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Food sources of early colonising arthropods: The importance of allochthonous input

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ABSTRACT

Arthropod predators and detritivores are among the first colonisers on land surfaces undergoing primary succession. In the absence of higher plants and herbivores, they may either have an allochthonous food source (i.e. of geographically distant origin) or local food source that is sustained by e.g. microorganisms. By studying spiders and collembolans on sites along chronosequences on recently emerged nunataks (ice-free land in glacial areas), we analysed whether the food source of early colonisers was of local or distant origin. Also, we measured the potential changes in trophic position with increasing site age. With stable carbon and nitrogen isotope analysis of both spiders and collembolans, we determined that allochthonous food sources are important on the youngest sites. The allochthonous food sources may explain how arthropods can persist in the absence of local primary productivity. Also, some spider species may increase their ability to survive by shifting their trophic position as the community composition changes. The results indicate that a wolf spider species shifted towards a lower trophic level with increasing site age. By contrast, no shifts in trophic position were observed for sheet-web spiders or collembolans.

Introduction

The general view of primary succession, where primary productivity is needed before invertebrates can colonise, is challenged by studies showing that arthropod predators and detritivores are among the first colonisers on virgin land (Hodkinson et al. 2002). This has been reported from a number of substrates that are subjected to primary succession, e.g. glacier forelands (Kaufmann 2001; Hodkinson et al. 2004), lava fields and pyroclastic flows (Ashmole et al. 1992; Sugg and Edwards 1998; Edwards and Thornton 2001). In the absence of higher plants and herbivores, predators and detritivores may either feed on allochthonous food source (i.e. of geographically distant origin) or local resources out of the decomposer system. The local resources are then either supported by allochthonous nutrient input (as suggested by Ashmole et al. 1992; Hodkinson et al. 2002) or by local microorganisms. In the present paper, we use stable isotope analyses to determine the potential importance of allochthonous food resources for predators and detritivores at primary succession sites. Further, we analyse whether or not these arthropods change their diet at different successional stages.

At primary succession sites, the organic matter of recently emerged substrates contains more of the heavy carbon isotope, ^{13}C, than older vegetated soils (Bardgett et al. 2007). This difference in ^{13}C content can be used to trace the source of carbon in the food web because the ^{13}C content increases only slightly (0.5–1.0‰) from one trophic level to another (Deniro and Epstein 1978; Minagawa and Wada 1984). Indeed, this method has been used to identify the relative importance of allochthonous food sources, e.g. terrestrial sources for aquatic food webs (Rau 1980) and vice versa (Collier et al. 2002), but so far, not to trace food sources during primary succession. The relative amount of the heavy isotope of nitrogen, ^{15}N, increases step-wise from one trophic level to another (Minagawa and Wada 1984; Oelbermann and Scheu 2002; Vanderklift and Ponsard 2003; Wise et al. 2006), which enables studies of trophic position of arthropods. Changes in trophic position of generalist predators have been detected during primary succession, suggesting that during early stages of community assembly they mainly feed on detritivores but gradually shift to predators when these become relatively abundant (König et al. 2011). In the presence of plants, a shift towards herbivory has been observed for collembolan species (Endlweber et al. 2009) and for species that feed on microorganisms we expect a shift towards microorganisms that use plant material as food resource.

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Classic sites for studies of primary succession are patches of land that emerge following glacier retreat. To take into account not only the temporal factor of assembly but also the spatial factor of the influx of allochthonous organisms, we set out to characterise primary food web assembly on nunataks (ice-free land in glacial areas) in Iceland. Since the end of the 19th century, the Vatnajökull glacier in Iceland has decreased in volume by about 10% (Björnsson 2009) and consequently nunataks have increased both in number and size. Thus, they have the restricted boundaries of islands and chronological sequences of primary succession. The first colonisers on the nunataks are detritivorous dipterans and collembolans, spiders and mites, which may be either detritivorous or predators (Ingimarsdóttir et al. 2013). Three spider species and two collembolan species were chosen for this study, which all were present on soils of different age and on more than one nunatak. The spiders are sheet-web spiders (Linyphiidae), *Meioneta nigripes* (Simon, 1884) and *Collinsia holmgreni* (Thorell, 1871), and a wolf spider (Lycosidae), *Pardosa palustris* (Linnaeus, 1758). Both sheet-web spider species are common on sparsely vegetated land (Agnarsson 1996) and *M. nigripes* is recognised as an early coloniser (Lindroth 1973; Hodkinson et al. 2004). The wolf spider, *P. palustris*, is associated with a variety of habitats (Agnarsson 1996). The collembolan species are *Pseudisotoma sensibilis* (Tullberg, 1876) which is associated with a variety of habitats, and *Desoria olivacea* (Tullberg, 1871) which is abundant in wet habitats (Fjellberg 2007).

