

# Invertebrate community assembly along proglacial chronosequences in the high Arctic

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## Summary

1. Invertebrate community assembly is described for two contrasting proglacial chronosequences (over 1900 years) at Kongsfjord, W. Spitsbergen, Svalbard.
2. Three hypotheses were tested: (1) community assembly is deterministic, directional and predictable; (2) succession is inextricably linked to plant community and soil development; and (3) dispersal is a rate-limiting factor for community assembly.
3. Communities, dominated by omnivores and detritivores, are more complex than supposed previously. Herbivore species were few but predators, parasitoids and hyperparasitoids were abundant.
4. Species fell within one of eight defined groups with respect to colonization. This relates to ecophysiological tolerances, need for facilitation or dependence on other species. Spiders, surface-active Collembola and drought-resistant cryptostigmatic mites arrived before vascular plants established and soils developed. Later colonizers required site facilitation through soil development or host availability.
5. Comparisons between the proglacial area of Midtre Lovénbre, a land-terminating glacier, and three Lovén Islands, released from beneath a tidewater glacier, showed similarities in community composition and species abundance with respect to successional stage, suggesting determinism and direction in community development.
6. Most common species on Midtre Lovénbre colonized the Lovén Islands rapidly, suggesting that dispersal does not seriously restrict community development on the time scales involved. Some minor species associated with older soils appear not yet to have reached the islands.

*Key-words:* colonization, dispersal, facilitation, food-web, succession, Svalbard.

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## Introduction

Community assembly following glacier regression in the high Arctic is poorly understood and quantitative studies documenting the development of communities along proglacial chronosequences are surprisingly absent. The importance of allochthonous energy and nutrients (living invertebrates and wind-blown detritus) for initial colonization of new substrates, in the high Arctic and elsewhere was emphasized recently (Hodkinson *et al.* 2001; Hodkinson, Webb & Coulson 2002). This paper describes the subsequent assembly of invertebrate communities on proglacial chronosequences at Kongsfjord, W. Spitsbergen, Svalbard, for which soil

and plant community development are already characterized (Hodkinson, Coulson & Webb 2003). Outside the high Arctic, soil development and plant succession on glacier forelands is investigated widely (Matthews 1992; Chapin *et al.* 1994) but, with the exception of studies on Rotmoos Glacier, Austria (Kaufmann 2001, 2002; Kaufmann & Raffl 2002; Kaufmann, Fuchs & Gosterxeier 2002), detailed data on animal community assembly along glacial chronosequences are lacking. Limited data, however, are available for selected groups such as spiders (Zingerle 1999). By contrast, community assembly on other newly exposed substrates has been studied widely, usually at lower latitudes (e.g. Lindroth *et al.* 1973; Majer 1989; Ashmole *et al.* 1992; Miles & Walton 1993; Crawford, Sugg & Edwards 1995; Hodkinson *et al.* 2002).

Our primary objectives were to describe, measure and model patterns and rates of invertebrate community assembly following glacial retreat, using selected proglacial

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areas of known chronology. In particular, we tested three linked hypotheses, namely that (1) invertebrate community assembly is deterministic and directional and therefore predictable; (2) invertebrate succession is linked inextricably to plant community and soil development and (3) dispersal, linked to ecophysiological adaptability, is a rate-limiting factor for invertebrate community assembly.

Community assembly for a 1900-year chronosequence along the proglacial area of a land-terminating glacier, the Midtre Lovénbre, was compared with that (over *c.* 1000 years) on the nearby Lovén Islands (see Hodkinson *et al.* 2003). These small islands in Kongsfjord were released successively from beneath the ice during the regression of the main valley glacier, the Kongsbre. They lie 3 km from the mainland shore and are separated by *c.* 1 km of open water. Midtre Lovénbre communities developed on bare nutrient-poor moraines in proximity to the cooling effect of a large glacier but with unrestricted access to colonizing organisms from adjacent areas. The 'isolated' Lovén Island communities, by contrast, developed on glacial diamicton, receiving significant nutrient enrichment from surrounding marine ecosystems (Alsos, Elvebakk & Gabrielsen 1998; Hodkinson *et al.* 2003).

The invertebrate fauna of Svalbard is relatively well known, particularly for the Kongsfjord area (Coulson & Refseth 2004). The ecophysiology, population biology and dispersal characteristics of many of the dominant species are well established and provide background for the interpretation of community assembly data (Bale *et al.* 1997; Hodkinson *et al.* 1998; Coulson *et al.* 2002; Coulson, Hodkinson & Webb 2003a,b).

#### STUDY SITES

Sites (Table 1) were adjacent to Ny-Ålesund, Kongsfjord, West Spitsbergen, Svalbard. On Midtre Lovénbre foreland, seven sampling plots (approx. 20 × 30 m), were established at roughly equal distances along a transect of 1.7 km across the proglacial area. Starting at the glacier snout, sites 1–5 lay on the moraine, site 6 on the sandur below the terminal moraine and site 7 a little to one side on a raised rock ridge beyond the sandur. Plot 7 was relatively undisturbed by recent glaciation (Hodkinson *et al.* 2003). The Lovén islands chronosequence comprised sites on three islands, Storholmen, Midtholmen and Leirholmen. Each island plot (approximately 30 m diameter) was situated on the shallow down slope below the crest of the island. For both chronosequences plant cover, plant species richness, depth of soil organic horizon, percentage soil organic matter, soil nitrogen and soil moisture increased over time, whereas soil pH and average soil particle size decreased (Hodkinson *et al.* 2003). By contrast with the oldest Midtre Lovénbre site, the oldest Lovén Islands sites had a slightly lower vascular plant species richness and higher Bryophyte cover: the dominant species, nevertheless, tended to remain the same. Organic soil depth, however, was greater

**Table 1.** Study sites on Kongsfjord, Spitsbergen, Svalbard. Sites were aged in 2000 by either aerial/ground photography (P) or radiocarbon dating (RC); see Hodkinson *et al.* (2003) for full details

Site	Location	Age (years)
<i>Chronosequence 1</i>		
Midtre Lovénbre 7	N 78°54'534' E 12°04'537'	BP 1926–1820
Midtre Lovénbre 6	N 78°54'200' E 12°06'763'	150
Midtre Lovénbre 5	N 78°54'082' E 12°06'339'	100
Midtre Lovénbre 4	N 78°53'984' E 12°06'085'	60
Midtre Lovénbre 3	N 78°53'816' E 12°05'590'	37
Midtre Lovénbre 2	N 78°53'704' E 12°05'262'	16
Midtre Lovénbre 1	N 78°53'653' E 12°04'797'	2
<i>Chronosequence 2</i>		
Storholmen (S)	N 78°55'860' E 12°13'617'	BP 968–926
Midtholmen (M)	N 78°55'914' E 12°18'156'	BP 1174–1058
Leirholmen (L)	N 78°55'215' E 12°20'285'	100

on the Lovén Islands, resulting presumably from nutrient enrichment and impeded drainage. Table 1 gives locations, altitudes and ages of sites and plots. Plot ages were estimated from land-based and aerial photography, coupled with radiocarbon dating of soil organic matter (Hodkinson *et al.* 2003).

#### Methods

Several techniques were used to sample invertebrates. Four-centimetre-diameter cores were taken randomly in late July 2000 from within each plot ( $n = 40$  or 20 per plot for Midtre Lovénbre and Lovén Islands, respectively) and extracted for soil microarthropods using modified Macfadyen high gradient heat extractors (Leinaas 1978). Parallel sets of identical soil cores ( $n = 20$  per plot) were extracted for Enchytraeidae and larval Chironomidae using wet funnel extraction (O'Connor 1962). On the shallow soils (< 4 cm depth) of Midtre Lovénbre and Leirholmen each core, comprising the top 4 cm of substrate containing a complete soil profile, was inverted before extraction. On the deeper organic soils of Midtholmen and Storholmen (> 4 cm) cores were divided horizontally before extraction. Midtre Lovénbre and Lovén Island sites were sampled in mid July to early August 2000 and 2001, respectively.

Pitfall and yellow sticky traps provided additional data on species present. Water-filled pitfall traps (5 cm diameter, 3 × 5 per site, 1 m spacing) were operated continuously from 16 July to 3 August 2000 on Midtre Lovénbre plots and from 17 July to 6 August 2001 on

the Lovén Islands plots. Yellow sticky traps (doubled, each area 400 cm<sup>2</sup>, 4 per plot) were operated continuously from 17 July to 6 August on 2001 on Midtre Lovénbre (Coulson *et al.* 2003a).

