing the lower humus layer and the uppermost litter layer (Berg 2010). The highest diversity measures came from France (Ponge *et al*. 2003), from a community with an unusually high population density.

Conclusions

Inconsistency in methods used between the different studies makes it hard to draw conclusions from this review. Some areas where standardized protocols or more thorough method descriptions would enable generalizations in the future are therefore pinpointed in the discussion section. For future work it would be beneficial if all studies looking at these questions would; use a consistent area or volume for each extraction (and clearly state the volume used), give diversity values for each sampling occasion or as a mean (never as an accumulated value) and state if the diversity indices are standardized by individuals or samples and at what spatial scale they are measured.

We can show that both species richness and diversity indices in these studies had values within the range reported from other systems, and studies from Sweden generally reported lower species richness than studies from more southern countries. The reason why the richness should be lower in northern countries is unclear and should make an interesting issue for future studies.

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Appendix A. Habitat information and diversity indices for 25 data-sets used in this literature review. Species richness values marked with * can be considered measured at the level of gamma-diversity. Forest habitats are classified according to dominant tree species; Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Mixed coniferous (any coniferous trees), Spruce (*Piceetum* spp.), Pine (*Pinetum* spp.). Geography: C = central, S = south, W = west, E = east, N = north.

Reference	Geography	Forest age	Forest habitat	SR (total)	α (mean)	abundance	H′	1/D
Bååth et al. 1980	Sweden (N)	23	Scots pine	16		33 270	2.16	7.29
Bengtsson & Rundgren 1988	Sweden (S-E)	60-80	Mixed coniferous	23		10 500	2.19	5.40
Bengtsson & Rundgren 1988	Sweden (S-E)	60-80	Mixed coniferous	21		17 400	2.09	5.01
Bengtsson & Rundgren 1988	Sweden (S-E)	60-80	Mixed coniferous	20		25 100	1.77	3.59
Bengtsson & Rundgren 1988	Sweden (S-E)	60-80	Mixed coniferous	15		12 100	1.85	4.19
Chernova & Kuznetsova 2000	Russia (C-W)	90	Spruce	31	22.8	20 248		
Chernova & Kuznetsova 2000	Russia (C-W)	110	Spruce	31	21.8	5 569		
Chernova & Kuznetsova 2000	Russia (C-W)	110	Pine (mesic bilberry)	40	19.4	55 256		
Chernova & Kuznetsova 2000	Russia (C-W)	50	Pine (xeric lichen)	41	20.4	29 995		
Huhta et al. 1986	Finland (S)	50	Scots pine	34		81 200		
Huhta et al. 1986	Finland (S)	30	Scots pine	25		72 700		
Ingelög et al. 1977	Sweden (C)	150-300	Scots pine	16		7 324	2.01	6.24
Kuznetsova 2006	Russia (C-W)	110	Spruce	54*	18.2	34 600	2.14	5.02
Kuznetsova 2009	Russia (S-E, European)	?	Mixed coniferous	33		35 333	2.28	6.74
Lindberg & Bengtsson 2006	Sweden (S-W)	30	Norway spruce	20	14.8	65 000	1.80	4.41
Malmström et al. 2008	Sweden (C-E)	100-120	Mixed coniferous	22	14.9	35 000		6.91
Malmström et al. 2009	Sweden (C-E)	115	Mixed coniferous	22	20.7	76 660		6.48
Persson et al. 1980	Sweden (C)	120	Scots pine	26		60 000		
Pflug & Wolters 2002	Sweden (N)	?	Norway spruce	38		77 000		
Pflug & Wolters 2002	Sweden (S)	?	Norway spruce	30		59 000		
Pflug & Wolters 2002	Germany	?	Norway spruce	36		83 000		
Pflug & Wolters 2002	France (N-C)	?	Norway spruce	36		154 000		
Ponge et al. 2003	France (C)	20-50	Mixed coniferous	42*		62 134	2.59	8.88
Siira-Pietikäinen & Haimi 2009	Finland (C)	100	Norway spruce	19*		42 000	1.97	5.13
Siira-Pietikäinen et al. 2001a	Finland (C)	100	Mixed coniferous		19	45 775	1.94	
Siira-Pietikäinen et al. 2001b	Finland (C)	100	Norway spruce		13	54 000	2.21	