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Age and level of self-organization affect the small-scale distribution of springtails (Collembola)

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Abstract. In studies of community assembly, species are often assumed to have similar spatial distributions and responses to the environment regardless of age or size. Under this assumption, it is possible to use species and species-level traits in community composition studies. Here, we test this assumption for two species of soil-living arthropods (springtails: Collembola) with direct development but assumed differences in self-organizing behavior. We expected that the species with more pronounced social interactions (*Hypogastrura tullbergi*) should be less influenced by environmental factors and species interactions across all age classes, than *Folsomia quadrioculata* that is not known to exhibit social behavior. We used variance partitioning to examine the relative contributions of soil variables, vegetation composition, and other Collembola, vs. spatial variables (as a proxy for intraspecific interactions, i.e., self-organization), on the distribution of the two species and three of their age classes. We show that two coexisting species with clear aggregation patterns greatly differ in how much the environment contributes to affecting the species' spatial structure. Local *F. quadrioculata* abundance was explained by different spatial and environmental variables depending on age class. In contrast, for *H. tullbergi,* spatial variables explained more of the abundance variation in all age classes. These differences have implications for the general predictability of changes in spatial structuring of species, as self-organized species may be less likely to respond to changes in environmental factors. Our results show that because age classes may be differentially affected by environmental conditions, caution should be taken when assuming that species traits can be applied to all developmental stages in a species.

Key words: age classes; biological interaction; Collembola; environmental constrain; intraspecific interaction; Moran's eigenvector map analysis; population ecology; self-organization; soil fauna; spatial configuration; variance partitioning.

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INTRODUCTION

Relating the spatial structure of species and populations to environmental conditions is a first step to understanding the factors underlying species distributions and community composition (Cottenie 2005). This is important for management of both threatened species and pest species (Lima et al. 2009). To develop theories of community organization, we need to describe patterns that can be compared across systems, and this needs to be done at all the scales that could influence the system (Levin 1992). Analyses of spatial community distribution patterns commonly view all conspecifics as behaving similarly and as having the same traits (McGill et al. 2006) a practice that has been criticized by Violle et al. (2012). Rudolf and Rasmussen (2013) added to this criticism by emphasizing the risk of missing important differences between life stages (i.e., age classes) when traits are used at the species level. This risk seems especially high in species where food or habitat requirements are dramatically different between juveniles and adults, as in many amphibians and most insects. However, species that live in the same macro-habitat throughout their lives might also differ in their spatial distribution with age: For example, in connection with reproduction, feeding preferences, drought or temperature tolerance, and strength of interspecific interactions may show age-specific differences (Gilbert et al. 1999, Amarasekare and Sifuentes 2012).

Most populations show spatial structuring within their habitat (Tilman and Kareiva 1997). However, the degree of spatial structuring and its causes vary greatly among species. Both biotic and abiotic factors, including environmental conditions, interactions with other species and resources, may cause individuals to aggregate in specific areas (Wiens 1976). Species may also show "self-organized" spatial structuring (sensu Parrish and Edelstein-Keshet 1999), that is, a behavior not driven by specific habitat or environmental factors, but caused by internal factors within a population, such as responses on odor (pheromones), vocal or visual stimuli. Reasons for aggregation, not directly related to environmental variables, include reducing the risk for predation (Hamilton 1971), increasing reproductive success (Levitan and Young 1995), or improved ability to detect favorable patches (Leinaas et al. 2015), as well as other benefits of social group living (Benoit et al. 2009, Vanthournout et al. 2016). The degree to which self-organized behavior influences the spatial distribution of individuals depends on its relative dominance over sensitivity to environmental factors. In addition to these current conditions, present distribution patterns may to varying degree also reflect past structuring processes owing to dispersal limitation. Effects of these drivers on spatial distribution will in many organisms be age dependent, and comparison of juveniles vs. adults may reveal important components of the dynamics.

Space can be described in several different ways, and there are a number of methods for performing spatial analyses (Tilman and Kareiva 1997, Borcard et al. 2004, Griffith and Peres-Neto 2006, Beale et al. 2010). One of the most promising to capture spatial patterns at a range of scales simultaneously are Moran's eigenvector map (MEM) analyses (Borcard et al. 2004, 2011). Spatial variables can be interpreted as representing either dispersal constrains or biotic interactions causing distinct spatial distribution patterns not connected to environmental variables (Cottenie 2005). Fine-scale spatial patterns are more likely to be connected to biotic interactions. These fine-scale patterns are possible to capture by MEM analyses, whereas larger scale descriptors such as trend surface analyses usually fail (Borcard et al. 2004).

The Collembola (springtails) are excellent study organisms to test whether the species level is a reliable unit for spatial distribution analyses. Their lower dispersal ability compared to, for example, flying insects makes their immediate presence at a site much less stochastic. And with direct development, with juveniles and reproducing adult stages usually co-occurring in the same habitat (Hopkin 1997), age dependency will be more subtle and general, than the extreme differences in organisms with metamorphosis and switching of resources between juveniles and adults. However, in some Collembola species, age classes show different preferences regarding food quality (Jensen et al. 2006). This indicates that there may be age-related differences in behavior that can result in different distribution patterns even in this taxon, which can have effect on, for example, the function of the species in the ecosystem (Sato and Watanabe 2014). In addition, dispersal might be more restricted in young individuals (Johnson and Wellington 1983), both as a function of smaller size, but also due to a restricted ability to use all micro habitats because of a higher sensitivity to drought (Leinaas and Fjellberg 1985, Hertzberg and Leinaas 1998). Since eggs are deposited in batches, and often by aggregating adults (Hopkin 1997), reduced dispersal of smaller stages may lead to age differences in aggregating tendency even without self-organization of the juveniles. As collembolans have an important ecosystem functioning through their role in decomposition and nutrient cycling of soils (Petersen 1994), and different species and life stages may have different level of impact, it is important to understand underlying mechanisms for their spatial distribution to be able to predict potential changes in functioning (Wardle 2006).

The tendency to aggregate is diverse and widespread among collembolan taxa (Hopkin 1997 and references therein), ranging from species where environmental variation explains most of the local-scale distribution patterns (Hertzberg et al. 1994, Chauvat et al. 2014), to species with advanced coordinated group behavior (Lyford 1975, Leinaas 1981). This species-specific difference in self-organizing behavior makes studies on species distribution patterns particularly interesting. Attraction by chemical communication has been shown repeatedly in many Collembola since the first documentations in the 1970s (Mertens and Bourgoignie 1977, Verhoef and Nagelkerke 1977, Verhoef et al. 1977). In many species, aggregation pheromones have been studied by the tendency to aggregate in experimental arenas when exposed to substances excreted or extracted from conspecifics (Verhoef and Nagelkerke 1977, Verhoef et al. 1977, Benoit et al. 2009). Under field conditions however, such effects may not necessarily be sufficiently strong to clearly influence the spatial structuring of populations. The distribution of individuals may then be mainly explained by variation in environmental conditions, such as resources and humidity (Hertzberg et al. 1994, Chauvat et al. 2014). On the other hand, there are also species with advanced group behavior based on volatile pheromones keeping the members of the group together even when moving around (Mertens and Bourgoignie 1977, Leinaas 1983).