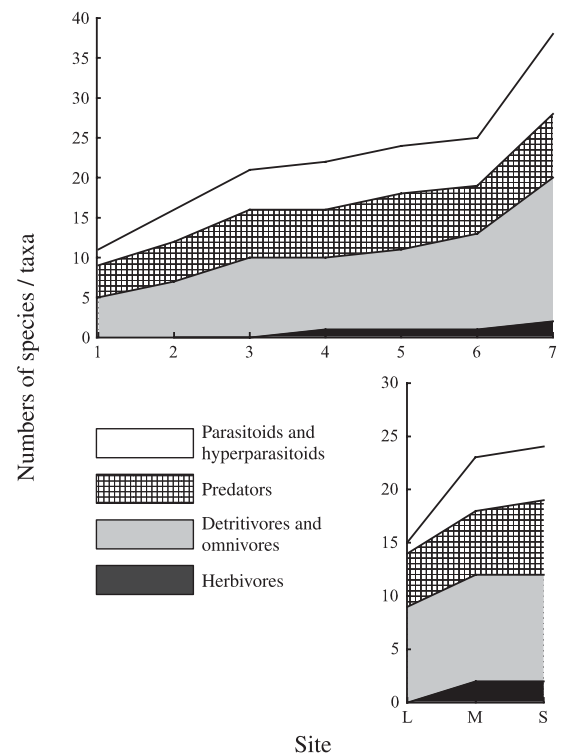
Species richness of soil testate amoebae was obtained from six soil cores per plot on Midtre Lovénbre. Soils were homogenized and subsamples examined on glass slides under a compound microscope. Numbers of species found during a 2-h search of six slides per plot were recorded. Lower than expected species richness at sites 6 and 7 was confirmed by examining four extra slides for 1 h.

Canonical correspondence analysis (CCA) was used to examine relationships between invertebrate community composition and site variables. Models based on linear regression were not significantly different from those using polynomial relationships (Makerenkov & Legendre 2002) and results presented use the linear model. CCA graphs were plotted using the Multivariate Statistical Package (mvsp) 3.1. (Kovach Computing Services). Species present at one site only were excluded from the analysis. CCA models, along orthogonal axes, the distribution of animal species (response variables) across sites with respect to environmental data for each site (explanatory variables). Results are displayed as diagrams plotting the correspondence (proximity) of species and sites to vector lines representing the explanatory variables. The closer the proximity, the greater the effect of that vector in determining the species distribution. Analyses are based on six explanatory variables, chronological age of site, soil surface pH, percentage vegetation cover, percentage cover by blue-green bacteria, plant species richness and percentage organic matter (OM) in the top 4 cm of soil. Variables are described fully in Hodkinson *et al.* (2003). The list was optimized from a larger set in which several variables, such as soil depth, soil moisture, soil clast size and soil nitrogen were serially correlated with those used. Adding these extra variables had minimal effect on the variation explained.

## Results

### SPECIES RICHNESS DURING COMMUNITY ASSEMBLY

The trophic composition of communities across the Midtre Lovénbre and Lovén Island chronosequences, derived from core, pitfall and yellow trap samples, is summarized in Fig. 1, with species listed by guild in Table 2. Taxonomic nomenclature follows Coulson & Refseth (2004) and Coulson *et al.* (2003a). All identified taxa with established populations are included. In addition, many Diptera (Nematocera and Muscomorpha) were caught by pitfalls and sticky traps (Coulson *et al.* 2003a) but taxonomic uncertainties prevented these groups being identified precisely and they are excluded from detailed analysis. They comprise predominantly non-resident adult Chironomidae (*c.* 18 species) blown in from surrounding aquatic breeding



**Fig. 1.** Trophic composition of higher invertebrate community across sites during community assembly on (a) Midtre Lovénbre and (b) Lovén Island chronosequences.

areas (Hodkinson *et al.* 1996b). However, one or two Svalbard chironomid species, particularly *Smittia* spp., are terrestrial, breeding in the transect soil (see Sendstad, Solem & Aagard 1976).

Some species caught by sticky and water traps parasitize or predate both resident and allochthonous prey species. These include several species of hymenopterous parasitoids, such as *Aclastus borealis* and *Gelis glacialis* (parasitizing spider cocoons), *Plectiscidea hyperboreus* and *Stenomacrus groenlandicus* (parasitizing Diptera: Nematocera) and *Atractodes pusillus* (parasitizing Diptera: Muscomorpha) (Coulson *et al.* 2003c), as well as species attacking sawfly and aphid hosts.

The striking feature about community composition (Fig. 1) was the low number of invertebrate herbivore species. Initial colonization was almost exclusively by detritivores/omnivores. Obligate herbivores, feeding on vascular plants, did not establish for 60 years, and then only a few species. Some Collembola, however, include cyanobacteria (blue-green bacteria) in a mixed diet (Hodkinson *et al.* 1994; Birkemoe & Liengen 2000). By contrast, predators and parasitoids feeding on the limited prey species were surprisingly species-rich. Communities on the oldest Lovén Islands contained a total species number intermediate between sites 6 and 7 on Midtre Lovénbre. For the most mature communities on Midtre Lovénbre and Lovén Island chronosequences, species in each guild represented, respectively: herbivores 5% and 8%, detritivores/omnivores 47% and 42%, predators 21% and 29% and parasitoids 26% and 21% of total species.

**Table 2.** Presence or absence of all higher invertebrate and testate amoeba (Rhizopoda) species at sites along Midtre Lovénbre and Lovén Island chronosequences. Note that the higher invertebrates are divided into trophic groupings. For testate amoebae\* indicates the most common species

Higher invertebrates		Midtre Lovénbre							Lovén Islands		
		1	2	3	4	5	6	7	Leir	Midt	Stor
Herbivores											
Symphyta	<i>Prontoprístia amentorum</i>				x	x	x	x		x	x
Aphidoidea	<i>Acyrthosiphon svalbardicum</i>							x		x	x
Detritivores/Omnivores											
Collembola											
	<i>Isotoma anglicana</i>	x	x	x	x	x	x	x	x	x	x
	<i>Hypogastrura tullbergi</i>	x	x	x	x	x	x	x	x	x	x
	<i>Sminthurides inequalis</i>	x	x	x	x	x	x	x	x	x	x
	<i>Folsomia quadrioculata</i>	x	x	x	x	x	x	x	x	x	
	<i>Folsomia bisetosa</i>							x			
	<i>Sminthurinus concolor</i>							x			
	<i>Onychiurus groenlandicus</i>										
	<i>Ceratophysella longispina</i>										
	<i>Hypogastrura viatica</i>								x		
Acarina											
Cryptostigmata											
	<i>Camisia anomia</i>	x	x	x	x	x	x	x	x	x	x
	<i>Tectocephus velatus</i>		x	x	x	x	x	x	x		
	<i>Diapterobates notatus</i>			x	x	x	x	x	x	x	x
	<i>Mycobates sarekensis</i>			x							
	<i>Hermannia reticulata</i>					x	x	x		x	x
	<i>Ceratoppia hoeli</i>										
	<i>Oppiella neerlandica</i>									x	x
	Unknown <i>Brachythionius?</i>										
	Enchytraeidae			x	x	x	x	x	x	x	x
	Chironomidae			x	x	x	x	x		x	x
Predators											
Acarina											
	Gamasida sp. 1	x	x	x	x	x	x	x	x	x	x
	Gamasida sp. 2 ( <i>Zircon</i> sp.)			x	x	x	x	x	x		x
	Gamasida sp. 3					x	x	x			
	Prostigmata								x	x	x
Arachnida											
	<i>Meioneta nigripes</i>	x	x	x	x	x					
	<i>Erigone psychrophila</i>	x	x	x	x	x			x		
	<i>Erigone arctica</i>		x	x	x	x	x	x		x	x
	<i>Halorates spetsbergensis</i>	x	x	x	x	x	x	x	x	x	x
	<i>Hilaira glacialis</i>						x	x		x	x
	Diptera									x	x
	<i>Parasyrphus tarsatus</i>										
Parasitoids (Hymenoptera)											
Ichneumonidae											
	<i>Stenomacrus groenlandicus</i>	x	x	x	x	x	x	x	x	x	x
	<i>Aclastus borealis</i>	x	x	x	x	x	x	x			
	<i>Plectiscidea hyperborea</i>		x	x	x	x	x	x		x	
	<i>Atractodes pusillus</i>		x	x	x	x	x	x	x		
	<i>Gelis glacialis</i>			x	x	x	x	x			
	<i>Synodites lineiger</i>										
	Braconidae										
	<i>Ichneutes hyperboreus</i>				x	x	x	x		x	x
	<i>Diaeretiella rapae</i>									x	x
	Megaspilidae										
	<i>Dendrocerus bifoveatus</i>									x	x
	Cynipidae										
	<i>Alloxysta</i> sp.									x	x
	Total species	11	16	21	22	24	25	38	16	24	24
Rhizopoda											
	<i>Diffflugia</i> sp.	x*	x	x		x	x				
	<i>Centropyxis cassis</i>		x*	x*	x*	x*	x*	x*			
	<i>Trigonopyxis arcuata</i>				x	x	x				
	<i>Euglypha tuberculata</i>				x						
	<i>Cyclopyxis arcelloides</i>					x	x	x			
	<i>Arcella vulgaris</i>					x					
	<i>Arcella cinctus</i>					x					
	<i>Trinema/Carythion</i>					x					
	<i>Nebela tinctoria</i>							x			
	<i>Centropyxis platystoma</i>									x	
	Total species	1	2	2	3	7	5	3			

