Oecologia
DOI 10.1007/s00442-012-2334-8

COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Primary assembly of soil communities: disentangling the effect of dispersal and local environment

María Ingimarsdóttir · Tancredi Caruso ·
Jörgen Ripa · Ólöf Birna Magnúsdóttir ·
Massimo Migliorini · Katarina Hedlund

Received: 1 November 2011 / Accepted: 10 April 2012

Abstract It has long been recognised that dispersal abilities and environmental factors are important in shaping invertebrate communities, but their relative importance for primary soil community assembly has not yet been disentangled. By studying soil communities along chronosequences on four recently emerged nunataks (ice-free land in glacial areas) in Iceland, we replicated environmental conditions spatially at various geographical distances. This allowed us to determine the underlying factors of primary community assembly with the help of metacommunity theories that predict different levels of dispersal constraints and effects of the local environment. Comparing community assembly of the nunataks with that of non-isolated deglaciated areas indicated that isolation of a few kilometres did not affect the colonisation of the soil invertebrates. When accounting for effects of geographical distances, soil age and plant richness explained a significant part of the variance observed in the distribution of the oribatid mites and collembola communities, respectively. Furthermore, null model analyses revealed less co-occurrence than expected by chance and also convergence in the body size ratio of co-occurring oribatids, which is consistent with species sorting. Geographical distances influenced species composition, indicating that the community is also assembled by dispersal, e.g. mass effect. When all the results are linked together, they demonstrate that local environmental factors are important in structuring the soil community assembly, but are accompanied with effects of dispersal that may "override" the visible effect of the local environment.

Keywords Collembola · Colonisation · Metacommunity · Oribatida · Variance partitioning

Introduction

It has long been understood that community assembly can be linked to environmental factors (e.g. Diamond 1975; Chase and Leibold 2003), but can also be explained by dispersal constraints (Hubbell 2001). To determine their relative importance, four models of community assembly have been suggested within the metacommunity framework (Leibold et al. 2004). The neutral theory predicts species to be ecologically similar, hence not requiring specific habitats, but constrained by dispersal (Hubbell 2001). The other three perspectives all predict differences

Communicated by Roland Brandl.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2334-8) contains supplementary material, which is available to authorized users.

M. Ingimarsdóttir (✉) · J. Ripa · K. Hedlund
Department of Biology, Lund University, Sölvegatan 37,
223 62 Lund, Sweden
e-mail: maria.ingimarsdottir@biol.lu.se

M. Ingimarsdóttir
The Icelandic Institute of Natural History, Urriðaholtsstræti 6-8,
P.O. Box 125, 212 Garðabær, Iceland

T. Caruso
Institut für Biologie, Plant Ecology, Freie Universität Berlin,
14195 Berlin, Germany

Ó. B. Magnúsdóttir
Institute of Biology, University of Iceland, Askja, Sturlugötu 7,
101 Reykjavík, Iceland

M. Migliorini
Department of Evolutionary Biology, University of Siena,
via A. Moro n° 2, 53100 Siena, Italy

in species traits as well as degree of dispersal constraints. The patch dynamics perspective predicts a low dispersal rate so that at any given time some suitable patches are unoccupied (Leibold et al. 2004). The species sorting perspective predicts the dispersal to be frequent enough so that a species can rapidly disperse to a suitable location. Thus, the niche requirements (local environment) control what organisms are present (Chase and Leibold 2003). In a mass effect system, the dispersal rate is so high that organisms are present in habitats both where they are good and where they are poor competitors (source–sink relationships) (Shmida and Wilson 1985).

Here, we want to disentangle the underlying processes of primary community assembly of soil arthropods and hence to determine the effects of environmental and dispersal factors on recently deglaciated areas. So far, plant community assembly has been well studied on glacier forelands worldwide (e.g. Matthews 1992), but the assembly of invertebrates, including soil arthropods, has achieved attention mainly during the last decade (Kaufmann et al. 2002; Hodkinson et al. 2004; Hågvar et al. 2009; Hågvar 2010). In these studies, changes of soil communities along chronosequences have been associated with environmental factors, but not with factors concerning dispersal. To also identify the effect of geographical distances, we studied invertebrate communities along chronosequences on nunataks, which are ice-free islands within a glacial environment. Since the end of the nineteenth century, Vatnajökull glacier in Iceland has decreased in volume by about 10 % (Björnsson 2009) and consequently nunataks have increased both in number and size. Each nunatak has a community assembly which starts with dispersal from other parts of the metacommunity, e.g. the mainland or other nunataks. The chronosequences among and within nunataks allowed us to spatially replicate environmental conditions at various geographical distances, and offered a unique opportunity to determine effects of geographical isolation and local environment on community assembly.