Materials and methods

Sampling sites

The fieldwork was performed on nunataks in Vatnajökull glacier in SE-Iceland. In the summer of 2008 the study was conducted along a chronosequence of sites on four nunataks on the southeast part of the glacier. The sites comprised 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 older nunatak, Esjufjöll, has been partly icefree, at least since the last glaciation (Björnsson personal communication), 10,000 years ago. The time since deglaciation, within each nunatak, was estimated with various methods, e.g. by comparing old and new maps and photos, and with help of mapping that has previously been done with global positioning system (gps) (see Ingimarsdóttir et al. 2013). Each site age was determined with a range of 10–30 years, except for the youngest sites that we know are 0–3 years old and the older site of the eight year old Maríusker, which we know is 3–8 years old. The median age of each site is used in the analyses (Table 1). Three transects were located along the chronosequence on each nunatak and as possible, they were located in different directions from the oldest central part of each nunatak to encompass different parts of the nunatak. Sampling plots (5 m × 5 m) were located along the transects within two sites on Maríusker and three and four sites on Bræðrasker nunatak and Kárasker and Esjufjöll nunataks, respectively. In the summer of 2009, Maríusker was visited again along with two additional nunataks that are located on the southwest part of the Vatnajökull glacier. The nunatak Vöttur was first seen on aerial photos in 1992 (Guðmundsson 2009) and Húsbóndi emerged around year 2000 (Guðmundsson 2005). Further knowledge of site age within the Vöttur and Húsbóndi nunataks was missing so each was regarded as one site. The nunatak Húsbóndi was only 900 m^2 in size so only two plots were placed there. On the nunatak Vöttur, three plots were randomly chosen to be included in this study.

Five pitfall traps (6.3 cm diameter, 6.5 cm depth) were placed randomly within each plot, containing 4% formaldehyde with additional detergent. The trapping period in 2008 was from 27 June to 1 August on Maríusker, 3–24 July on Bræðrasker, 29 June to 24 July on Kárasker and 8–29 July on Esjufjöll. The trapping period on Húsbóndi and Vöttur was from 13 July to 27 July 2009 and on Maríusker from 10 to 31 July 2009. Due to flooding and soil movements, only three traps from each plot could be used for analyses, and for the same reason only one or two traps could be used from each plot on Maríusker 2008. After each trapping period the formaldehyde solution was rinsed off the samples and the samples were preserved in 70% ethanol for almost three years, before the stable isotope analyses.

Soil samples of 10 cm × 10 cm and 5 cm depth were taken with a knife or spoon, when the soil was loose, to measure the isotopic value of the soil organic matter. All stones (>5 mm) were removed and then a subsample (approx. 7 g) of three soil samples per plot were oven-dried at 100 °C for about 24 h, weighed and then burned in an oven at 600 °C for 10 h to determine the loss of ignition that gives the organic matter of the soils.

Stable isotopes analyses

All spiders and collembolans were counted and identified to species, except for juveniles of the sheet-web spiders. The abundance was standardised to catch per trap per day. The five species that were chosen for this study were all found in sufficient number (at least three spider specimens and 25–50 collembola specimens per site, during the whole trapping period) on different sites and on at least two nunataks (Table 1). The specimens were dried at 60 °C for about 24 h. The dried wolf spider specimens were ground in a ball mill before they were weighed (with the range of 0.13–0.15 mg) into tin capsules. The whole body of the sheet-web spiders was weighed into tin capsules when possible. *M. nigripes* is a small spider species so in most cases 1½ specimen was needed to reach the required weight. Therefore, the isotopic values of *M. nigripes* contain a mixture of two specimens. This means that the number of replicates for this species was reduced to one or two per plot. A few samples of the other spider species were also a mixture of two specimens. Each collembolan sample consists of several collembolans. A subsample from one dried soil sample per plot was sieved with a mesh size of approximately 2 mm, crushed with a mortar into homogenous powder, and weighed into tin capsules so that the organic carbon in each sample would be within the range of 0.2–1.0 mg, when possible.

Analyses of the amount and ^{13}C ratios of soil carbon, as well as the ^{13}C and ^{15}N isotope ratios of the arthropods, were performed with an Isoprime isotope ratio mass spectrometer (Isoprime Ltd., Cheadle, UK) coupled to a Eurovector CN elemental analyser (Eurovector, Milan, Italy) using continuous flow. The isotope ratios are expressed as the deviation (‰) from a standard Pee Dee Belemnite (PDB) for carbon and from atmospheric N_2 for nitrogen: δ^{13}C or δ^{15}N (‰) = $(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standard deviation of isotope measurements of standard material (peach leaves, NIST) was ±0.2‰ for δ^{15}N and ±0.1‰ for δ^{13}C.

Changes in isotopic ratio of carbon and nitrogen following formaldehyde and ethanol treatments have been described (e.g. Ponsard and Amlou 1999; Sticht et al. 2006), but others have found only minor effects of the use of these preservatives on invertebrates (Sarakinos et al. 2002; Syväranta et al. 2008). Prior to the analyses, we compared the isotopic values of laboratory reared moths (*Agrotis segetum*) that had been preserved in a freezer with those preserved with formaldehyde/ethanol. We found no significant differences. According to these results, and because all the arthropods were preserved in the same way, no corrections were made of the isotopic values.