## COLONIZATION PATTERNS

*Midtre Lovénbreen*

Initial colonization was by detritivores/omnivores and their predators and parasitoids (Table 2). The first incomers at site 1 (2 years) were the surface-active Collembola *Isotoma anglicana*, *Hypogastrura tullbergi* and *Sminthurides inaequalis armatus*, together with the cryptostigmatic mite *Camisia anomia* and, surprisingly, the occasional terrestrial chironomid larva. Common predators included one species of gamasid mite and two species of spider, *Meioneta nigripes* and *Erigone psychrophila*. The single resident parasitoid was *S. groenlandicus*. Herbivores were absent.

Community complexity increased slowly (Table 2) and after 60 years a further soil-dwelling collembolan, *Folsomia quadrioculata* and two additional cryptostigmatic mites, *Dipterobates notatus* and *Tectocephus velatus*, were added to the detritivore/omnivores. Enchytraeidae first appeared after 37 years. It was, however, 60 years (site 4) before the first herbivore of higher plants, the sawfly *Prontoprissa amentorum*, established together with its parasitoid *Ichneutes hyperboreus*. Over the same time interval, a single predatory mite species was added, one spider species disappeared and a further two, *Erigone arctica* and *Halorates spetsbergensis*, entered the community.

Community development continued equally slowly between sites 5 and 6 (100–150 years) with two detritivore/omnivores, the collembolans *Folsomia bisetosa* and *Sminthurinus concolor* added, together with a further predatory gamasid mite and the spider *Hilaira glacialis*. A major transition, however, occurred at site 7 (1900 years) with the inclusion, of the relatively sedentary soil dwelling collembolans *Onychiurus groenlandicus* and *Ceratophysella longispina* and several additional mites including *Ceratoppia hoeli*, *Oppiella neerlandica* and *Brachythonus* sp. Establishment of the aphid *Acyrtosiphon svalbardicum*, feeding on *Dryas octopetala*, was accompanied by the addition of several aphid parasitoids and hyperparasitoids, namely *Diaeretiella rapae* (M'Intosh) (Braconidae) (= *Trioxys* sp. of Coulson *et al.* 2003a), *Dendrocercus bifoveatus* (Kieffer) (Ceraphronoidea, Megaspilidae) and *Alloxysta* sp. (Cynipidae), as well as larvae of the aphidophagous *Parasyrphus tarsatus* (Syrphidae).

Testate amoebae (Rhizopoda) (Table 2) were present throughout the Midtre Lovénbreen transect. A single species, *Difflugia* sp., was found at site 1 and the species that was to become dominant at remaining sites, *Centropyxis cassis*, appeared at site 2. This was followed by increasing species richness up to site 5 (100 years), but richness then declined. This decline appears real, as confirmed by extra samples from the older sites revealing no additional species.

*Lovén islands*

Comparisons between the Lovén Islands and Midtre Lovénbreen reveal many similarities but some differences.

Leirholmen is chronologically of similar age to site 5: Midtholmen and Storholmen are intermediate between sites 6 and 7.

The same four common Collembola species that first colonized Midtre Lovénbreen were present on all islands but some of the later soil-dwelling species, such as *O. groenlandicus*, were not found. An additional species, *Hypogastrura viatica*, absent from Midtre Lovénbreen, was abundant on Leirholmen but not found on the older islands.

Mites showed similar species consistency, with the early colonizers of Midtre Lovénbreen present on all islands. Similarly, *T. velatus* was present at the younger but missing from the oldest sites on both chronosequences. Some Midtre Lovénbreen species, notably *Mycobates sarakensis* and *C. hoeli*, were absent from all islands. Terrestrial chironomid larvae and Enchytraeidae were present throughout the island sites. Predatory mite species were well represented on all islands and *E. psychrophila* and *H. spetsbergensis* were again the first spider colonists, with the former preceding the latter. The herbivores *P. amentorum* and *A. svalbardicum* were not found on Leirholmen, but were present on Midtholmen and Storholmen.

Hymenoptera appeared less diverse than on Midtre Lovénbreen. *S. groenlandicus* was again ubiquitous on the islands but the remaining ichneumonids were sporadic (*P. hyperborea* on Midtholmen, *A. pusillus* on Leirholmen) or absent (*A. borealis*, *G. glacialis*). Of the remaining species *I. borealis*, *D. bifoveatus* and *Alloxysta* were again associated with herbivores only on Midtholmen and Storholmen, but *D. rapae* was not found.

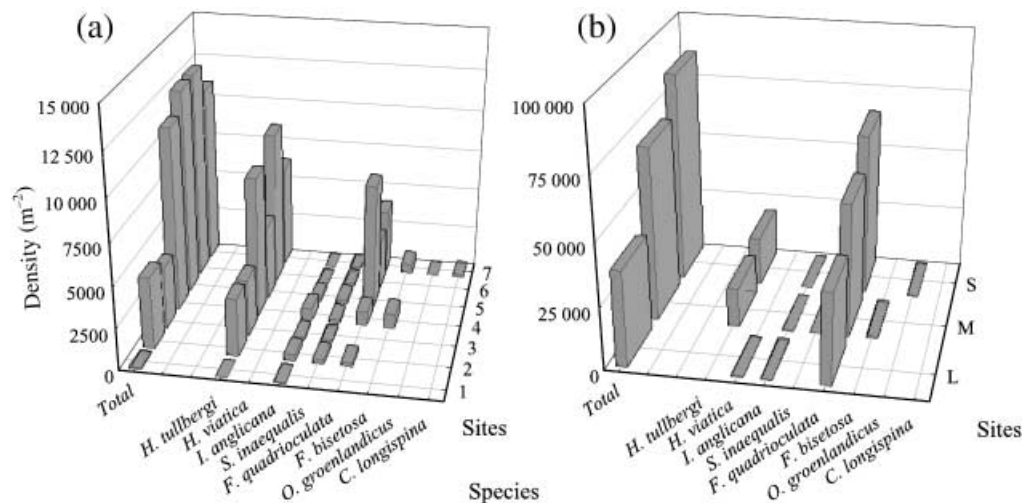
## POPULATION DENSITIES

Table 3 summarizes Kruskal–Wallace tests for significant differences in invertebrate population densities among sites on Midtre Lovénbreen and Lovén Island chronosequences. Abundances of all taxa differed significantly among sites across Midtre Lovénbreen. Similar significant differences were found among Collembola, Enchytraeidae and predatory mites on the Lovén Islands but cryptostigmatic mite and chironomid populations were similar.