The study organisms, collembolans and oribatid mites, are small wingless arthropods that provide important functions in soil and litter as detritivores and fungivores. They can be very species rich and abundant, and they differ in terms of traits, e.g. body size (Hopkin 1997; Krantz and Walter 2009). According to theories developed in terms of the species sorting perspective, related species of a similar trophic level show non-random patterns in terms of co-occurrences and traits. Species in communities that are influenced by competition co-occur less often than expected by chance, and the species that do co-occur differ in traits to reduce the overlap in resource use. When species composition is mainly influenced by the environment, species traits are similar (Hutchinson 1959; MacArthur and Levins 1967; Diamond 1975; Leibold 1998; Chase and Leibold 2003; Dayan and Simberloff 2005).

Previous studies that have disentangled the effect of local environment and geographical distances on soil communities have used the help of experimental design (Åström and Bengtsson 2011) or studied oribatids on smaller scales (<1.5 km) in homogenous landscapes (Lindo and Winchester 2009; Caruso et al. 2012). Hence, the focus of this study is to identify the drivers of primary community assembly of collembolans and oribatids at various geographical distances on deglaciated land.

Materials and methods

Study sites

Communities of collembolans and oribatids were studied on nunataks within the Vatnajökull glacier in southeast Iceland in 2008. The study was conducted along chronosequences on four nunataks, that is the youngest parts of one old nunatak and three nunataks that had emerged from the glacier during the last 70 years, namely Kárasker (1930s; Björnsson 1958), Bræðrasker (1961; Einarsson 1998) and Maríusker (2000). The oldest nunatak, Esjufjöll, has been partly icefree since at least the last glaciation (10,000 years; Björnsson H., personal communication).

Sampling

To achieve spatial replication of age of the land (hereafter called soil age) and environmental factors within and among nunataks, three transects were located on each nunatak, each extending from the recently deglaciated terrain to the oldest part of the nunatak. On Esjufjöll, we did not extend beyond 100 years old soil, but one additional transect was located partially on older soils to include communities on later stages of the assembly. Along each transect, 5 × 5 m sampling plots were located on soil of different age: two plots on Maríusker, but three and four on the Bræðrasker nunatak and the Kárasker and Esjufjöll nunataks, respectively.

The soil age was, on Esjufjöll, roughly estimated from the results of lichenometric dating (Dabski and Angiel 2010; Dabski personal communication), but on the other nunataks, soil age was estimated by comparing maps and photos of different ages. With these methods, we determined the soil age with a range of 10–30 years. Mapping with a global positioning system (GPS) in 2005 gave the age of the youngest part of each nunatak (0–3 years). The median age was used in the analyses (Table 1). The size of each nunatak and its distance from other unglaciated land types, i.e. another nunatak, mountain and lowland

(Table 2), were estimated from a Spot 5 satellite image from 2004, using ArcGIS 9 software (ESRI).

To characterise the plant community within each plot, four 5-m parallel transects were analysed across each plot, placed at 1, 2, 3 and 4 m from their reference edge. Plant species richness (i.e. number of vascular plant species) and total cover of vegetation (including mosses, lichens and biological crust), stones (>5 cm), gravel (0.5–5 cm) and sand (<0.5 cm) was measured using the line-intercept method as described by Magnússon and Magnússon (2000) and Magnússon et al. (2009). Three pitfall traps (6.3 cm diameter, 6.5 cm depth) with rainroof covers were placed randomly within each plot, each containing 4 % formaldehyde with additional detergent. As the fieldwork was done on foot, the trapping period varied slightly among the nunataks, 27 June to 1 August in Maríusker, 3–24 July in Bræðrasker, 29 June to 24 July in Kárasker and 8–29 July in Esjufjöll. On the youngest nunatak, Maríusker, only one or two traps could be used from four of the plots due to flooding and soil movements. Three soil samples of 10 × 10 cm and 5 cm deep were taken randomly in each plot. The samples were put in paper bags and watered regularly until they were extracted 2–4 weeks later. Soil fauna was extracted for 3 days per sample within a period of 3 weeks, using modified Macfadyen funnels (Macfadyen 1961). The extracted fauna was preserved in 50 % ethylene glycol. Subsamples from the same soil samples were taken for measuring the organic matter in the soil. They were oven-dried at 100 °C for about 24 h, weighed, and burned in an oven at 600 °C for 10 h before they were reweighed. The loss on ignition gave the organic content of the soils.

Adult oribatids and all collembolans were determined to species or genus level using the literature (Balogh and Mahunka 1983; Marshall et al. 1987; Bernini et al. 1995; Fjellberg 1998; Subias 2004; Weigmann 2006; Fjellberg 2007). Size of collembolans was taken from the literature (Fjellberg 1998, 2007), but that of oribatids was measured under a microscope. Oribatid juveniles were excluded from all analyses. Before analyses, the species data from the pitfall traps and soil samples within each plot were combined, and because the number of specimens caught by the two methods was not comparable, the presence/absence data was used for the analyses. As it is difficult to distinguish between established and transient (dispersing) invertebrates, we assumed that all species present may establish.