In this study, we investigate the relative importance of environmental factors vs. self-organized intraspecific behavior for the small-scale spatial distribution of species and age classes within two collembolan species, *Hypogastrura tullbergi* (Schäffer) and *Folsomia quadrioculata* (Tullberg). Both species show clear tendencies to aggregate in high Arctic tundra meadows (Hertzberg et al. 1994, Sømme and Birkemoe 1999). Based on available information, we predicted that the underlying mechanisms for the spatial aggregation would differ between the two species. In patchy habitats, *F. quadrioculata* may be seen to aggregate where food conditions are favorable (Hertzberg et al. 1994), while its drought sensitivity may further affect its spatial distribution (Hertzberg and Leinaas 1998). However, no distinct group coordination has been observed in this or any related species in the field, nor during extensive lab studies of the species (Sengupta 2015). We therefore hypothesize that environmental constrains will be more important than self-organized aggregation in this species. In contrast, *H. tullbergi* belongs to a genus where advanced coordinated group behavior is common (Lyford 1975, Simon 1975, Mertens and Bourgoignie 1977, Leinaas 1983, Leinaas et al. 2015). Although less striking in *H. tullbergi* than many other species of the genus, we nevertheless hypothesized that the spatial structuring of this species would have a more distinct self-organized component than *F. quadrioculata.* We also expected the two species to differ in how age classes vary in their responses to environmental factors. Age-dependent effects of environmental stressors such as drought is hypothesized to be more pronounced in the sensitive *F. quadrioculata* (Hertzberg and Leinaas 1998). In contrast, all age stages appear much more robust in *H. tullbergi*, as even the smallest animals are seen active together with larger ones even in fairly dry habitats (H. P. Leinaas, *personal observation*). Hence, we hypothesized that potential difference in sensitivity between age classes in this species will not have consequences for spatial structuring between the age classes, as it is expected to be counteracted by the predicted self-organized aggregation.

Both species were studied within an area of ~6 m^2 in a homogeneous dry meadow in the high Arctic ecosystem on Svalbard; in this particular habitat, they are among the most dominant species of Collembola (Fjellberg 1994). We disentangled the relative effect of environmental constrains (soil properties, vegetation, and other Collembola) from that of spatial factors (self-organization, or dispersal limitations) by variance partitioning of the explained spatial variation in abundance of each species or age class. Additionally, we discuss the ecological relevance of the specific explanatory variables explaining the distribution of each species and age class and the potential consequences of using species-level data in analyses if age classes show different spatial structuring.

METHODS

Study species

To disentangle the relative effect of environmental and inter-species factors on spatial distribution of individuals, we selected two species living in the same habitat, but with contrasting degrees of grouping behavior.

Folsomia quadrioculata is a Holarctic species, distributed from the high Arctic to the warmer temperate zone (Potapov 2001). It occupies a wide range of habitat types and is often a numerically dominant species. It is a typical litter-dwelling (hemiedaphic) drought-sensitive species (Hertzberg and Leinaas 1998) and shows limited ability to move across open surfaces (Hertzberg et al. 1994). Adults reproduce throughout the season whenever temperature permits (Sengupta et al. 2017). In the Arctic, the life cycle typically extends over more than one year (Birkemoe and Sømme 1998), and in heterogeneous habitats, it may show strongly aggregated distribution (Hertzberg et al. 1994).

Hypogastrura tullbergi has a restricted circumpolar distribution, and in Europe, it is only found in the high Arctic islands of Svalbard (Fjellberg 1998). It is a surface-living (epi-edaphic) species, common in drier habitats of the tundra (Fjellberg 1998). On Svalbard, it appears to have a two-year life cycle, with reproduction concentrated to early summer (Birkemoe and Leinaas 1999). *Hypogastrura* spp. often exhibit distinct social interactions, and several species have advanced grouping behavior including coordinated activity and synchronization of life-history events within large groups of clustering individuals (Lyford 1975, Leinaas 1983). Although *H. tullbergi* has not been shown to have similar social behavior, it often aggregates in small groups (H. P. Leinaas, *personal observation*). Moreover, groups of *H. tullbergi* kept in culture tend to synchronize molting (Birkemoe and Leinaas 2000), which is a clear sign of social interaction (Leinaas 1983).

Study area and sampling design

To disentangle the relative effect of environmental and spatial factors on spatial distribution of individuals, it is useful to include species with contrasting life-history strategies and differing degrees of social behavior. For this, we selected a high Arctic meadow situated approximately 2 km southeast of Ny-Ålesund, Svalbard (78°55′ N, 11°59′ E). This meadow was characterized by a *Cassiope tetragona*/*Dryas octopetala* vegetation type with 50–100% coverage (Appendix S1: Fig. S1). The organic layer was situated on top of coarse stones and silt and varied between 0.5 and 6 cm in thickness.

An area of approximately 3.5 × 2 m was chosen, on the basis of a continuous cover of the dwarf-shrub *C. tetragona* (L.) D.Don (Arctic bell-heather). The scale was selected to capture the likely area that the focal species use and interact within during a season. The sampling area was divided into 35 squares, each 35 × 49 cm, and the squares sampled at two different intensities (i.e., number of 10-cm^2 soil cores taken). The exact measures of the sampled area (3.43 × 1.75 m) depended on the position of the randomly chosen intensive sampling squares. Cores were taken with a soil corer to include humus (0.5–6 cm) and the first 2 cm of mineral soil. Five squares were randomly chosen for intensive sampling to study small-scale aggregation of Collembola; here, 35 soil cores were taken in each square. The edges of adjacent cores were at least 3.5 cm apart. In the remaining 30 squares, one core was taken at the center of the square (Appendix S1: Fig. S2). This design resulted in a total of 205 soil cores taken.

Collembola sampling, determination, and measurement

The samples were collected during 3 d (4–6 August 1995). Each soil core was divided into one layer containing the vegetation and humus and one consisting of 2 cm of mineral soil, to later extract soil fauna from each layer. Collembola are primarily found in the organic layers, although some species are found in the upper part of the mineral soil (Petersen and Luxton 1982). The sampling of the upper most 2 cm is likely to include also all individuals from the mineral soil. During field sampling, an additional sample of the humus layer (7 × 7 cm) surrounding each soil core (Appendix S1: Fig. S2B) was collected by hand and stored in plastic bags for analysis of soil properties.

The collembolans were extracted within one week of field collection in a standard manner using a modified Macfadyen (1961) high-gradient extractor (Leinaas 1978). Four dominant species (>96% of total abundance) were identified

(Fjellberg 1980) and body lengths of all individuals within these measured in 0.06-mm intervals at 16× magnification in a stereo-microscope. The two most dominant species, *F. quadrioculata* and *H. tullbergi*, were classified into three size classes based on body length (measured from the base of anal spines to the tip of head). In these species of Collembola, body length is strongly correlated with age (Birkemoe and Sømme 1998). We assume that these size classes represent three age classes (following Birkemoe and Sømme [1998]): hatchlings (<0.40 mm), juveniles (0.40–0.89 or 0.40–0.82 mm, for *F. quadrioculata* and *H. tullbergi,* respectively), and adults (>0.89 or >0.82 mm). Maximum lengths for the species are 1.3 mm for *F. quadrioculata* and 1.5 mm for *H. tullbergi* (Fjellberg 1998, Potapov 2001). The abundances of the two species and the three age classes of each species were used as response variables.