Total Collembola on Midtre Lovénbreen (Fig. 2a) (maximum = 12 000 m<sup>-2</sup>) were consistently lower than on the Lovén Islands (Fig. 2b) (maximum = 80 000 m<sup>-2</sup>) for sites of equivalent age. In general, Collembola densities increased with site age, becoming maximal at or beyond 100 years. On Midtre Lovénbreen *H. tullbergi* tended to be numerically dominant, with *F. quadrioculata* second and *I. anglicana* and *S. inaequalis* almost invariably present but at lower densities (< 1000 m<sup>-2</sup>). Remaining species formed minor components of the community. By contrast, numerical dominance was reversed on the Lovén Islands, with *F. quadrioculata* dominant, *I. anglicana* and *S. inaequalis* generally present at low population densities, and other species occurring sporadically. *H. tullbergi* remained the second

**Table 3.** Results of Kruskal–Wallace tests for significant differences in the abundance of soil invertebrates among sites on Midtre Lovénbre and Lovén Island chronosequences. Species present at one site are excluded. For mites, Collembola and Chironomidae  $n = 40$  or  $20$  on Midtre Lovénbre and Lovén Island sites, respectively. For Enchytraeidae  $n = 20$  throughout

	Midtre Lovénbre		Lovén Islands	
	H	P	H	P
Total mites	151.65	< 0.001	2.99	NS
<i>C. anomia</i>	116.44	< 0.001	1.32	NS
<i>D. notatus</i>	98.49	< 0.001	2.16	NS
<i>T. velatus</i>	99.94	< 0.001	4.48	NS
Total Collembola	136.28	< 0.001	12.78	< 0.01
<i>H. tullbergi</i>	111.94	< 0.001	36.42	< 0.001
<i>I. anglicana</i>	44.77	< 0.001	6.26	< 0.05
<i>S. inaequalis</i>	17.46	< 0.05	2.11	NS
<i>F. quadrioculata</i>	177.78	< 0.001	11.20	< 0.01
Enchytraeidae	11.58	< 0.05	19.11	< 0.001
Chironomidae	23.69	< 0.001	0.06	NS
Predatory mites	56.29	< 0.001	7.97	< 0.05

**Fig. 2.** Mean population densities  $m^{-2}$  for total and individual species of Collembola at sites across (a) Midtre Lovénbre and (b) Lovén Island chronosequences.

dominant species on Midtholmen and Storholmen but was largely replaced by *H. viatica* on Leirholmen.

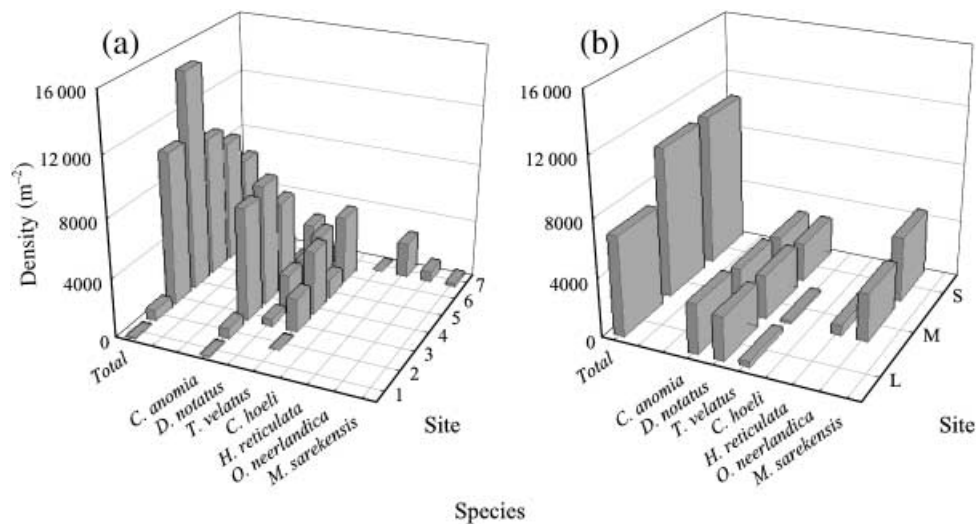
Total cryptostigmatic mites on Midtre Lovénbre (Fig. 3a) increased gradually from sites 1–4 (maximum =  $15\,000\ m^{-2}$ ) and then declined steadily to site 7 ( $6000\ m^{-2}$ ). *C. anomia* was dominant, particularly at the youngest sites (1–4), with *D. notatus* or *T. velatus* second or third in rank abundance ( $< 4000\ m^{-2}$ ). Among remaining species, only *Hermannia reticulata* reached significant densities at site 7 ( $2000\ m^{-2}$ ). Species abundances were more equitable on the Lovén Islands with *C. anomia*, and *D. notatus* displaying similar densities ( $2\text{--}3000\ m^{-2}$ ) and *O. neerlandica* becoming relatively abundant on Midtholmen and Storholmen ( $3\text{--}400\ m^{-2}$ ). Populations of *H. reticulata*, where present, were less than at site 7 ( $< 1000\ m^{-2}$ ).

Densities of larval Chironomidae (Fig. 4a) were surprisingly higher in heat-extracted soil samples than in O'Connor wet extractions and data for the former are presented. Densities on Midtre Lovénbre varied among

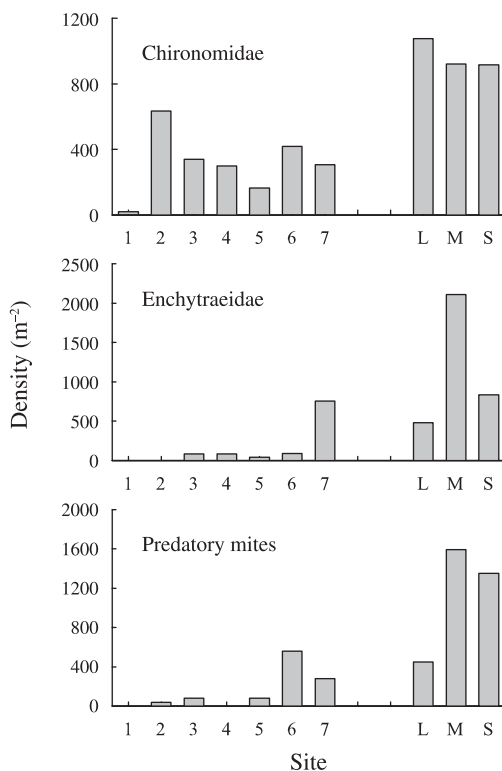
sites with a maximum ( $600\ m^{-2}$ ) at site 2. Site 1 supported a pioneer population of  $25\ m^{-2}$  but other sites were variable within the range  $200\text{--}400\ m^{-2}$ . Lovén Island populations, however, were similar ( $900\text{--}1100\ m^{-2}$ ) and about 2–3 times those on Midtre Lovénbre.

Enchytraeidae populations (Fig. 4b) were consistently higher in wet extractions. Densities differed significantly among sites on Midtre Lovénbre, resulting primarily from a higher population at site 7 ( $800\ m^{-2}$ ). Sites 3–6 supported broadly similar densities ( $< 200\ m^{-2}$ ). Populations on the Lovén Islands were consistently higher ( $500\text{--}2100\ m^{-2}$ ) than at comparable sites on Midtre Lovénbre, with Midtholmen significantly higher than the remaining islands.

Populations of predatory mites (Gamasida + Prostigmata) were present throughout both chronosequences. Densities on Midtre Lovénbre generally increased from a small number of scattered individuals  $m^{-2}$  at site 1, through measurable populations ( $4\text{--}111\ m^{-2}$ ) at sites 2, 3 and 5 to significant populations at sites 6 and 7 ( $350\text{--}550\ m^{-2}$ ).



**Fig. 3.** Mean population densities  $m^{-2}$  for total and individual species of cryptostigmatic mites at sites across (a) Midtre Lovénbre and (b) Lovén Island chronosequences.



**Fig. 4.** Mean population densities  $m^{-2}$  for (a) total terrestrial chironomid larvae, (b) total Enchytraeidae and (c) total cryptostigmatic mites at sites across the Midtre Lovénbre and Lovén Island chronosequences.

Site 4 was unusual in that only a sparse population was found. Population density on Leirholmen ( $500 m^{-2}$ ) was comparable with site 6 but those on Midtholmen and Storholmen ( $1200$ – $1500 m^{-2}$ ) were twice the Midtre Lovénbre maximum and probably reflected the higher numbers of Collembola present.