Statistical analyses

To determine the effect of geographical distances and local environment on soil community assembly, we separated

Table 1 Average values of the environmental factors that were measured for each plot and each soil age

Soil age (years)	No. plots	Altitude (m a.s.l.)	Organic matter (%)	Plant richness[a]	Vegetation cover (%)	Stone cover (%)	Gravel cover (%)	Sand cover (%)
Maríusker								
1.5	3	460	0.9	0.7	0.0	33.0	41.3	25.7
5.5	3	483	0.5	4.3	0.3	62.0	30.0	7.7
Bræðrasker								
1.5	3	615	1.2	0.0	0.0	53.0	27.3	19.7
25	3	642	1.2	5.7	0.0	57.0	36.3	6.7
45	3	694	1.6	10.3	6.3	71.7	20.7	1.3
Kárasker								
1.5	3	571	1.4	0.3	0.0	23.7	33.0	43.3
25	3	642	3.0	14.0	7.0	51.7	34.7	6.7
45	3	671	1.9	14.3	5.7	57.0	33.0	4.3
68	3	702	6.5	12.7	16.3	66.7	14.3	2.7
Esjufjöll								
0	2	572	2.1	14.0	2.0	28.5	48.5	21.0
1.5	3	521	1.1	6.0	0.0	27.7	39.7	33.0
10	1	579	1.2	19.0	9.0	26.0	58.0	7.0
25	3	549	1.4	17.3	23.3	27.3	40.0	9.3
33	1	631	1.5	24.0	52.0	30.0	18.0	0.0
55	3	611	1.5	21.3	21.3	25.3	40.0	13.3
90	4	657	1.4	19.3	22.3	17.8	49.3	10.8
2,200	1	728	25.4	28.0	100.0	0.0	0.0	0.0

[a] Number of vascular plant species

Table 2 The nunataks studied in Vatnajökull, Iceland, summer 2008

Nunatak	Nunatak age (years)	Size (km^2)	Distance (km) over glacier to nearest		
			Lowland	Highland	Nunatak
Maríusker	8	0.02	5.1	1.9	4.1
Bræðrasker	47	0.25	9.6	6.8	1.3
Kárasker	73	0.87	9.4	7.6	1.3
Esjufjöll	>10,000	9.40	13.3	6.4	1.0

Nunatak age number of years since each nunatak started emerging

the analyses of the environmental and geographical factors. Many environmental factors co-vary in a study that is performed along chronosequences. Thus, the major environmental factors were selected and collinear factors excluded from the analyses (Legendre and Legendre 1998). This was done with a principal component analysis (PCA) on log-transformed environmental data (see Tables 1 and 2 for the environmental factors), which allowed us to visualise which environmental factors co-varied and to choose the representative environmental factors (Fig. 1; Legendre and Legendre 1998; Gotelli and Ellison 2004). The following factors were chosen: the soil age, the age of the nunatak, i.e. how many years the nunatak has been visible and thus subjected to community assembly, and plant species richness. To determine the effects of geographical distances on community assembly, a model based on Moran's eigenvector mapping was employed (Borcard and Legendre 2002; Dray et al. 2006). A multivariate extension of Akaike's information criterion was used to choose the most parsimonious spatial model. See online resource 1 for details on the procedure followed in the present analysis. The chosen environmental factors and the Moran's eigenvectors of geographical distances were then analysed with a redundancy analysis of the collembolan and oribatid species composition. The variance explained by the two sets of factors (the environment and geographical distances) was determined with variance partitioning (Borcard et al. 1992). Statistical significance of the chosen environmental factors was tested with a Monte Carlo permutation test. All multivariate statistical analyses were performed with R version 2.10 (R Development Core Team 2006, http://www.R-project.org) using the vegan (Oksanen et al. 2006) and spacemakeR (Dray et al. 2006) packages.

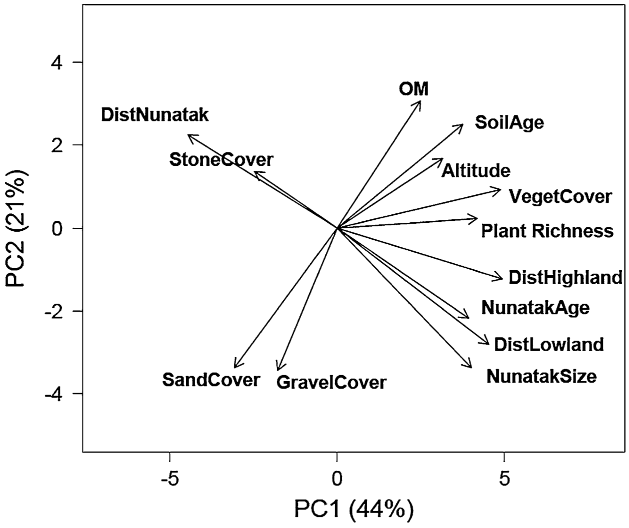

Fig. 1 Principal component analysis (PCA) of the environmental factors. The factor coordinates (*arrows*) are built from the PC1 and PC2 eigenvector coefficients and allow visualisation of major patterns in the correlation among factors and the selection of the representative factors of the major environmental gradients