Procedure for analysis

The analyzing procedure to test the main hypotheses of different structuring factors (1) between the two species and (2) between age classes within each species was done in eight steps:

1. Explanatory variables: Measure environmental variables grouped into: soil properties, vegetation composition, and other Collembola (see *Environmental variables*). And create spatial variables (MEM-variables, see *Spatial variables*).
2. Standardize/generalize data (for details see *Statistical analysis*).
3. Select spatial variables based on forward selection of eight response variables (three age classes and total number of each species) and environmental variables based on prior ecological knowledge (see *Spatial variables* and *Environmental variables* for details on each selection procedure).
4. Determine whether there is a spatially structured distribution that could be explained (see *Spatial autocorrelation of species abundances*).
5. Make multiple linear regression models assuming Gaussian distribution. Eight response variables × 4 explanatory components (three groups of environmental variables and one for spatial variables, see point one) = 32 models.
6. Create 32 multiple regression models with log link and assuming negative binomial distribution to handle skewness and overdispersion in the data. Compare the relative contribution of components between each paired Gaussian/negative binomial model (manually), to verify whether models assuming Gaussian distribution show approximately the same result. Variance partitioning must be done with a linear model with identity link and Gaussian distribution.
7. Combine the variables from all four components (from point five) into one explanatory dataset per response variable and make one multiple linear regression assuming Gaussian distribution for each (eight models).
8. Variance partitioning between components based on models from point five and seven.

The variance partitioning in step 8 disentangles the amount of explained variation that can be attributed to either spatial variables, soil properties, vegetation composition, or other Collembola. By comparing the relative importance of these structuring factors between the two species and between the three age classes of each species, we determine whether the spatial distribution of individuals within these groups is structured by the same or different factors.

Explanatory variables

*Environmental variables.—*To evaluate the importance of external factors for the spatial structuring of the two species (and each age class), we included three sets of external explanatory variables: (1) soil properties, (2) vegetation composition, and (3) other Collembola.

1. Springtails live mainly in the organic part of the soil (Hopkin 1997), and their abundance is affected by soil variables such as humidity and food quality (Kaczmarek 1975, Rantalainen et al. 2004). Soil properties were measured either in the humus of the soil-fauna sample or from the soil (humus) surrounding each sample core (Appendix S1: Fig. S2B) and consisted of five variables: thickness of humus layer, soil moisture, relative amount of soil organic matter, microbial activity, and amount of active fungal hyphae. The thickness of the humus layer in each soil core was

measured to the nearest 0.25 cm in the field. Soil moisture of the sampled humus cores with vegetation was measured and expressed as proportion (%) water loss after drying the samples at 105°C for 24 h, following extraction of Collembola. The soil collected around each soil core was stored at 2°C; within 1 week after sampling, it was homogenized and two subsamples were taken: 1.5 g for measurements of relative fungi content (1 g for ergosterol analysis, 0.5 g for dry weight) and 1.5 g for analyses of microbial activity. The relative amount of soil organic matter was measured by ignition loss (600°C in 2 h) of soil samples used to measure microbial activity, and given as g per g of dry weight (i.e., relative amount). Microbial activity was measured by relative CO_2-production (soil respiration) 10 d after sampling. This was determined by incubation of 1.5 g (wet weight) soil in a 50-mL hypodermic syringe (Terumo, Egham, Surrey, UK) with canola needles for 48 h. The needles were stuck into silicon to ensure no gas exchange with the environments. In all syringes, a Whatman glass microfiber filter (25 mm diameter) soaked in distilled water was added to prevent desiccation of the soil during the incubation period. The soil was incubated in darkness at approximately 16.5°C (max 17.6°C, min 15.6°C), that is, as stable a temperature as the local facilities allowed. The onset of incubation was delayed by 12 h from the first to the last sample. Gas samples were sucked into evacuated ($<10^{-4}$ MPa) 10-mL glass vials (10-CV, effective volume 12 mL; Chromacol, London, UK) with butyl rubber stoppers (type 20-B3P; Chromacol) covered with a layer of silicon, after 2, 24, and 48 h. The incubation volume in the syringe was reduced by 12 mL for each sample taken, the initial volume being 60 mL. Six syringes without soil but with a soaked glass microfiber filter were sampled along with the incubated soil and used a controls. The glass vials were stored and analyzed on a gas chromatograph according to Sitaula et al. (1992) within 5 months after sampling. Due to the long period of storage, an adjustment of CO_2 concentrations in the vials was necessary. Sitaula et al. (1992) found a linear relationship between days of storage and loss of CO_2 from glass vials (0.2% loss per day) over a period of 60 d. This relationship was extrapolated and used to adjust for the CO_2 concentration measured. The soil for fungal measurements was transferred to a deep-freezer straight after sorting and analyzed after 2 months. The amount of ergosterol was determined to estimate the biologically active fungal biomass (Seitz et al. 1977). A slightly modified version of the total neutral-extractable method by Davis and Lamar (1992) was used. One milliliter of hexane and 4 mL of 10% KOH in methanol were added to approximately 1 g of wet soil (0.5 g dry weight). The samples were sonicated for 15 min, left for 45 min to cool, and then refluxed at 70°C for 30 min. After cooling, 1 mL of H_2O and 2 mL of hexane were added. The samples were vortexed for 30 s and centrifuged, and the hexane phase was transferred to another test tube. Two milliliters of hexane was added to the old tubes, after which they were vortexed and centrifuged once more to yield as much of the extract as possible. The hexane was evaporated in a vacuum centrifuge at 40°C, and the samples were dissolved in methanol by heating at 40°C for 15 and 1-min sonicating. Prior to the HPLC analyses, the samples were stored in the freezer for a week and then filtered through a 0.5-mm Teflon syringe filter (Millex LCR-4; Millipore, Milford, Massachusetts, USA). The ergosterol analysis was carried out at the ecology department, University of Lund.

2. Vegetation composition (mosaic of plant species) has been shown to influence soil-fauna communities in the Arctic, even in relatively homogenous vegetation types (Coulson et al. 2003). We therefore collected data on vegetation composition and included this as presence/absence of six plant species or taxonomic groups: bryophytes, lichens, grasses, small polar willow (*Salix polaris* Wahlenb.), Arctic bell-heather (*C. tetragona*), and purple saxifrage (*Saxifraga oppositifolia* L.). This was done within all 7 × 7 cm squares prior to soil core sampling. Most vascular plants were identified to species level (only species occurring in more than five squares were

included in analyses) but for bryophytes, lichens, and grasses, no further distinction was made due to time constrains. Within these three groups, the variation in quality for the springtails was regarded as unimportant. For one of the clusters with 35 squares within a 35 × 49 cm areas, the data were lost but recovered from photographs taken of each square at the sampling date, and the composition showed the same pattern as for the rest of the data.

3. To determine whether competition from other Collembola could affect the population structure of the two focal species, the abundance of two other relatively abundant species (*Oligaphorura groenlandica* (Tullberg) and *Isotoma anglicana* (Lubbock)) and the abundance of the other focal species were included as explanatory variables. Additionally, the abundance of the remaining observed collembolans pooled together was included as a fourth explanatory variable.

*Spatial variables.—*The effect of physical distance between conspecifics (aggregation patterns) on their abundance was determined based on analyses of spatial autocorrelation patterns. Based on the Euclidean distance between samples, a new set of independent spatial variables describing different scales of spatial autocorrelation are created, that is, distance-based Moran's eigenvector map (dbMEM) variables (Borcard et al. 2011). Each dbMEM-variable represents an autocorrelation pattern at a given scale. These capture the spatial relation between all sampling points in the design without any information about relation to the response variables to be analyzed. These variables are subsequently used as explanatory variables in the variance partitioning used to disentangle the importance of spatial vs. environmental drivers.

