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Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates

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Glaciers are retreating and predatory invertebrates rapidly colonize deglaciated, barren ground. The paradox of establishing predators before plants and herbivores has been explained by wind-driven input of invertebrate prey. Here we present an alternative explanation and a novel glacier foreland food web by showing that pioneer predators eat locally produced midges containing 21,000 years old ancient carbon released by the melting glacier. Ancient carbon was assimilated by aquatic midge larvae, and terrestrial adults achieved a radiocarbon age of 1040 years. Terrestrial spiders, harvestmen and beetles feeding on adult midges had radiocarbon ages of 340–1100 years. Water beetles assumed to eat midge larvae reached radiocarbon ages of 1100–1200 years. Because both aquatic and terrestrial pioneer communities use ancient carbon, the term "primary succession" is questionable in glacier forelands. If our "old" invertebrates had been collected as subfossils and radiocarbon dated, their age would have been overestimated by up to 1100 years.

Glaciers are melting and retreating worldwide[1–3]. Large areas of barren ground are opened for colonization by a broad range of life forms. This colonization, which is a complex and multifaceted process[4–6], has received much attention as melting glaciers are an iconic symbol of climate change[7]. However, the colonization of pioneer organisms on barren ground has long remained enigmatic because their succession does not follow the common sequence; autotrophic plants first, followed by herbivores, and then predators. On the contrary, heterotrophic organisms, like predatory beetles, spiders and harvestmen are early colonizers that typically establish before any visible autotrophs[8–12]. This seemingly ecological paradox is thought to be explained by wind-driven input of invertebrate prey[9,13,14]. However, melting glaciers have been shown to release biogeochemically diverse organic matter, a portion of which consists of ancient carbon with radiocarbon ages that range from 600 to 8,500 years[15]. Interestingly, the bioavailability of glacier-derived ancient carbon is positively correlated with increasing radiocarbon age[16]. This suggests that truly old carbon has a great potential to enter into contemporary food webs, which was corroborated by recent work highlighting the role of melting glaciers for carbon cycling in glacier forelands, glacier-fed streams and coastal estuaries[15–18]. For example, ancient carbon can be a significant or complementary energy source for pioneer heterotrophic microbial communities in glacier forelands following glacial retreat[18] and it enters into low trophic levels in food webs of glacier-fed rivers[17] and coastal oceans[16]. It is also known that ancient carbon from peat can be assimilated by aquatic organisms. For example, oldsquaw ducks, *Clangula hyemalis*, can have substantial amounts of ancient carbon in their muscle tissue if they feed on freshwater invertebrates in lakes and ponds receiving particulate peat carbon[19]. Yet, the potential entry of ancient carbon into modern food webs remains poorly understood, particularly the transfer of ancient carbon from low to high trophic food web levels.

Here we show that ancient carbon released by a melting glacier rapidly enters high trophic levels in both aquatic and terrestrial communities on pristine ground, resulting in living invertebrates with a high radiocarbon age. We also document a combined aquatic and terrestrial food web from a recently deglaciated moraine landscape, which challenges the classic "predator first" hypothesis.

Results

Ancient carbon feeds pioneer animals. Our study area, the Midtdalsbreen Glacier and its foreland, is part of Hardangerjøkulen, a 73 km^2 large glacier in central-south Norway. The foreland (60°34′N; 7°28′E), nearly 1400 m above sea level, is characterized by harsh environmental conditions, particularly during winter. Midtdalsbreen has retreated 154 m during 2001–2011, and 34 m in 2010. Samples of surface soil taken 20 m from the glacier edge in September 2010 contained organic matter which was in average 21,000 years old (Supplementary S1). We assume that this results from a mix of three different carbon pools, i.e. recent organic material blown onto the glacier surface, 4,000–8,000 years old carbon from the time when the glacier was absent periodically[20], and organic material from the "Ålesund interstadial" (38,000–35,000 BP) when the ice sheet over south Norway was strongly reduced[21–23]. As the pristine moraine ground was inhabited by surface-active microarthropods and predatory beetles, spiders, and harvestmen before higher plants had been established[4,11,24,25], we suspected that ancient carbon could enter the pioneer food webs and serve as an energy source. Invertebrates for radiocarbon analyses were sampled on a 2005 moraine in 2011 and 2012, about 100 m from the ice edge. The aerial photo from 2007 (Fig. 1) shows the actual landscape, with some of the dated moraines.