The species composition was further analysed to determine the role of species interactions on the species composition. Species co-occurrence was tested for non-random patterns following Gotelli (2000) and Gotelli and Entsminger (2010), using 5,000 randomisations of the original data matrix and algorithm SIM 9 in Gotelli (2000) to create null expectations. Random matrices had the same number of species and samples as the original matrix. Null model analysis was also performed on size ratios within the collembolan and oribatid communities. The assumption was that patterns for soil arthropod size are, at least in part, an indirect proxy to species niche differentiation so differences in size ratios imply that interspecific competition is structuring the community. This test was performed both at plot level and for each sample (pit-fall traps and soil samples) within Esjufjöll only, as that was the only nunatak that contained enough species, of both oribatids and collembolans, for the test. The size difference, on a log-scale, to each species nearest neighbour (i.e. the size ratio) was calculated for each species within each plot/sample with more than one species present. The average of all size ratios was then calculated as a total mean nearest neighbour distance. The observed mean nearest neighbour distance was tested against a null distribution generated by drawing 10,000 sets of species, equal in number within each plot/sample to the observed community, from the total pool of species found at the nunatak (Peres-Neto 2004).

Results

Community assembly

Collembolans were abundant in samples from all nunataks. In total, around 6,700 collembolans and 1,380 oribatids were found, of which all collembolans and the 870 oribatid adults were determined to genus or species (Tables 3, 4). The majority of the juvenile mites (86 %) were present in the oldest plot on Esjufjöll, which was also the most

Table 3 The oribatid species (subspecies in parentheses) present on the different locations along the chronosequences on each nunatak and the total number of species on each soil age

Species	Soil age (years)				
	≤10 (M, B, K, E)	25–33 (B, K, E)	45–55 (B, K, E)	68–90 (K, E)	2,200 (E)
Bankisoma lanceolata (*islandica*)					E
Belba compta					E
Camisia (*Ensicamisia*) *lapponica*		E		K, E	
Ceratozetes sellnicki		E	E	E	E
Dissorhina ornata					E
Eupelops plicatus					E
Liebstadia similis				E	E
Liochthonius clavatus	E				
Liochthonius sellnicki		E		E	E
Liochthonius strenzkei	E				
Liochthonius tuxeni					E
Neobrachychthonius marginatus			E		
Nothrus silvestris					E
Oppiella (*Moritsoppia*) *translamellata*					E
Oppiella nova			B	K	
Oppiella (*Rhinoppia*) *subpectinata*					E
Oribatula tibialis		E	B, E	E	E
Pantelozetes paolii	E			E	E
Quadroppia quadricarinata					E
Scheloribates laevigatus		E	E	E	E
Scutovertex sculptus				E	E
Suctobelba regia		E			E
Suctobelba trigona					E
Suctobelbella acutidens			E	E	E
Synchthonius crenulatus					E
Tectocepheus velatus (*sarekensis*)		E			
Tectocepheus velatus (*velatus*)	B, E	E	K, E	K, E	E
Trichoribates myrica		E	E	E	E
Trichoribates setiger		E	E	E	E
Total number of species	4	10	9	13	23

M Maríusker, *B* Bræðrasker, *K* Kárasker, *E* Esjufjöll

species rich (Table 3). The collembolan communities were dominated by the surface-active *Desoria olivacea* and *Pseudisotoma sensibilis* that were present in 40 and 41 out of 45 plots, respectively. More sedentary collembolans were present in plots of 45 years and older on Bræðrasker and Kárasker and of 25 years and older on Esjufjöll. No oribatid species were found on Maríusker and only a few species were found on Bræðrasker and Kárasker (Table 3). Generally, the community was dominated by the surface active species *Tectocepheus velatus*, which was present in 20 out of 45 plots, *Oribatula tibialis*, and rather sedentary species that were mainly found in the oldest plots of Esjufjöll.

Geographical and environmental effects

When disentangling the effects of geographical and environmental factors, the variation in species composition differed between the two taxa (Fig. 2b, c). Less than 30 % of the variation was explained for the collembolan communities while almost 60 % was explained for the oribatid communities. The variation explained of the oribatid and collembolan communities, attributed uniquely to geographical distances, was higher than the amount explained by environmental factors only (Fig. 2). Half the explained variation was shared between both factors. When removing the conditional effect of geographical distances, plant species richness and soil age

Table 4 The collembolan species present on the different locations along the chronosequences on each nunatak and the total number of species on each soil age