Moran's eigenvector map analyses are suitable for testing spatial patterns at all possible scales within the sampled area (Borcard et al. 2004). We determined a truncation threshold of 35 cm using "spantree" in the R package vegan (Oksanen et al. 2015) and used the package PCNM to first create a distance matrix based on Euclidean distances and then compute the MEM-variables based on principal coordinate analysis (Legendre et al. 2012). We used the definition by Borcard et al. (2004), and only included eigenvectors with positive spatial autocorrelation, which gave a total of 30 significant MEM-variables. There was a spatial trend in most of our response variables (*x*- and *y*-coordinates), but for all but one variable, the selected MEM model explained all variation (no effect of pure trend) and therefore we excluded the trend in the final subset used as the component "spatial variables." For one of the response variables (juvenile *F. quadrioculata*), the full MEM model could not explain any variation significantly. As there was, however, a significant trend in the data, we used the *x*- and *y*-coordinates of samples in the forward selection to represent spatial variables when explaining the abundance variation of this group.

Statistical analysis

Collembola abundance data from the mineral soil and humus were pooled before the analyses. The abundance of the two focal species, or their age classes, was used as response variables. As the sampled area was identical for all soil cores, the actual values were used. Samples with missing environmental variables (due to loss of data) were removed from analyses, and this gave a total number of 197 samples (Appendix S1: Fig. S2A).

To allow comparisons between regressions, all explanatory variables were centered and the response abundance data were standardized prior to analysis (Schielzeth 2010). There was no strong correlation between the variables within or between any of the four components: soil properties, vegetation composition, other Collembola, and spatial variables (Pearson $r < 0.5$; Appendix S1: Table S1). All analyses mentioned in the methods were done in R version 3.3.1 (R Core Team 2016), specific packages given for each analysis.

*Spatial autocorrelation of species abundances.—*To detect whether the focal species had a spatially structured distribution, the total abundance data for each species were tested for spatial autocorrelations. For this purpose, we calculated a *z*-score based on the difference in observed and expected Moran's *I* (O'Sullivan and Unwin 2010), using the Spatial Autocorrelation (Morans *I*) tool in ArcMap (ESRI 2014). Correlograms were constructed for visualization, using R packages pgirmess (Giraudoux 2015) and spdep (Bivand 2015), with Moran's *I* statistics and two-sided autocorrelation tests.

*Variance partitioning.—*To determine the relative contribution of the four components of explanatory variables (soil properties, vegetation composition, other Collembola, and spatial variables), we performed multiple linear regressions, using function lm in R with Gaussian distribution. The influence of the explanatory components on the abundance of one focal group at a time was analyzed by including (1) all components together ("total model"), (2) one component at a time ("single model"), and (3) one as explanatory and the three other as co-variables ("pure effect"), in the regressions. The amount of variability explained by each component was assessed through variance partitioning based on sum of squares decomposition and compared with the residuals from each regression (Legendre and Legendre 1998; using varpart from the package vegan, with the lm-function), after Borcard et al. (2011). This enabled us to detect the proportion explained by the "pure effect" of one of the components, that is, what can only be explained by that set of explanatory variables and not by any of the others, and how much of the variation that was explained by the joint effect of two or more variables.

The environmental components (soil properties, other Collembola, and vegetation composition) consisted of 4–6 variables each (see *Environmental variables* under *Explenatory variables* section and Appendix S2: Tables S1–S3) and were selected based on prior knowledge and availability of data. To minimize the risk of overestimation of the impact of the MEM values compared to the other components in variation partitioning, sometimes considered as a problem with MEM analyses (Gilbert and Bennett 2010), we determined the variables to be included in the final model by using forward selection (double stopping criteria, after (Blanchet et al. 2008), using package "packfor" in R (Dray et al. 2013). To use a selection procedure (Akaike's information criterion-based or *P*-value-based) to only include a subset of all created MEM-variables is a standard procedure in variation partitioning between spatial and environmental components (Borcard et al. 2011). This resulted in 1–5 MEM-variables for each spatial model found to explain the variation in the response variables (further details in Appendix S1: page 3 and Appendix S2: Figs S1–S2).

There was no strong correlation between the variables within or between any of the four components (Pearson $r < 0.5$; Appendix S1: Table S1). Differences between species and age classes were estimated by comparing the proportion of variation explained by the different fractions in the variation partitioning.

*Negative binomial regressions.—*Because the data for most age classes did not meet the assumption of Gaussian (normal) distribution and included many zeros, we also analyzed the data with negative binomial regressions (see Appendix S3 for method details and results). However, these regressions do not permit variation partitioning to be performed. We compared the results from the two different regression methods (Gaussian and negative binomial) to determine whether they showed similar results, as an evaluation of whether the result from the variation partitioning (based on Gaussian regressions) could be trusted. Since the data did not meet the assumption of Gaussian distribution, the effect size and significance level of each variable in the regressions cannot be compared with those found in other studies (Legendre and Legendre 2012). For this, the results from the negative binomial regressions should be used. However, the results from the variance partitioning are valid for comparisons between species and age classes within the study.

Results

We found 6834 collembolan individuals in our study, of which 4089 were *Folsomia quadrioculata* and 1830 *Hypogastrura tullbergi*. The remaining 915 individuals belonged to other species, of which the most common were *Oligaphorura groenlandica* (446 individuals) and *Isotoma anglicana* (197 individuals).

In *F. quadrioculata,* the juveniles were quantitatively dominant over the other age classes, and they were mainly found in the humus (2316 individuals) but still abundant in the mineral soil (509 individuals; Fig. 1). The other two age classes occurred in similar proportions in the humus and mineral soil (hatchlings: 283 vs. 147 individuals, and adults: 411 vs. 329 individuals, respectively). By contrast, *H. tullbergi* occurred almost exclusively in the humus, with only three individuals found in the mineral soil (Fig. 1). Also for this species, the juveniles had the highest overall abundance (852 individuals), but the distribution was more even between the three age classes (393 hatchlings and 526 adults).

Both *F. quadrioculata* and especially *H. tullbergi* showed aggregated spatial patterns as expected (z-score 3.29 and 12.68, respectively, $P < 0.001$) with weak positive spatial autocorrelations at short distances (up to 60 or 40 cm, respectively; Fig. 2). In other words, both species had a moderately clumped distribution with higher abundance in certain parts of the sampled area. The abundance densities varied from 1000 to 85,000 ind/m^2 for *F. quadrioculata* (average 20,000 ind/m^2) and from 0 to 54,000 ind/m^2 for *H. tullbergi* (average 9000 ind/m^2). The strongest positive autocorrelation of *F. quadrioculata* was found at 60 cm and an even stronger negative autocorrelation appeared at 2 m (Fig. 2A). *Hypogastrura tullbergi* had the strongest autocorrelation at the shortest distance class (20 cm; Fig. 2B). This, together with the higher z-score, indicates that *H. tullbergi* had a more pronounced clumped distribution.