Many parasitoid Hymenoptera were taken in water traps at all sites. The Midtre Lovénbre fauna (Fig. 5a) was dominated by four Ichneumonidae, *S. groenlandicus*,

*P. hyperborea*, *A. borealis* and *A. pusillus*. Brachypterous forms of *S. groenlandicus* indicate its resident status. The abundance trend for these species was a progressive increase, from a low at site 1 to a peak at the midpoint of the transect (sites 3–5) and then a gradual decline at sites 6–7. *G. glacialis* and *S. lineiger*, were taken at low densities on sticky traps but were absent from water traps. Remaining Hymenoptera were less abundant and their distribution reflected that of potential herbivore hosts. Thus, *I. hyperboreus* was consistently present at low densities at sites 4–7, but *S. lineiger* was infrequent and only at site 7. Similarly, the aphid parasitoids/hyperparasitoids all occurred only at site 7. By contrast, *S. groenlandicus* was again the dominant species on all Lovén Islands (Fig. 5b), the herbivore parasitoids/hyperparasitoids occurred at similar densities to Midtre Lovénbre but catches of the remaining species were lower and more sporadic.

Total spider catches in water traps on Midtre Lovénbre tended to increase gradually from sites 1–7 (Fig. 6a). This reflected catches of indeterminate juveniles and masked individual species trends related to distribution. Numerically dominant species were *H. spetsbergensis* and two *Erigone* species. *M. nigripes* and *H. glacialis* became increasingly important in the early and latter stages of succession, respectively. The Lovén Islands (Fig. 6b) followed similar trends, with highest spider numbers trapped on the oldest islands and the same rankings of species abundance. One species associated with the early succession on Midtre Lovénbre, *M. nigripes*, was not found.

#### VARIATIONS IN SPECIES DEMOGRAPHY

Some abundant collembolans, such as *H. tullbergi*, differed in population body size distribution across the Midtre Lovénbre (Fig. 7). Body length correlates with Collembola age (Petersen 1971), and on this criterion the population age structure of *H. tullbergi* varied

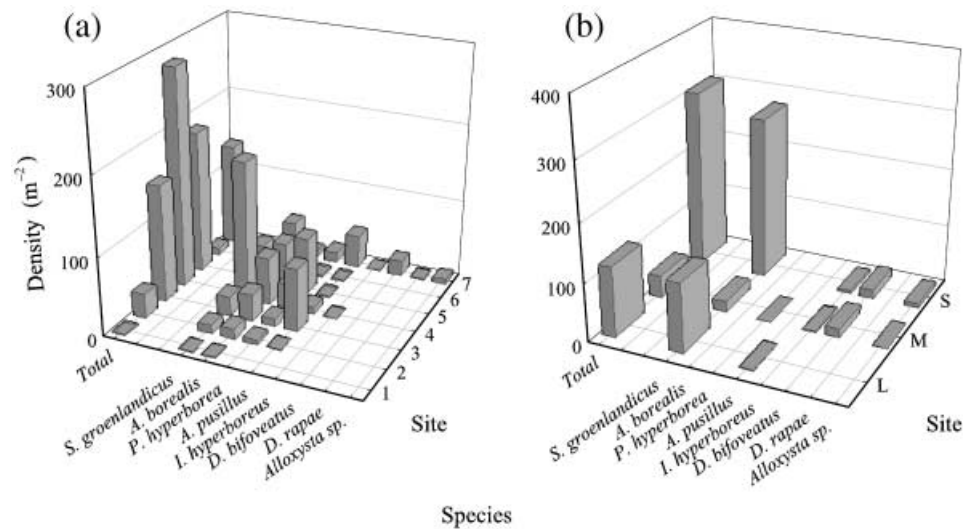


Fig. 5. Total pitfall catches of all Hymenoptera and totals for individual species at sites across (a) Midtre Lovénbre and (b) Lovén Island chronosequences.

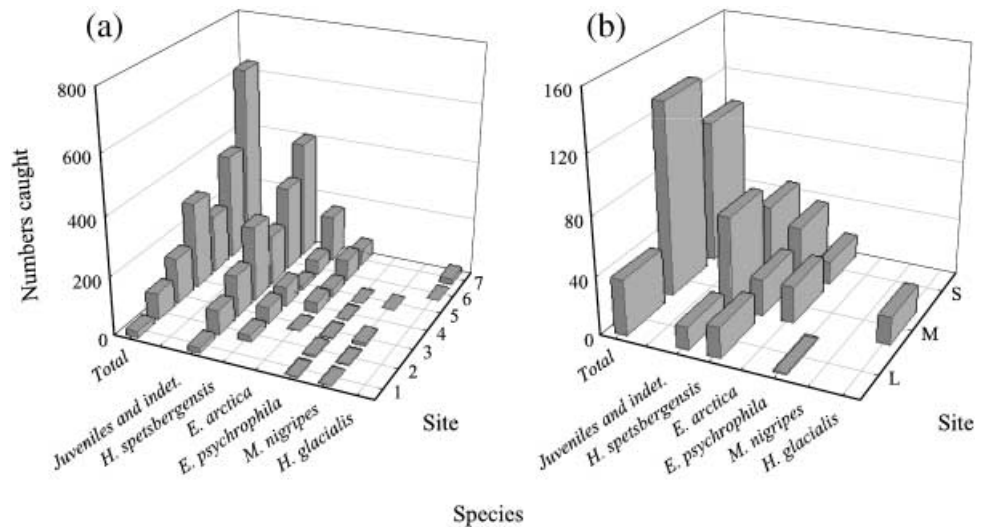


Fig. 6. Total pitfall catches of all Areneae and totals for individual species at sites across (a) Midtre Lovénbre and (b) Lovén Island chronosequences.

among sites. At younger sites (1–3) the population comprised mainly of older adult individuals (length > 0.85 mm; Birkemoe & Sømme 1998) compared with a greater proportion of juveniles at sites 4–7.

#### CANONICAL CORRESPONDENCE ANALYSIS

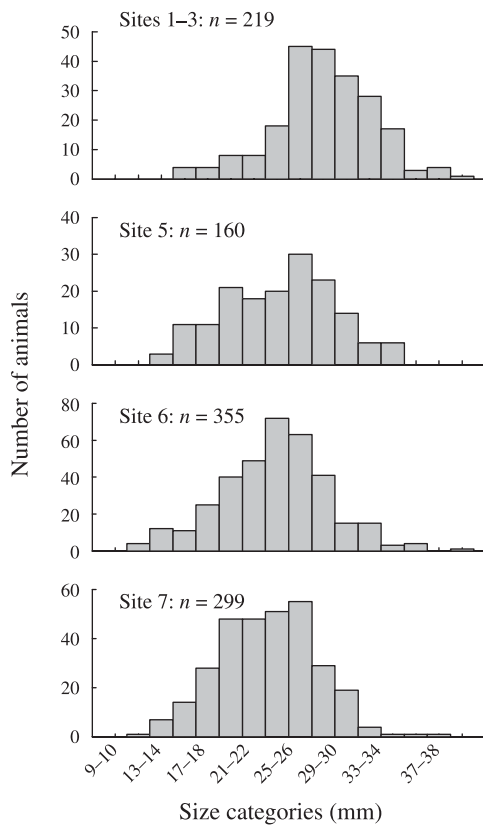
Figure 8 compares CCA ordinations for Midtre Lovénbre sites alone and with the addition of the Lovén Island data. Analyses demonstrated strong relationships (> 85% of variation explained by the first three axes), confirming directional trends already apparent in the data. Thus, most species and sites ordinated along the first and second axes adjacent to vector lines representing site age, percentage cover and percentage OM. This suggests that site age and the associated factors, percentage cover and percentage OM were the best predictor variables for many, but not all invertebrate taxa.

Thus *O. neerlandica* (8), Enchytraeidae (3), *F. quadriculata* (12), predatory mites (10) and *H. reticulata* (7) all tend to associate strongly with older sites. *D. notatus* (5), and Chironomidae (1) lie along the time axis but closer to the centroid, suggesting less dependence on time but no strong association with the other factors. By contrast, some earlier colonizers, such as *I. anglicana* (10), *S. inaequalis* (11), *T. velatus* (6) and *C. anomia* (4), lie closer to other vectors such as vascular plant species richness, percentage blue-green and pH.