Species	Soil age (years)				
	≤10 (M, B, K, E)	25–33 (B, K, E)	45–55 (B, K, E)	68–90 (K, E)	2,200 (E)
Anurophorus laricis			K		
Arrhoppalites principalis			B		
Ceratophysiella sp.	E	E		K	
Chaetophorura arctica				E	
Desoria olivacea	M, B, K, E	B, K, E	B, K, E	K, E	
Desoria tolya	M, E	B, E	K, E	K, E	E
Entomobrya sp.			E	K	
Folsomia brevicauda	E	E	B	K	E
Folsomia quadrioculata	E		E		E
Friesia truncata		E	E	E	
Heterosminthurus claviger	M, E	E	K, E	K, E	E
Isotoma anglicana	M, B, E	K, E	B, K, E	E	E
Lepidocyrtus lignorum	B, E	E	B, E	K, E	E
Mesaphorura sp.	K	E	E	E	E
Micranurida pygmaea	E				
Neanura muscorum				E	
Oligophorura groenlandica	E		B		
Oligophorura schoetti			B, K		
Parisotoma notabilis		E	B, E	K	E
Protaphorura sp.	E		K	K	
Pseudanurophorus binoculatus					E
Pseudisotoma sensibilis	M, B, K, E	B, K, E	B, K, E	K, E	
Sminthurides malmgreni	M, E	K, E	K		E
Sminthurides schoetti		E			
Tetracanthella arctica	E				
Willemia denisi				K	
Total number of species	15	13	18	16	10

M Maríusker, *B* Bræðrasker, *K* Kárasker, *E* Esjufjöll

were still statistically significant in the redundancy analysis (Table 5). Plant species richness determined the collembolan species composition while soil age that of the oribatids. Being aware that the plot including most oribatid species was also by far the oldest plot, the analysis was also performed excluding that plot, but the results did not change significantly.

Species co-occurrence and body size

The hypothesis that species co-occur randomly, as expected according to the neutral theory, was rejected because the species distribution of collembolans and oribatids was significantly different from a random distribution (Table 6). The pattern of species occurrence had a positive effect size, which means that species tend to co-occur less frequently than expected under a random community assembly. The extent to how much they avoid each other was considerably higher for collembolans than for oribatids.

The differences in body size ratio of co-occurring collembolans were not different from a random distribution (Table 7). A significant convergence in body size ratio was observed in the oribatid communities from the pit-fall traps, but not from the soil samples (Table 7). This may be partly because pit-fall traps caught both surface-active and sedentary species while the soil samples mainly included sedentary species. Accordingly, the majority of organisms sampled from soil were small species, varying less in size than the species caught in pit-fall traps.

Discussion

Colonisation rate and effects of local environment

The knowledge of how geographical distances and environmental factors shape communities of collembolans and

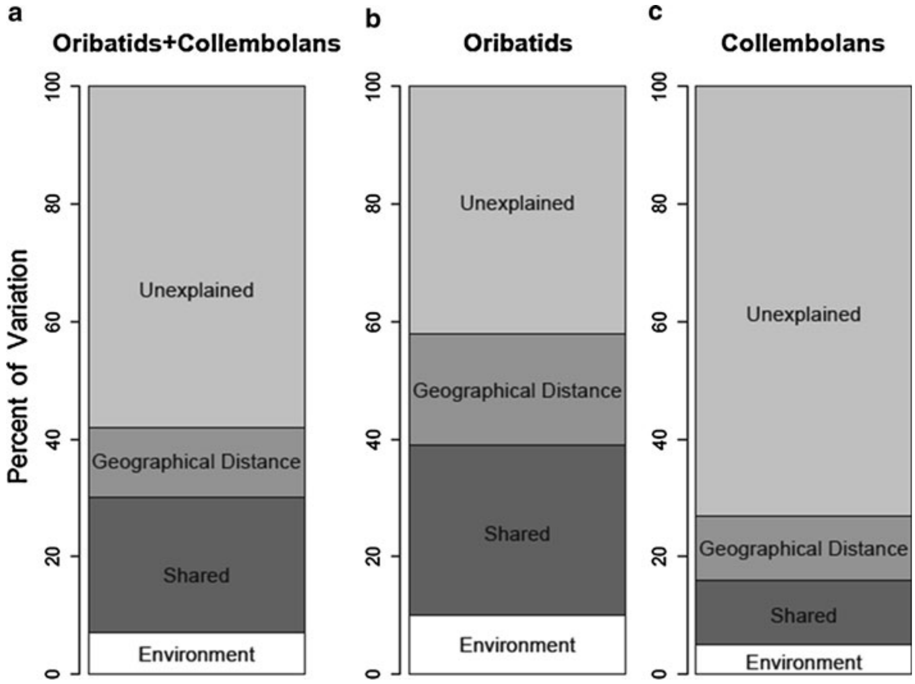

Fig. 2 Variance partitioning from a redundancy analysis shows the amount of variance that can be explained by geographical distances and environmental factors for species composition of **a** oribatids and collembolans, **b** oribatids and **c** collembolans. The shared part can be explained by both geographical distances and environmental factors

Table 5 The effect of environmental factors on the community structures after removing the conditional effects of the geographical distances, analysed by redundancy analysis and Monte Carlo permutation test

Factor	Oribatids + collembolans	Oribatids	Collembolans
Plant richness	$\boldsymbol{P < 0.005}$	$P = 0.370$	$\boldsymbol{P < 0.005}$
Nunatak age	$P = 0.155$	$P = 0.155$	$P = 0.335$
Soil age	$\boldsymbol{P < 0.005}$	$\boldsymbol{P < 0.005}$	$P = 0.215$