Factors structuring spatial patterns of age classes

In *F. quadrioculata*, a larger part of the variation of abundance could be explained in adults (32%) than in hatchlings (15%) or juveniles (13%; Table 1A). Both soil properties and other Collembola (especially the spatially structured soil properties or other Collembola, that is, the joint contribution with MEM-variables) explained large proportions of the variation in adult abundance, but none in the hatchlings. Variation in juvenile abundances was mostly explained by other Collembola (Table 1A, Fig. 3A). In contrast, the pure spatial variables explained most of the variation in the abundance of hatchlings, but none in the adults (Table 1A, Fig. 3A). The exact variables from each component that contributed to the explained variation can be found in Appendix S2:

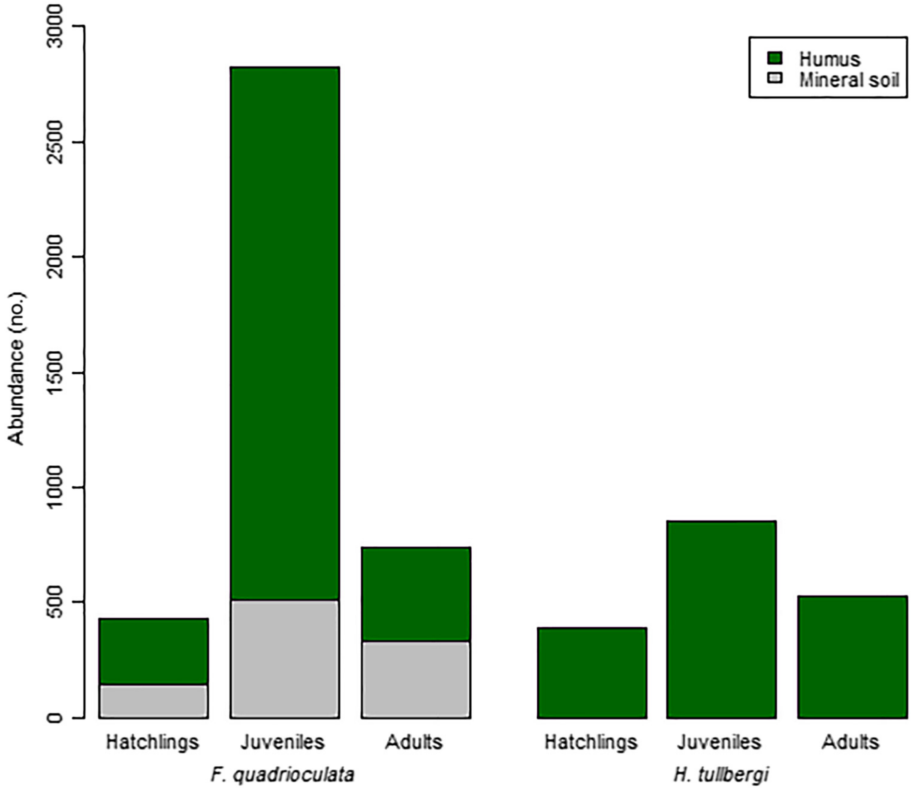

Fig. 1. Abundance of the three age classes of *Folsomia quadrioculata* and *Hypogastrura tullbergi*, divided between humus (including vegetation) and mineral soil, including only the 197 samples used in analyses.

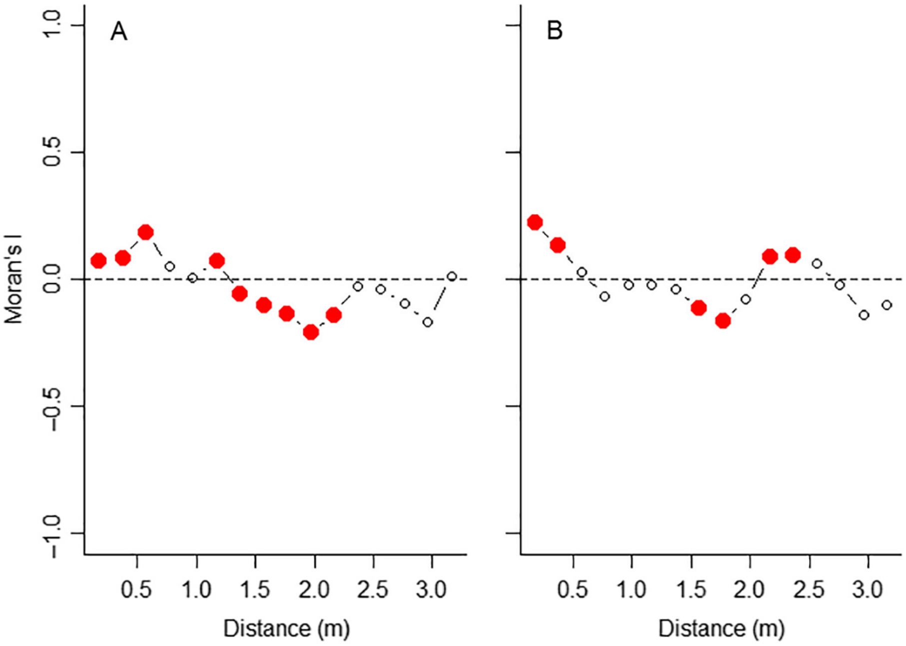

Fig. 2. Both focal species had moderately clumped distributions with correlated abundances at short distances, as shown by correlograms with the distances of spatial autocorrelation in abundance of (A) *Folsomia quadrioculata* and (B) *Hypogastrura tullbergi*. Distance classes of 20 cm, filled (red) dots indicate significant autocorrelation (two-sided Moran's test, $P < 0.05$).

Table 1. Variation explained by each of four explanatory components for the abundance of hatchlings, juveniles, and adults for (A) *Folsomia quadrioculata* and (B) *Hypogastrura tullbergi* based on multiple linear regression models assuming Gaussian distribution.

	Hatchlings		Juveniles		Adults	
Characteristic	Single model	Pure effect	Single model	Pure effect	Single model	Pure effect
(A) *F. quadrioculata*						
Soil properties	−0.001 (5, 192)	−0.015 (5, 176)	0.031 (5, 192)*	−0.002 (5, 180)	0.134 (5, 192)***	0.013 (5, 176)
Other Collembola	0.014 (4, 193)	0.007 (4, 176)	0.108 (4, 193)***	0.083 (4, 180)***	0.249 (4, 193)***	0.091 (4, 176)***
Vegetation	0.018 (6, 191)	0.038 (6, 176)*	−0.002 (6, 191)	−0.007 (6, 180)	0.050 (6, 191)*	0.013 (6, 176)
Spatial	0.107 (5, 192)***	0.144 (5, 176)***	0.041 (2, 195)**	0.006 (1, 180)	0.153 (5, 192)***	0.024 (5, 176)
Total model	0.154 (20, 177)***	–	0.128 (16, 181)***	–	0.315 (20, 177)***	–
(B) *H. tullbergi*						
Soil properties	−0.001 (5, 192)	0.026 (5, 179)*	−0.194 (5, 192)	−0.013 (5, 179)	0.014 (5, 192)	−0.002 (5, 178)
Other Collembola	0.003 (4, 193)	−0.003 (4, 179)	0.011 (4, 193)	−0.003 (4, 179)	0.040 (4, 193)*	0.052 (4, 178)**
Vegetation	0.044 (6, 191)*	0.044 (6, 179)*	0.064 (6, 191)**	0.032 (6, 179)	0.115 (6, 191)***	0.035 (6, 178)*
Spatial	0.160 (2, 195)***	0.154 (2, 179)***	0.105 (2, 195)***	0.083 (2, 179)***	0.182 (3, 194)***	0.079 (3, 178)***
Total model	0.221 (17, 180)***	–	0.125 (17, 180)***	–	0.248 (18, 179)***	–

Notes: Values are the adjusted R^2 values (df of model and residual given within parentheses). Single model, including only the variables from one component. Pure effect, also including the other components as co-variables. Total model includes all variables from the four components together. Detailed results can be found in Appendix S2: Tables S1–S5. Total number of samples = 197.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