#### Discussion

One problem in chronosequence studies that substitute space for time (Pickett 1989) is that prevailing conditions at any location have probably varied over the long time scales involved. For example, Kaufmann (2002) demonstrated faster community development on

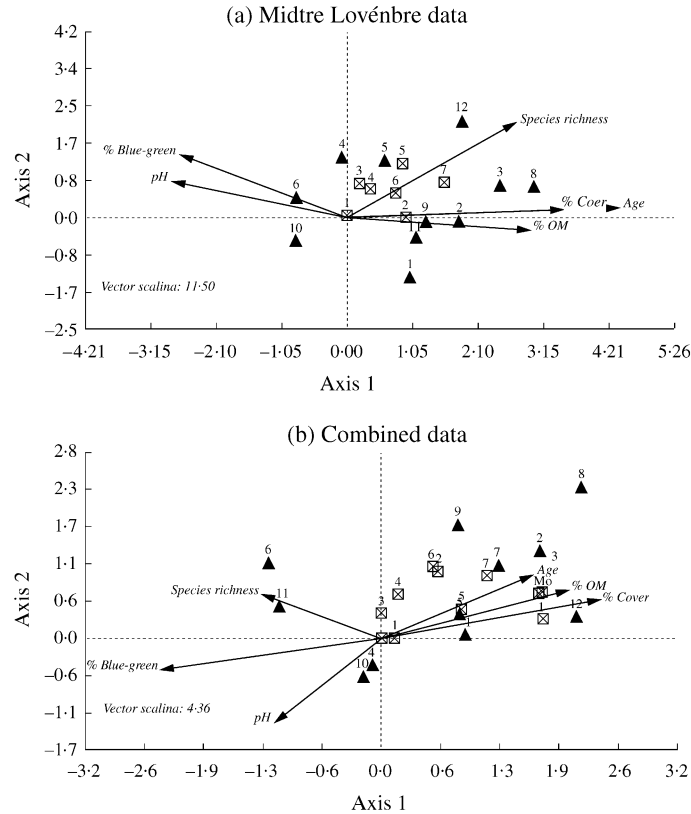




**Fig. 7.** Changes in the size distribution of *H. tullbergi* across the Midtre Lovénbre. Measurements are graticule units.

Rotmoos Glacier foreland over the last 30 y compared with the previous 30–50 years, linked to marginally warmer temperatures. Another confounding factor is rapid colonization of glacier forelands from lateral vegetated areas, as occurs on Rotmoos. Lack of such areas around Midtre Lovénbre, however, reduces this possibility significantly for soil animals, at least at sites 1–5, where the direction of colonization most probably corresponded with the long time axis of the chronosequence. Furthermore, because of low community diversity, there was little evidence of strong topographical variation in community composition at sites of equivalent age, as evident on Rotmoos (Kaufmann & Raffl 2002). Despite such potential limitations chronosequences provide unique insights into community assembly that cannot be replicated by short-term experimentation.

Time scales for community assembly were slow, reflecting harsh environmental conditions extending over hundreds to thousands of years, longer by an order of magnitude than most studies elsewhere (Matthews 1992). Nevertheless, the composition of animal communities developing on Midtre Lovénbre and Lovén Island chronosequences were broadly similar, despite their contrasting histories and situations. Thus the fauna of Leirholmen after 100 years corresponded closely with that of Midtre Lovénbre site 5, paralleling the established similarities in the soil and vegetation



**Fig. 8.** Results of CCA (axis 1 plotted against axis 2) for (a) the Midtre Lovénbre data alone and (b) combined data with the Lovén Island data added. Closed triangles represent individual animal species or groups, open squares represent sites and directional vector arrows represent the explanatory variables. See text for full explanation of trends.

(Hodkinson *et al.* 2003). Thus *I. anglicana*, *F. quadrioculata*, *Hypogastrura* spp., *C. anomia* and *T. velatus* were the dominant soil microarthropods, *H. spetsbergensis* and *E. psychrophila* the dominant spiders, *S. groenlandicus* and *A. pusillus* the dominant parasitoids and Enchytraeidae and terrestrial chironomids were present. Differences included the substitution of *H. tullbergi* by *H. viatica* on Leirholmen and the absence of some of the common Midtre Lovénbre species, such as *S. inaequalis* and *E. arctica*. These latter species, nevertheless, were present on the older islands. Similarly, the faunas of Midtholmen and Storholmen largely mirrored that of site 7, but lacked some minor species. Common additional elements included the herbivores *P. amentorum* and *A. svalbardicum*, together with the parasitoids *I. hyperboreus*, *D. bifoveatus*, *D. rapae* and *Alloxysta* sp., the spider *H. glacialis*, the syrphid *P. tarsatus* and the microarthropods *H. reticulata* and *O. neerlandica*. Lovén Island communities contained many flightless species that have dispersed effectively across the marine water barrier to and between islands over the last 100–1000 years (Coulson *et al.* 2002). Some apparently more sedentary soil-dwelling microarthropod species, however, such as *F. bisetosa*, *O. groenlandicus*, *M. sarekensis*, *C. hoeli* and a *Brachytho-nius* sp., together with parasitoids such as *A. borealis*, *G. glacialis* and *S. lineiger*, were absent from island samples. Enchytraeidae and *F. quadrioculata*, were significantly more abundant on the older islands than on Midtre Lovénbre, probably reflecting their better exploitation of deeper, moister organic soils.

Colonization rates by testate amoebae on Midtre Lovénbre contrasted strongly with those for volcanic tephra on Deception Island, South Shetland (Smith 1985). *Diffugia* sp. occurred within 1 year and three species were present after 60 years compared with the elapse of 150 years before first colonization of unfavourable sites on Deception. The apparent decline in species richness between sites 5–7 is, however, difficult to explain.

In addition to variations between chronosequences, more subtle differences may occur within species populations across the chronosequence. Varying population age structure of *H. tullbergi* across Midtre Lovénbre may thus result from poor recruitment related to low food availability and high desiccation stress, to which hatching Collembola are particularly susceptible (Birkemoe & Leinaas 1999). Alternatively, it may reflect differential dispersal of mature animals from favourable adjoining sites (Johnson & Wellington 1983; Hertzberg 1997; Hertzberg & Leinaas 1998). Mature Collembola often have a greater tendency to disperse than juveniles.

The chronosequences chosen showed strong directional trends for several factors and it is unsurprising that these often emerged as good predictors of species distributions. Factors linked positively to site age, or distance from the glacier, included soil OM, moisture, depth, clast size and total nitrogen as well as vegetation cover and vascular plant species richness. Other factors, such as cyanobacteria cover, were less dependent on

site age. Together these factors provide the environmental template for invertebrate colonization. Community assembly is, however, complex depending on the interplay between the ecology, ecophysiology and dispersal characteristics of individual species. Eight categories of colonizers, each with their characteristic demands can be recognized, namely:

(a) *Species independent of vascular plant establishment*. Includes surface-active species subsisting on allochthonous inputs of prey items or organic detritus. These are the first colonizers, including spiders such as *H. spetsbergensis*, *M. nigripes* and *E. psychrophila* and darker pigmented Collembola with protective pigmentation such as *I. anglicana*, *S. inaequalis* and *H. tullbergi*. Species are often highly dispersive and show some drought resistance (Hodkinson *et al.* 1996a; Coulson *et al.* 2002). The mite *C. anomia* is an exception that is slow-moving but it is, nevertheless, highly robust and drought-resistant and may be dispersed passively by other agencies (Hodkinson *et al.* 1996a; Coulson *et al.* 2002). These Collembola and mite species may feed on cyanobacteria or lichens as they become available.

(b) *Species dependent on soil formation linked to plant growth*. Includes Enchytraeidae and some soil-dwelling Collembola, such as *O. groenlandicus* and *F. bisetosa*. These are desiccation-susceptible species requiring deeper moist soils with a high organic content that tended to occur at older sites (Byzova, Uvarova & Petrova 1995; Hodkinson *et al.* 1996a; Birkemoe, Coulson & Sømme 2000).

(c) *Species dependent on cyanobacteria or lichen cover*. Embraces mites such as *T. velatus* and *D. notatus* whose population peaks corresponded with the maximum cover by blue-green bacteria or lichen. These are again desiccation-resistant surface-dwelling species (Hodkinson *et al.* 1996a).