According to radiocarbon dating, specimens of the wolf spider *Pardosa trailli*, the harvestman *Mitopus morio*, and the ground beetles *Nebria nivalis* and *Bembidion hastii*, were 340, 570, 690, and 1100 years old, respectively (Fig. 1 and Supplementary S1). This indicates that glacier foreland predators contain significant amounts of ancient carbon. Except for microarthropods, these are the invertebrates with highest surface activity on recently deglaciated ground, with *B. hastii* being the clearly most active[11]. However, to understand the transport of ancient carbon up to the predator level, the prey must be identified. A potential prey for all four predators is surface active springtails (Collembola), which showed considerable surface-activity on the pioneer ground[11,25]. Surprisingly, only minor amounts of ancient carbon was found in springtails, as *Bourletiella hortensis* and a mix of four Isotomidae springtail species were each radiocarbon-dated to about 60 years old (Supplementary S1). Our next step to identify the prey was gut analyses. Although the liquid gut content of spiders does not give visually clues, the gut content of the three other predators contained well-preserved chitinous parts of their invertebrate prey. Microscopic studies of their gut contents revealed very few remnants of springtail prey, but a significant, although varying amount of adult chironomid midge remnants, i.e. facet eyes, antennae and other typical fragments (Supplementary S2). Surface active chironomid midges collected on a six-year-old moraine had a radiocarbon age of 1040 years (Fig. 1 and Supplementary S1). Thus these midges apparently transported ancient carbon to all four predators (Fig. 1). Most of these chironomids were small Orthocladiinae and Tanytarsini species, whose larvae develop in water or moist soil. Since zooplankton can ingest small particles containing ancient carbon in rivers[17], it is likely that the midge larvae in our study developed in glacial meltwater dams and ingested organic particles containing ancient carbon. Chironomids can be carried far by wind[14], but the presence of ancient carbon indicates that many of them must have developed locally.

Previous studies have shown that ancient and bioavailable carbon is metabolized at low trophic levels[16–19]. Our results extend these findings by showing an extensive *in situ* use of ancient carbon by several organisms in a glacial foreland, and that ancient carbon enters high trophic levels of the recent food web soon after deglaciation. In our case, the chironomids transferred the ancient carbon from freshwater to terrestrial habitats. They thus may play a pivotal role in glacial foreland ecosystems by buffering energy limitation by using and transporting ancient carbon. This situation differs from primary succession that starts without ancient carbon. Because energy for pioneer organisms is partly delivered by the glacier, the term "primary succession" is questionable in glacier forelands. A further extension of our results relates to the dating of fossil organisms. If some of our "old" invertebrates had been collected as subfossils and radiocarbon dated, their true age would have been overestimated by up to 1100 years.

A pioneer food web. The pioneer food web on barren ground includes aquatic and terrestrial habitats (Fig. 2). Ancient carbon in freshwater is assimilated by larvae of chironomid midges, and further transported to terrestrial predators via adult, flying midges. We also recorded ancient carbon in aquatic predators. In a dam younger than