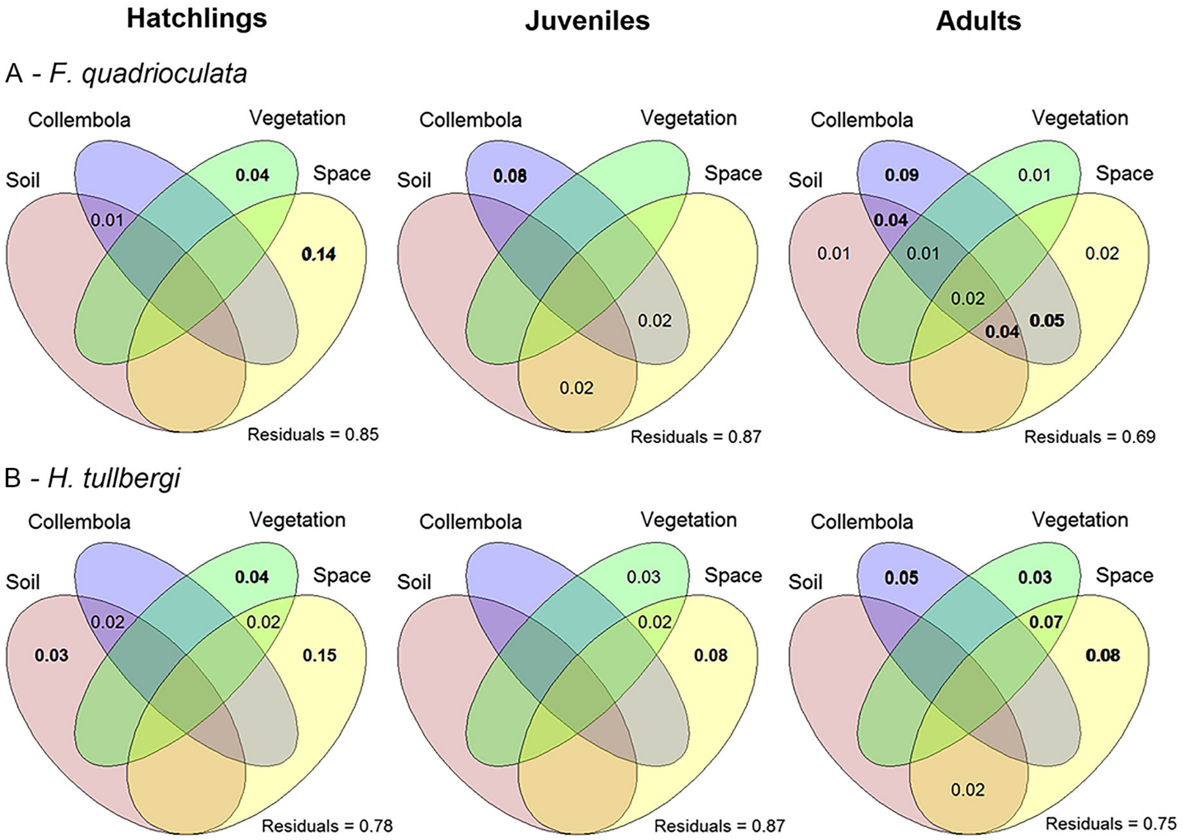

Fig. 3. Variation in abundance of (A) *Folsomia quadrioculata* and (B) *Hypogastrura tullbergi* for three age classes, explained by the four components: soil properties, abundance of other Collembola, vegetation composition, and spatial autocorrelation. The proportion of variation explained by each fraction (adjR^2-values) is written in bold to indicate significance ($P < 0.05$). Overlapping areas represent joint contribution by two or more components (from variance partitioning); non-overlapping parts are the pure effect of each component when the three others are included as co-variables. Fields without a number are not contributing to the explained variation (adj$R^2 < 0.01$, NS) and can have negative adjR^2-values. Colors are used to separate the components.

Tables S1–S5, most contributing variables corresponded to the ones found for the total abundance (Table 3) with some minor differences between the age classes. In *H. tullbergi*, almost the same proportion of the variation was explained in hatchlings as in adults and in total abundance (≈25%), but for juveniles, only 13% was explained (Table 1B). For all age classes, the spatial variables alone (when removing the effect of other variables, that is, pure model as compared to single model) explained most of the variation. The spatial variables are interpreted as self-organization and thus indicate that social interactions were the strongest structuring factor for all stages of *H. tullbergi*. For adults, the joint spatial and vegetation fraction (i.e., spatially structured vegetation) contributed almost as much to explaining the variation (Table 1B, Fig. 3B).

Factors structuring spatial abundance distribution of species

The explanatory models described the abundance distribution of the two species equally well, and the proportion of explained variation in abundance was 30% for *F. quadrioculata* and 27% for *H. tullbergi*. However, the two species differed in the factors explaining this variation. Soil properties, other Collembola species, vegetation composition, and spatial variables all significantly contributed to variation in the abundance of *F. quadrioculata*,

Table 2. The proportions of variation explained by each of the four explanatory components for the total abundance of the two species *Folsomia quadrioculata* and *Hypogastrura tullbergi*.

	F. quadrioculata		*H. tullbergi*	
Characteristic	Single model	Pure effect	Single model	Pure effect
Soil properties	0.07 (5, 192)**	0.01 (5, 177)	−0.02 (5, 192)	−0.01 (5, 177)
Other Collembola	0.17 (4, 193)***	0.12 (4, 177)***	0.01 (4, 193)	0.01 (4, 177)
Vegetation	0.02 (6, 191)	0.03 (6, 177)*	0.09 (6, 191)***	0.03 (6, 177)
Spatial (MEM)	0.14 (4, 193)***	0.10 (4, 177)***	0.23 (4, 193)***	0.19 (4, 177)***
Total model	0.30 (19, 178)***	–	0.27 (19, 178)***	–

Notes: MEM, Moran's eigenvector map. Values are the adjusted R^2 values (df of model, residual given within parentheses), giving the total variation explained by each model from multiple regression (single model) and the variation explained when the other components are included as co-variables (pure effect). All different fractions from variation partitioning are shown in Fig. 4. "Total model" includes all variables from the four components together. For all, multiple linear regression models assuming Gaussian distribution are used. Total number of samples = 197.

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

although all effects were not significant when accounting for the variation in the other components and the vegetation only explained the variation when accounting for the others (single model vs. pure effect in Table 2, Fig. 4A). In contrast, spatial variables explained the largest part of the variation in abundance of *H. tullbergi*, with an additional effect of vegetation (Table 2, Fig. 4B). Pure space accounted for 70% of the total explained variation (0.19 out of 0.27 in Table 2), indicating that spatial effects not correlated with variation in environmental variables, therefore interpreted as intraspecific interactions (self-organization), were most important for structuring the abundance distribution of *H. tullbergi*.

Of the soil variables, humus volume had a positive effect and relative amount of organic material a negative effect on the abundance of *F. quadrioculata* (multiple regression with all five soil properties: adjR^2 = 0.074, $P < 0.001$; Table 3A), while there was no effect of any of the soil properties on *H. tullbergi* (adjR^2 = −0.02, P = 0.87).