Values in bold indicate the rejection of the null hypothesis at $P \leq 0.05$

Table 6 Species co-occurrence analysis for testing whether species distributions can be approximated by random distributions generated by statistical models (null model analysis)

Assemblage	Obs C score[a]	Sim C score[b]	Effect size[c]	P value[d]
Collembolans + oribatids (all plots)	7.6	5.8	11.2	<0.001
Collembolans (all plots)	12.7	10.4	8.31	<0.001
Oribatids (all plots)	2.2	1.9	2.1	0.03
Collembolans (Esjufjöll)	5	4.5	4.4	<0.001
Oribatids (Esjufjöll)	1.6	1.4	2.3	0.03

[a] Observed *C* score

[b] Simulated *C* score after 5,000 randomisations with random matrices having the same number of species and samples as the original matrix

[c] The *C* score measures the extent by which species are not co-occurring and the effect size scales the difference between the real and simulated *C* score in units of standard deviations, which allows the comparison of different assemblages

[d] Tail probability of observed *C* score obtained by random permutations. The null hypothesis is that species co-occur neither more (negative effect size) nor less (positive effect size) frequently than expected under a random distribution

oribatids is important as it helps us to understand the underlying mechanisms of the assembly of soil communities. Collembolans have been shown to reach virgin isolated habitats within a few years (Lindroth 1973; Thornton et al. 1988; Schneider et al. 2011) and establish before oribatids (Lindroth 1973). However, in several studies on primary community assembly, soil invertebrates are either not sampled or not present (Edwards and Thornton 2001; Abe 2006). Here, we determine the effect of long distances on the rate of community assembly by comparing the assembly of the nunataks with glacier forelands, which are similar habitats with well-known chronosequences but are not isolated by distance. Most studies have been performed on glacier forelands that are geographically far apart, as in Iceland (Lindroth 1965), Austria (Kaufmann et al. 2002), Norway (Hågvar et al. 2009; Hågvar 2010) and Svalbard (Hodkinson et al. 2004). Thus, we cannot compare the exact species composition of the nunataks and the glacier forelands. However, our results and that of others show that, on both nunataks and glacier forelands, surface-active collembolans are among the early colonisers, establishing within the first 30 years (Lindroth 1965; Kaufmann et al. 2002; Hodkinson et al. 2004; Hågvar 2010), along with a few surface-active oribatids, e.g. *T. velatus* (Hodkinson et al. 2004; Hågvar et al. 2009). The more sedentary collembolan and oribatid species start establishing in 30- to

Table 7 Size ratio analysis for testing whether the collembolan and oribatid communities show divergence (bigger difference in size than expected by chance) or convergence (smaller difference in size than expected by chance) in size ratio

	No. species	Neutral MNND	Observed MNND	*P* value
Collembolans				
Plots	22	0.187	0.199	0.47
Pitfall traps	18	0.371	0.320	0.059
Soil samples	12	0.401	0.312	0.18
Oribatids				
Plots	28	0.155	0.133	0.28
Pitfall traps	13	0.223	0.169	0.041
Soil samples	25	0.203	0.173	0.42

MNND mean distance to nearest neighbour

60-year-old soil on glacier forelands (Hodkinson et al. 2004; Hågvar et al. 2009; Hågvar 2010) which is similar to that on the nunataks. Thus, the isolation does not have a negative effect on the rate of the general soil community assembly. However, the geographical distances explained a substantial part of the variance in community composition indicating that community assembly can be partially explained by dispersal (Cottenie 2005).

The local environment significantly affected the community composition of both oribatids and collembolans. The effect of soil age on the assembly of oribatids is also observed by Hågvar et al. (2009). Soil age is highly correlated with organic matter, and oribatids feed on litter and soil microorganisms such as soil fungi (Siepel and de Ruiter-Dijkman 1993; Schneider and Maraun 2005). Hodkinson et al. (2004) concluded that some early colonisers are more associated with factors other than soil age, such as plant species richness. Collembolans are considered to mainly feed on fungi (reviewed by Hopkin 1997) and other microorganisms (Birkemoe and Liengen 2000). Thus, the driver of collembolan community assembly is probably not the plants themselves but rather a local environmental factor which facilitates both plant species richness and collembolans, or the plant litter affects microorganisms that collembolans feed on.

Community assembly and metacommunities

Of the four metacommunity perspectives, we can fit species sorting and mass effect models to our data, but neutral theory and patch dynamics perspectives are not important descriptors of community assembly. The patch dynamics perspective predicts that the dispersal rate is low so that organisms do not reach all the locations where they can establish (Leibold et al. 2004). Ecologically similar species, as is assumed for the neutral theory (Hubbell 2001), should not require specific habitats. Thus, patterns of species composition formed by the processes of patch dynamics or neutral theory should show no significant effect of the local environment (Cottenie 2005), which is opposite to our findings.