(d) *Species dependent on colonization by the host plant*. Obligate herbivores whose appearance corresponded with the first colonization by their plant host. Included *P. amentorum* on *S. polaris* and *A. svalbardicum* on *D. octopetala* (Strathdee & Bale 1995).

(e) *Specialized predators/parasitoids/hyperparasitoids dependent on resident host species*. Includes species such as *I. hyperboreus*, *S. lineiger*, *D. bifoveatus*, *D. rapae*, *Alloxysta* sp. and *P. tarsatus* associated with obligatory prey. Other species such as *A. borealis* and *G. glacialis* are associated more closely with spider species and were distributed more broadly (Coulson *et al.* 2003a).

(f) *Less specific general predators dependent on general availability of prey*. Includes predatory mites that reflect the abundance of potential prey species such as *F. quadrioculata*. This may give the misleading impression in CCA that prey and predator are responding similarly to the same environmental variables.

(g) *Poor dispersers*. Species occurring only in the oldest soils and having poor dispersal powers, being apparently absent from sites, where on the basis of similar soil characteristics they might be expected to occur. Includes the mites *H. reticulata*, *C. hoeli* and *O. neerlandica*.

(h) *Vagrants*. Species of unknown biology that are not permanently resident, e.g. allochthonous Chironomidae that may be present at any site at any time.

Thus, the concept of facilitation, used widely in plant succession (McCook 1994; Callaway & Walker 1997), is equally applicable to animal community assembly. Some species are facilitated by the presence of specific plants, others by the presence of suitable animal hosts. Some require no facilitation, yet others require long-term general facilitation through soil development associated with plant growth.

Patterns of invertebrate community assembly observed parallel those elsewhere, on diverse substrates from mine spoil, polder, mud, scree, glacial moraine, landfill to volcanic lava and ash. Despite the apparent lack of a deep species pool, the same functional groups of species were the first to colonize, namely spiders, surface-active Collembola and desiccation-resistant mites (cf. Meijer 1980; Hutson 1980; Moore & Luxton 1986; Crawford *et al.* 1995; Judd & Mason 1995; Thornton 1996; Mrzljak & Wiegleb 2000; Kaufmann 2001; Hodkinson *et al.* 2002; Kaufmann *et al.* 2002). The main elements missing were surface-active predatory beetles, such as Carabidae, and larger scavenging orthopteroid insect orders sometimes found in the tropics and elsewhere.

High Arctic terrestrial ecosystems have low net primary productivity ( $< 140 \text{ g C m}^{-2} \text{ year}^{-1}$ ) and low vascular plant species richness, with an essentially two-dimensional vegetation structure (Bliss & Matveyeva 1992). Ecological theory predicts low diversity communities with relatively simple food chains and low connectivity (Bazely & Jefferies 1997; Morin 1999). Is this realized? The food web is dominated by detritivore and omnivores throughout community assembly, with herbivores of vascular plants relatively late entrants, such that they are unlikely to impact significantly on the early direction of plant succession as observed elsewhere (Brown & Gange 1992). However, the food web, particularly at the older sites, is surprisingly complex (cf. Summerhayes & Elton 1923). It comprises relatively high proportions of hymenopterous parasitoids, some hyperparasitoids and a complex of predators, including several spider species, some gamasid and prostigmatic mites and an aphidophagous syrphid. Several larger Hymenoptera were captured at densities that appear to exceed those of their potential prey (Coulson *et al.* 2003a). This raises the question of how the system sustains such extended food chains with an apparently high parasite/predator loading. The answer appears to lie in the spatial structure of the community and the vagility of parasitoids. The low diversity of plant species produces an extensive vegetation mosaic of relatively uniform species composition. Some prey species exist at low densities across this mosaic and their location requires widespread searching, particularly by the larger parasitoids. Trap catches reflect aggregate numbers of vagile parasitoids searching through the area rather than the absolute numbers present at one time. Furthermore, allochthonous inputs of both

insects and detritus provide significant further continuing subsidies to the terrestrial food web in areas of low productivity (Polis *et al.* 1997; Hodkinson *et al.* 2002).

Returning to our initial hypotheses, the evidence suggests that community assembly was both deterministic and directional (Ward & Thornton 2000), with similar common predictable patterns, involving common suites of species, across both chronosequences. This relates to species requirements as listed previously, which determine their point of entry into the community. However, as for the plant community (Hodkinson *et al.* 2003) it is difficult to distinguish between chance and determinism by default, when the community progressively recruits from a limited pool of effectively dispersed species. Kaufmann (2002) reached similar conclusions for his more complex community on Rotmoos Glacier foreland – that community assembly was an ordered and predictable process linked to the varying biologies and tolerances of the colonizing species. Nevertheless, several earlier colonizers exist independently of vascular plants and soil development. Later colonizers depend more directly on characteristics of the developing soil or the presence of particular plant types or species, which facilitate their establishment.

Another conclusion common with the Rotmoos study is that for the more abundant invertebrates rates of dispersal do not appear seriously to limit colonization (Kaufmann 2001; Kaufmann *et al.* 2002). This is evidenced by the fact that the colonization is almost instantaneous. For many other species requiring facilitation, colonization of three separate islands 3 km from the mainland did not present an insurmountable barrier given the time scales involved, and there was high commonality of species at comparable successional stages. Several species survive extended passage on or in seawater (Coulson *et al.* 2002) and only in the case of the less common soil-dwelling microarthropods restricted to Midtre Lovén site 7 does weak dispersal ability appear to limit their realized distribution.

Invertebrate community assembly on proglacial chronosequences in the High Arctic thus shares many common features with successions elsewhere, but with a greatly extended time scale. This raises concern over the long-term vulnerability of these isolated island communities when subjected to rapidly accelerating climate change. Future change will almost certainly occur more rapidly than in the past (IPCC 2001).