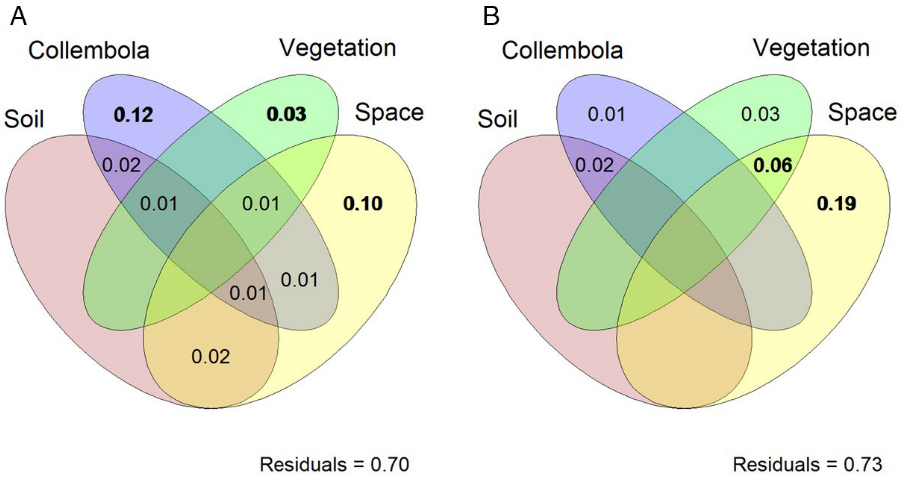

Fig. 4. Variation in total abundance of (A) *Folsomia quadrioculata* and (B) *Hypogastrura tullbergi*, explained by the four components: soil properties, abundance of other Collembola, vegetation composition, and spatial autocorrelation. Values given are the proportion of variation explained by each fraction (adjR^2-values), and bold numbers indicate significance ($P < 0.05$). Overlapping areas represent joint contribution by two or more components, and the non-overlapping parts are the pure effect of each component when the influence of the three others is considered as co-variables. Fields without a number are not contributing to the explained variation (adj$R^2 < 0.01$, NS) and can have negative adjR^2-values. Colors are used to separate the components.

Table 3. Linear multiple regressions (Gaussian distribution) on the abundance of *Folsomia quadrioculata* (left) and *Hypogastrura tullbergi* (right) explained by (A) soil properties (df = 5, 192), (B) abundance of other Collembola (df = 4, 193), or (C) vegetation composition (df = 6, 191).

	F. quadrioculata			*H. tullbergi*		
Characteristic	Estimate	t	P	Estimate	t	P
A						
Ergosterol† (mg/g)	2.559×10^{-3}	1.230	0.220	-3.46×10^{-4}	−0.159	0.874
Microbial activity (CO_2/g)	1.01×10^{3}	1.86	0.064	-2.484×10^{2}	−0.440	0.661
Water content (%)	1.241×10^{-2}	0.961	0.338	-1.121×10^{-2}	−0.829	0.408
Humus thickness (cm)	**2.163×10^{-1}**	**3.28**	**0.001**	-5.554×10^{-2}	−0.804	0.422
Organic material (g/g)	**−3.249**	**−3.323**	**0.001**	7.289×10^{-1}	0.712	0.478
B						
H. tullbergi	−0.001	−0.200	0.842	–	–	–
F. quadrioculata	–	–	–	−0.001	−0.200	0.842
Isotoma anglicana	**0.135**	**2.967**	**0.003**	−0.041	−0.812	0.418
Oligaphorura groenlandicus	0.057	1.794	0.074	0.087	2.538	0.012
Unidentified	**0.145**	**4.197**	**<0.001**	−0.018	−0.451	0.652
C						
Bryophytes	−0.526	−1.158	0.248	0.752	1.721	0.087
Lichens	−0.393	−2.762	0.006	**0.457**	**3.334**	**0.001**
Grasses	0.0264	0.162	0.872	0.210	1.340	0.182
Cassiope tetragona	0.1066	0.604	0.547	0.287	1.688	0.093
Saxifraga oppositifolia	0.1762	0.857	0.392	−0.176	−0.891	0.374
Salix polaris	0.0804	0.540	0.590	**0.421**	**2.940**	**0.004**

Notes: For abundance of *F. quadrioculata* explained by soil properties, $R^2 = 0.098$, adj$R^2 = 0.074$, $F = 4.15$, $P = 0.001$; for abundance of *H. tullbergi* explained by soil properties (NS), $R^2 = 0.009$, adj$R^2 = -0.016$, $F = 0.37$, $P = 0.87$. For abundance of *F. quadrioculata* explained by abundance of other Collembola, $R^2 = 0.188$, adj$R^2 = 0.171$, $F = 11.19$, $P < 0.001$; for abundance of *H. tullbergi* explained by abundance of other Collembola (NS), $R^2 = 0.033$, adj$R^2 = 0.012$, $F = 1.62$, $P = 0.17$. For abundance of *F. quadrioculata* explained by vegetation composition (NS), $R^2 = 0.050$, adj$R^2 = 0.021$, $F = 1.69$, $P = 0.126$; for abundance of *H. tullbergi* explained by vegetation composition, $R^2 = 0.120$, adj$R^2 = 0.092$, $F = 4.34$, $P < 0.001$. Bold values indicate variables with a significant contribution in models that explain the variation significantly.

† Ergosterol indicates the amount of fung. This and the estimates of microbial activity and organic material were measured per g soil (humus) dry weight.

The abundances of *I. anglicana* and unidentified collembolans had a positive relationship with abundance of *F. quadrioculata* (adj$R^2 = 0.171$, $P < 0.001$; Table 3B). The abundance of other Collembola had no effect on the abundance of *H. tullbergi* (adj$R^2 = 0.012$, $P = 0.17$).

Presence of lichens showed a negative relationship with *F. quadrioculata*, but the model with all the vegetation variables was not significant for this species (adj$R^2 = 0.020$, $P = 0.13$). In contrast, the vegetation composition did have an effect on *H. tullbergi* (adj$R^2 = 0.092$, $P < 0.001$), with presence of *Salix polaris* and lichens influencing the abundance positively (Table 3C).

In the spatial model of *F. quadrioculata* abundance, the first selected variable (MEM 2, contributing to 58% of the explained variation of that model) described a relatively large-scale pattern, with high positive autocorrelation at 10–30 cm and some significant positive autocorrelation up to 50 cm (Appendix S2: Fig. S1A). MEM 7 also described a quite large-scale pattern, while MEM 10 and MEM 18 described smaller scale patterns with positive and negative autocorrelations at many distances (Appendix S2: Fig. S1B–D). In the spatial model of *H. tullbergi* abundance, the four MEM-variables selected described the largest possible patterns detectable by our sampling design, with the strongest autocorrelation at the shortest distance (MEM1–4; Appendix S2: Fig. S2).

Comparison with analyses using negative binomial distribution data

The relative amount of variation explained when comparing the different components was similar regardless of regression method (Gaussian or negative binomial) for the abundance of both *F. quadrioculata* and *H. tullbergi* (compare Table 2 with Appendix S3: Table S23, total abundance) and of all age classes (compare Appendix S2:

Tables S1–S5 with Appendix S3: Tables S1–S23). There was a pure effect of all variables except the soil properties on total abundance of *F. quadrioculata* in a Gaussian regression, although vegetation composition did not contribute to the total model when using a negative binomial regression. When explaining the abundance of *H. tullbergi* using Gaussian regression, only the spatial variables showed a pure effect. Using a negative binomial regression instead revealed that both spatial variables and other Collembola contributed to the total model. Similar small differences between the two regression methods could be seen for the three age classes of both species. However, the relative contribution of the components was consistently similar between the methods.