The similar colonisation rates of nunataks and glacier forelands indicate a sufficient dispersal rate for the assumptions of the species sorting perspective (Leibold et al. 2004). The environmental factors are significantly associated with the assembly of the soil community, which is also consistent with the species sorting perspective. Furthermore, both collembolan species and oribatid species co-occur less frequently than expected by chance. This can be due to local environmental factors or competition, but it cannot be caused by random dispersal formed by either processes of the neutral theory or mass effect. Also, the oribatids that do co-occur show convergence in body size ratio, which may suggest a common environmental or foraging constraint structuring the community rather than competition (Leibold 1998).

The mass effect assumes a heterogeneous environment, with the corresponding species sorting processes, but emphasises the role of dispersal because species can be present in a habitat where they are poor competitors by frequent dispersal from other habitats. Thus, species composition will vary with both the local environment and geographical distances (Cottenie 2005). The results that are consistent with the mass effect perspective are the large amount of unexplained variation in the collembolan species composition, which may be caused by random variation (Borcard et al. 1992), and that the collembolans that do co-occur show random differences in body size ratio. These random patterns of the collembolans may be caused by the potentially high dispersal rate of collembolans, as the colonisation rate of collembolan species is higher than that of oribatids (Lindroth 1973; Hodkinson et al. 2004). This is in line with Åström and Bengtsson (2011) who found that the dispersal rate of collembolans was high enough for mass effect but lower for oribatids. The unexplained variance in species composition may, however, also be caused by overlooked environmental factors (Borcard et al. 1992). In light of these results, and combined with the results from the co-occurrence analysis showing that collembolans co-occur less than the oribatids, we suspect that we may have missed out an important factor that is structuring the collembolan community, e.g. the distribution of cyanobacteria which collembolans graze on (Birkemoe and Liengen 2000). More data are necessary to disentangle these alternative explanations of the observed patterns.

When the results are linked together, they demonstrate that the local environment is important in structuring soil community assembly but is accompanied with effects of dispersal. We therefore conclude that primary soil community assembly is consistent with both species sorting and mass effect perspectives, where the soil arthropod community is structured by dispersal with the filter of the environmental constraints determined by the temporal evolution of the soil. In the case of oribatids, and especially collembolans, the dispersal rate can be so high that species can persist in non-viable habitat patches due to intricate source–sink dynamics.

Acknowledgments The study was performed in Vatnajökull National Park. All the people who gave advices on the nunataks and the glacier, borrowed and transported equipment/supplies are thanked, especially Hálfdán and Helgi Björnsson, farmers at Kvísker, Öræfi. Arne Fjellberg assisted in identification of collembolans. Starri Heiðmarsson provided us with the outlines of the nunataks from 2005. We thank Alwyn Williams for his comments on the manuscript. T. Caruso was supported by the Alexander von Humboldt Foundation, EBESA IPY project n1 452, SCAR EBA Programs, and the Italian PNRA (Programma azionale di Ricerche in Antartide) with funding granted to Roberto Bargagli (University of Siena). The work was supported by Kvískerjasjóður, The Crafoord Foundation and Kungliga Fysiografiska Sällskapet i Lund.

References

Abe T (2006) Colonization of Nishino-Shima island by plants and arthropods 31 years after eruption. Pac Sci 60:355–365

Åström J, Bengtsson J (2011) Patch size matters more than dispersal distance in a mainland-island metacommunity. Oecologia 167:747–757. doi:10.1007/s00442-011-2024-y

Balogh J, Mahunka S (1983) Primitive oribatids of the Palaearctic region. Elsevier, Amsterdam

Bernini F, Castagnoli M, Nannelli R (1995) Arachnida Acari. Calderini, Bologna

Birkemoe T, Liengen T (2000) Does collembolan grazing influence nitrogen fixation by cyanobacteria in the high Arctic? Polar Biol 23:589–592. doi:10.1007/s003000000133

Björnsson S (1958) Könnunarferð í Kárasker. Jökull 8:15–17

Björnsson H (2009) Jöklar á Íslandi. Opna, Reykjavík

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecol Model 153:51–68

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055

Caruso T, Taormina M, Migliorini M (2012) Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. J Anim Ecol 81:214–221. doi:10.1111/j.1365-2656.2011.01886.x

Chase JM, Leibold MA (2003) Ecological niches: linking classic and contemporary approaches. University of Chicago Press, Chicago

Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett 8:1175–1182. doi:10.1111/j.1461-0248.2005.00820.x

Dabski M, Angiel P (2010) Geomorphic implications of the retreat of Breiðamerkurjökull at the southern part of the Skálabjörg ridge, Esjufjöll, Iceland. Jökull 60:185–197

Dayan T, Simberloff D (2005) Ecological and community-wide character displacement: the next generation. Ecol Lett 8:875–894. doi:10.1111/j.1461-0248.2005.00791.x

Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, pp 342–444

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Model 196:483–493

Edwards JS, Thornton IWB (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VI. The pioneer arthropod community of Motmot. J Biogeogr 28:1379–1388