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## References

- Alsos, I.G., Elvebakk, A. & Gabrielsen, G.W. (1998) Vegetation exploitation by barnacle geese *Branta leucopsis* during incubation on Svalbard. *Polar Research*, **17**, 1–14.
- Ashmole, N.P., Ormomi, P., Ashmole, M. & Martin, J.L. (1992) Primary faunal succession in volcanic terrain: lava and cave studies on the Canary Islands. *Biological Journal of the Linnean Society*, **46**, 207–234.
- Bale, J.S., Hodkinson, I.D., Block, W., Webb, N.R., Coulson, S.C. & Strathdee, A. (1997) Life strategies of arctic terrestrial arthropods. *Ecology of Arctic Environments* (eds S.J. Woodin & M. Marquiss), pp. 137–165. Blackwell Science, Oxford.
- Bazely, D.R. & Jefferies, R.L. (1997) Trophic interactions in Arctic ecosystems and the occurrence of a terrestrial trophic cascade. *Ecology of Arctic Environments* (eds S.J. Woodin & M. Marquiss), pp. 183–207. Blackwell Science, Oxford.
- Birkemoe, T., Coulson, S.J. & Sømme, L. (2000) Life cycles and population dynamics of enchytraeids (Oligochaeta) from the High Arctic. *Canadian Journal of Zoology*, **78**, 2079–2086.
- Birkemoe, T. & Leinaas, H.P. (1999) Reproductive biology of the arctic collembolan *Hypogastrura tullbergi*. *Ecography*, **22**, 31–39.
- Birkemoe, T. & Liengen, T. (2000) Does collembolan grazing influence nitrogen fixation by cyanobacteria in the high Arctic? *Polar Biology*, **23**, 589–592.
- Birkemoe, T. & Sømme, L. (1998) Population dynamics of two collembolan species in an Arctic tundra. *Pedobiologia*, **42**, 131–145.
- Bliss, L.C. & Matveyeva, N.V. (1992) Circumpolar Arctic vegetation. *Arctic Ecosystems in a Changing Environment. An Ecophysiological Perspective* (eds S.F. Chapin, R.L. Jefferies, J.F. Reynolds, G.R. Shave & J. Svoboda), pp. 59–89. Academic Press, London.
- Brown, V.K. & Gange, A.C. (1992) Secondary plant succession – how is it modified by insect herbivory. *Vegetatio*, **101**, 3–13.
- Byzova, J.B., Uvarov, A.V. & Petrova, A.D. (1995) Seasonal changes in communities of soil invertebrates in tundra ecosystems of Hornsund, Spitsbergen. *Polish Polar Research*, **16**, 245–266.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.
- Chapin, F.S., Walker, L.R., Fastie, C.L. & Sharman, L.C. (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**, 149–175.
- Coulson, S.J., Hodkinson, I.D. & Webb, N.R. (2003a) Aerial dispersal of invertebrates over a High Arctic glacier foreland. *Polar Biology*, **26**, 530–537.
- Coulson, S.J., Hodkinson, I.D. & Webb, N.R. (2003b) Micro-scale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. *Ecography*, **26**, 801–809.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R. & Harrison, J.A. (2002) Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. *Functional Ecology*, **16**, 353–356.
- Coulson, S.J. & Refseth, D. (2004) The terrestrial and freshwater invertebrate fauna of Svalbard including Jan Mayen. *A Catalogue of the Svalbard Terrestrial and Marine Animals: Invertebrates, Fishes, Birds and Mammals* (eds H. Strøm & H. Goldman). Skrifter 201. Norwegian Polar Institute, Tromsø, in press.
- Coulson, S.J., Jussila, R., Hodkinson, I.D. & Webb, N.R. (2003c) *Synodites lineiger* (Thomson, 1893) (Hymenoptera: Ichneumonidae) new to Svalbard, with an updated list of ichneumonid species from the archipelago. *Norwegian Journal of Entomology*, **50**, 55–56.
- Crawford, R.L., Sugg, P.M. & Edwards, J.S. (1995) Spider arrival and primary establishment on terrain depopulated by volcanic-eruption at Mount St. Helens, Washington. *American Midland Naturalist*, **133**, 60–75.
- Hertzberg, K. (1997) Migration of Collembola in a patchy environment. *Pedobiologia*, **41**, 494–505.
- Hertzberg, K. & Leinaas, H.P. (1998) Drought stress as a mortality factor in two pairs of sympatric species of Collembola at Spitsbergen, Svalbard. *Polar Biology*, **19**, 302–306.
- Hodkinson, I.D., Coulson, S.J., Harrison, J.S. & Webb, N.R. (2001) What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic – some counter intuitive ideas on community assembly. *Oikos*, **94**, 349–352.
- Hodkinson, I.D., Coulson, S.J. & Webb, N.R. (2003) Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north west Svalbard. *Journal of Ecology*, **91**, 651–663.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R. & Block, W. (1996a) Can high Arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology*, **10**, 314–321.
- Hodkinson, I.D., Coulson, S., Webb, N.R., Block, W., Strathdee, A.T. & Bale, J.S. (1994) Feeding studies on *Onychiurus arcticus* (Tullberg) (Collembola, Onychiuridae) on West Spitsbergen. *Polar Biology*, **14**, 17–19.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R., Block, W., Strathdee, A.T., Bale, J.S. & Worland, M.R. (1996b) Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos*, **75**, 241–248.
- Hodkinson, I.D., Webb, N.R., Bale, J.S., Block, W., Coulson, S.J. & Strathdee, A.T. (1998) Global change and Arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. *Arctic and Alpine Research*, **30**, 306–313.
- Hodkinson, I.D., Webb, N.R. & Coulson, S.J. (2002) Primary community assembly on land – the missing stages: why are the heterotrophic organisms always there first. *Journal of Ecology*, **90**, 569–577.
- Hutson, B.R. (1980) Colonization of industrial reclamation sites by Acari, Collembola and other invertebrates. *Journal of Applied Ecology*, **17**, 255–275.
- IPCC (2001) *Summaries for Policymakers WG I 'Climate Change 2001: the Scientific Basis'. Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report: Contributions of IPCC Working Groups*. Cambridge University Press, Cambridge.
- Johnson, D.L. & Wellington, W.G. (1983) Dispersal of the collembolan, *Folsomia candida* (Willem), as a function of age. *Canadian Journal of Zoology*, **61**, 2534–2538.
- Judd, K.W. & Mason, C.F. (1995) Colonization of a restored landfill site by invertebrates, with particular reference to the Coleoptera. *Pedobiologia*, **39**, 116–125.
- Kaufmann, R. (2001) Invertebrate succession on an alpine glacier foreland. *Ecology*, **82**, 2261–2278.
- Kaufmann, R. (2002) Glacier foreland colonisation: distinguishing between short-term and long-term effects of climate change. *Oecologia*, **130**, 470–475.
- Kaufmann, R., Fuchs, M. & Gosterxeier, N. (2002) The soil fauna of an alpine glacier foreland: colonization and succession. *Arctic, Antarctic and Alpine Research*, **34**, 242–250.
- Kaufmann, R. & Raffl, C. (2002) Diversity in primary succession: the chronosequence of a glacier foreland. *Global Mountain Biodiversity: a Global Assessment* (eds C. Korner & E. Spehn), pp. 179–192. Parthenon, London.
- Leinaas, H.P. (1978) Sampling of soil microarthropods from coniferous forest podzol. *Norwegian Journal of Entomology*, **25**, 57–62.

- Lindroth, C.H., Andersson, H., Bodvarsson, H. & Richter, S.H. (1973) Surtsey Iceland. The development of a new fauna 1963–70: terrestrial invertebrates. *Entomologica Scandinavica Supplement*, **5**, 1–280.
- Majer, J.D. (1989) *Animals in Primary Succession. The Role of Fauna in Reclaimed Lands*. Cambridge University Press, Cambridge.
- Makerenkov, V. & Legendre, P. (2002) Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecology*, **83**, 1146–1161.
- Matthews, J.A. (1992) *The Ecology of Recently Deglaciated Terrain*. Cambridge University Press, Cambridge.
- McCook, L.J. (1994) Understanding ecological community succession – causal models and theories, a review. *Vegetatio*, **110**, 115–147.
- Meijer, J. (1980) The development of some elements of the arthropod fauna of a new polder. *Oecologia*, **45**, 220–235.
- Miles, J. & Walton, D.W.H. (1993) Primary succession revisited. *Primary Succession on Land* (eds J. Miles & D.W. H. Walton), pp. 295–302. Blackwell Science, Oxford.
- Moore, F.R. & Luxton, M.S. (1986) The collembolan fauna of two coal shale tips in Northwest England. *Pedobiologia*, **29**, 359–366.
- Morin, P.J. (1999) *Community Ecology*. Blackwell Science, Oxford.
- Mrzljak, J. & Wiegleb, G. (2000) Spider colonization of former brown coal mining areas – time or structure dependent? *Landscape and Urban Planning*, **51**, 131–146.
- O'Connor, F.B. (1962) The extraction of Enchytraeidae from soil. *Progress in Soil Zoology* (ed. P.W. Murphy), pp. 279–285. Butterworths, London.
- Petersen, H. (1971) Methods for estimation of growth of Collembola in cultures and in the field, exemplified by preliminary results for *Onychiurus furcifer* (Börner). *Annales de Zoologie, Écologie Animale*, **3**, 235–254.
- Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. *Long-Term Studies in Ecology* (ed. G. Likens), pp. 110–135. Springer-Verlag, Heidelberg.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.
- Sendstad, E., Solem, J.O. & Aagard, K. (1976) Studies of terrestrial chironomids (Diptera) from Spitsbergen. *Norwegian Journal of Entomology*, **24**, 91–98.
- Smith, H.G. (1985) The colonization of volcanic tephra on Deception Island by Protozoa: long term trends. *British Antarctic Survey Bulletin*, **66**, 19–33.
- Strathdee, A.T. & Bale, J.S. (1995) Factors limiting the distribution of *Acyrtosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. *Polar Biology*, **15**, 375–380.
- Summerhayes, V.S. & Elton, C. (1923) Contributions to the ecology of Spitsbergen and Bear Island. *Journal of Ecology*, **11**, 214–287.
- Thornton, I.W.B. (1996) The origins and development of island biotas as illustrated by Krakatau. *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes* (eds A. Keast & S. Miller), pp. 67–90. SPB Academic Publishing, Amsterdam.
- Ward, S.A. & Thornton, I.W.B. (2000) Chance and determinism in the development of isolated communities. *Global Ecology and Biogeography*, **9**, 7–18.
- Zingerle, V. (1999) Spider and harvestman communities along a glaciation transect in the Italian Dolomites. *Journal of Arachnology*, **27**, 222–228.

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