DISCUSSION

Different structuring factors depending on species and age class

The relative importance of intraspecific interactions (e.g., self-organization), interspecific interactions, and abiotic constrains for the spatial distribution of organisms is one of the key questions in ecology to be able to predict population dynamics and species diversity patterns. To develop theories of the mechanisms governing this, we first need to discover and quantify these patterns (Levin 1992). In studies of communities of species with direct development, individuals within a species are often treated as if they are influenced by environmental and biotic factors in the same way (Martins da Silva et al. 2016, Widenfalk et al. 2016). If this is true, then species-level traits can be used to examine the factors explaining species distributions and community composition (Vandewalle et al. 2010). However, we found that this assumption depends on species identity and did only hold for one of two studied Collembola species. This questions the use of species-level traits in community studies where many species with different life strategies and degree of intraspecific interaction coexist (see Violle et al. 2012, for a discussion in the context of plant traits).

The two springtail species showed contrasting relationships to spatial and environmental factors, which appeared to reflect differences in their social interaction. We found that in *Folsomia quadrioculata*, variation in abundance was both related to environmental and biotic (inter- and intraspecific) variables. However, for *Hypogastrura tullbergi*, variation in abundance was mainly related to spatial factors, suggesting that spatial structuring in this species was largely caused by intraspecific interactions (self-organization). In the extreme case, self-organized structuring would result in that only a restricted part of high-quality patches are occupied by the species. This means that the link between patch occupancy and patch quality is weakened. In conclusion, our predictions about a general difference in structuring factors between the two species were confirmed.

More importantly, however, we found that the different age classes within *F. quadrioculata* were differentially affected by spatial or environmental factors. Analyzing all age classes together indicated that all four explanatory components explain some part of the spatial structuring of this species; however, for each age class, distinct different components and variables within each component are of importance (more details on the specific differences in section *Species- and age-specific responses to spatial and environmental factors*). Thus, drawing conclusions from the species-level data will hide possible explanations about the causes of spatial structuring as the mechanistic understanding is clearer when knowing the age class that responds to a given variable. For *H. tullbergi*, we found that variation in abundance in all age classes was mainly explained by spatial factors, indicating self-organized aggregation. For this species, pooled data give the same picture as if analyzing the age classes separately. As individuals of different size within a population may have different functionality (Rudolf and Rasmussen 2013), knowing whether all age classes are structured similarly or not would help when predicting shifts in the functions provided from a species or organism group if the function is supported mainly by one or some of the age classes.

Species- and age-specific responses to spatial and environmental factors

As shown by the correlograms (Fig. 2A) and especially by the MEM-variables selected for the models of each age class abundance (Appendix S2: Table S4), the spatial structure of *F. quadrioculata* was not consistent between age classes. In contrast, all age classes were structured similarly for *H. tullbergi*, which also showed strongest aggregation patterns at short distances (20–35 cm) in line with the hypothesis of self-organized behavior.

The factors explaining variation in abundance differed between the age classes of *F. quadrioculata*, with pure space being most important for hatchlings but not for the other two age classes. With apparently fairly low dispersal ability, the distribution of *F. quadrioculata* hatchlings is likely to be closely connected to the patches best suited for egg disposal. The species deposit their eggs in batches (Sengupta 2015), often with batches from several females together (H. P. Leinaas, *personal observation*) resulting in an aggregated distribution. In the present study, a larger proportion of hatchlings than older juveniles were found in the mineral soil with limited resources but stable humidity conditions, suggesting that eggs are deposited in locations selected to reduce risk of dehydration. This agrees with the fact that also fairly high number of adults (presumably reproducing) was found in the mineral soil. Hatchlings are more sensitive to desiccation than eggs (Leinaas and Fjellberg 1985), and the advantage of this reproductive behavior may to a large extent be linked to increased survival of the first sensitive period after hatching.

As they grow, *F. quadrioculata* juveniles will disperse and find areas with favorable foraging conditions. We are not aware of any studies showing facilitation between springtail species. A positive relation to other Collembola thus suggests that individuals of many springtail species are attracted to high-quality micro-patches in the soil, but that these high-quality patches are not explained by our environmental variables.

Folsomia quadrioculata reproduces continuously throughout the summer (Sømme and Birkemoe 1999). The adults found in the present study are hence individuals that either seek favorable foraging sites or are looking for suitable patches for mating and oviposition. Thus, it is not surprising that they responded both to the spatial and environmental variables. A thick humus layer conserves water during dry periods and might reflect seasonal moisture conditions for the springtails better than the measured moisture content (Vegter et al. 1988). The soil properties that explained high abundance of the adults (thick humus layer and low relative amount of organic material) indicates that beneficial microhabitats are those that ensure protection from dehydration and consist of litter that decomposes quickly (much microbial activity). The negative effect of organic material on abundance was unexpected. It might be caused by the effect of slow decomposing low-quality litter likely to have less microbial and fungal activity, and thus, providing a lower amount of food (Rantalainen et al. 2004).

In *H. tullbergi*, the spatial variables explained the largest part of variation in abundance and almost the same MEM-variables were included for all age classes indicating that they were all structured in the same way. Thus, the spatial structuring appears to reflect self-organization independent of size and reproductive status of the individuals, that is, by social interaction common to all age classes. This agrees with the mode of chemical communication (pheromones) previously observed in other *Hypogastrura* species with more advanced group behavior (Mertens and Bourgoignie 1977, Leinaas 1983).

In addition to pure spatial variables, the joint contribution of vegetation and space explained a substantial part of the variation in all *H. tullbergi* age classes. Lichens had a positive effect on the abundance of *H. tullbergi*. The positive correlation between lichens and three of the four chosen MEM-variables (r values 0.28–0.38, $P < 0.001$) resulted in a joint contribution of vegetation and space detected for this species. This agrees with many surface-dwelling collembolan species in drought-exposed habitats relying on lichens as primary food (Leinaas and Fjellberg 1985). By contrast, the abundance of *F. quadrioculata* showed a negative effect of lichens, which for this drought-sensitive species may be explained by lichens often being associated with the driest patches on the ground.

Consequences of differences between species and age classes and ways to handle them

Although both species showed a clear tendency to aggregate in their common habitat, they nevertheless differ greatly in how much the environment vs. self-organization contributes to the spatial structure of the species. This may have great implications for the general predictability of changes in spatial structuring of species with environmental changes (e.g., land use or climate change), as self-organized species might not respond as predicted to changes in environmental conditions. This is further complicated by species- and age-specific differences in dispersal ability with consequences for how long effects of past structuring processes may last. Differences between age classes would have implications for modeling of population responses to environmental change. Our results emphasize that for species where age classes are differently affected by environmental conditions, the use of species-level data can give biased results. One way of handling this is through a species-level size-spectrum approaches, where the distribution of traits across size classes for each species is taken into consideration (Hartvig et al. 2011); this has been used recently to, for example, predict the consequences of species loss (Brose et al. 2017).

CONCLUSIONS

This study suggests that both degree of self-organization and developmental stage are of importance when understanding mechanisms shaping spatial distribution patterns of species. This phenomenon is not commonly considered when analyzing community assembly patterns (Maass et al. 2015), although it has also been shown previously for insects (Rudolf and Rasmussen 2013). If this is a general pattern, it means that for species that are structured in the same manner regardless of age (e.g., *Hypogastrura tullbergi*), species-level traits can be applied to all age classes. For other species in which the factors structuring abundance vary with age (e.g., *Folsomia quadrioculata*), there will be a clear difference in distribution between age classes. Such differences between age classes are well known for species switching habitats during development, such as many fishes, amphibians, and holometabolous insects (Aschenbrenner et al. 2016), but is less recognized for animal species that utilize the same macro-habitat through all life stages. The consequence is that using species-mean trait values to interpret the effect of environmental and spatial factors for population or community patterns could be misleading.

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