Einarsson E (1998) Ung og gömul jökulsker í Breiðamerkurjökli. Landnám og framvinda gróðurs. In: Árnason GS, Arnarson BG, Jörundsson EP, Svavarsdóttir G, Torfason Z (eds) Kvískerjabók. Sýslusafn Austur-Skaftafellssýslu, Höfn, pp 222–254

Fjellberg A (1998) The Collembola of Fennoscandia and Denmark. Part 1: Poduromorpha. Brill, Leiden

Fjellberg A (2007) The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona. Brill, Leiden

Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. Ecology 81:2606–2621

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Sunderland

Gotelli NJ, Entsminger GL (2010) EcoSim: null models software for ecology, 7th edn. Acquired Intelligence Inc. & Kesey-Bear, Jericho

Hågvar S (2010) Primary succession of springtails (Collembola) in a Norwegian glacier foreland. Arct Antarct Alp Res 42:422–429. doi:10.1657/1938-4246-42.4.422

Hågvar S, Solhoy T, Mong CE (2009) Primary succession of soil mites (Acari) in a Norwegian glacier foreland, with emphasis on oribatid species. Arct Antarct Alp Res 41:219–227. doi:10.1657/1938-4246-41.2.219

Hodkinson ID, Coulson SJ, Webb NR (2004) Invertebrate community assembly along proglacial chronosequences in the high Arctic. J Anim Ecol 73:556–568

Hopkin SF (1997) Biology of the springtails (Insecta: Collembola). Oxford University Press, Oxford

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat 93:145–159

Kaufmann R, Fuchs M, Gosterxeier N (2002) The soil fauna of an Alpine glacier foreland: colonization and succession. Arct Antarct Alp Res 34:242–250

Krantz GW, Walter DE (2009) A manual of acarology, 3rd edn. Texas Tech University Press, Lubbock

Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam

Leibold MA (1998) Similarity and local co-existence of species in regional biotas. Evol Ecol 12:95–110

Leibold MA et al (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613. doi:10.1111/j.1461-0248.2004.00608.x

Lindo Z, Winchester NN (2009) Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. Oecologia 160:817–825. doi:10.1007/s00442-009-1348-3

Lindroth CH (1965) Oikos. Acta Oecologica Scandinavica. Supplementum 6. Skaftafell, Iceland: a living glacial refugium. Munksgaard, Copenhagen

Lindroth CH (1973) Entomologica Scandinavica. Supplementum 5. Surtsey, Iceland: the development of a new fauna, 1963–1970: terrestrial invertebrates. Munksgaard, Copenhagen

MacArthur RH, Levins R (1967) Limiting similarity convergence and divergence of coexisting species. Am Nat 101:377–385

Macfadyen A (1961) Improved funnel-type extractors for soil arthropods. J Anim Ecol 30:171–184

Magnússon B, Magnússon SH (2000) Vegetation succession on Surtsey, Iceland, during 1990–1998 under the influence of breeding gulls. Surtsey Res 11:9–20

Magnússon B, Magnússon SH, Friðriksson S (2009) Development in plant colonization and succession on Surtsey during 1999–2008. Surtsey Res Prog Rep 12:57–76

Marshall VG, Reeves RM, Norton RA (1987) Catalogue of the Oribatida (Acari) of continental United States and Canada. Mem Entomol Soc Can 139:1–418

Matthews JA (1992) The ecology of recently deglaciated terrain. A geoecological approach to glacier forelands and primary succession. Cambridge University Press, Cambridge

Oksanen J, Kindt R, Legendre P, O'Hara RB (2006) Vegan: Community Ecology Package version 1.8-2

Peres-Neto PR (2004) Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. Oecologia 140:352–360. doi: 10.1007/s0042-004-1578-3

R Development Core Team (2006) R: a language and environment for statistical computing. In: R Foundation for Statistical Computing. Vienna, Austria

Schneider K, Maraun M (2005) Feeding preferences among dark pigmented fungal taxa ("Dematiacea") indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari). Pedobiologia 49:61–67. doi:10.1016/j.pedobi.2004.07.010

Schneider K, Christman MC, Fagan WF (2011) The influence of resource subsidies on cave invertebrates: results from an ecosystem-level manipulation experiment. Ecology 92:765–776. doi: 10.1890/10-0157.1

Shmida A, Wilson MV (1985) Biological determinants of species diversity. J Biogeogr 12:1–20

Siepel H, de Ruiter-Dijkman EM (1993) Feeding guilds of oribatid mites based on their carbohydrase activities. Soil Biol Biochem 25:1491–1497

Subias LS (2004) Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes, Oribatida) del mundo (1758–2002). Graellsia Monogr 60(número extraordinario): 3–305

Thornton IWB, New TR, McLaren DA, Sudarman HK, Vaughan PJ (1988) Air-borne arthropod fall-out on Anak Krakatau and a possible pre-vegetation pioneer community. Philos Trans R Soc Lond B 322:471–479. doi:10.1098/rstb.1988.0139

Weigmann G (2006) Acari, Actinochaetida. Hornilben (Oribatida). Goecke & Evers, Keltern