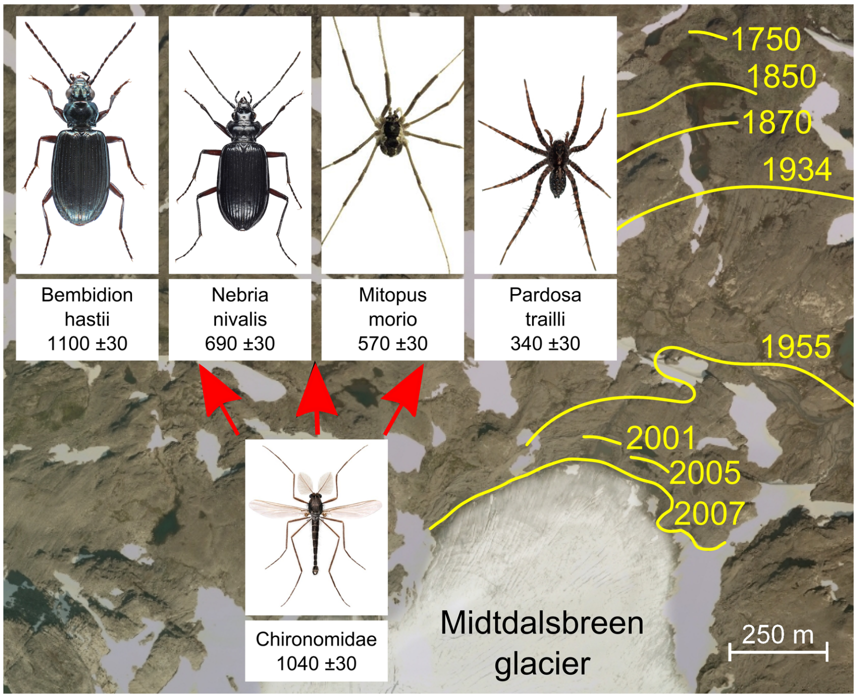

Figure 1 | Radiocarbon ages of chironomid midges and four predators collected in 2011 and 2012 on the 2005 moraine. The aerial photo of the glacier foreland, taken in 2007, shows several dated moraines. The melt water dam in Supplementary S3 is situated just inside the 2005 moraine. Aerial photo source© Norway Digital. O. Hanssen and G. H. Morka are acknowledged for the beetle and spider photos, and H. Elven is acknowledged for the Chironomidae drawing.

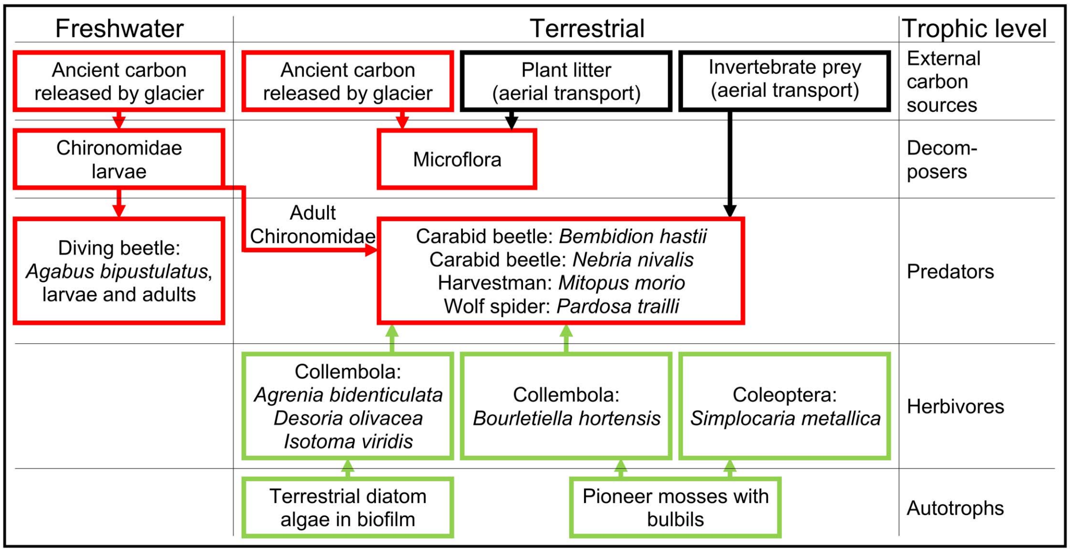

Figure 2 | Food web on pioneer ground, combining aquatic and terrestrial habitats. In both habitats, it is distinguished between autotrophs, herbivores, predators, decomposers and external sources of carbon and energy. Red boxes show flow of ancient carbon, green boxes flow of chlorophyll-produced carbon, and black boxes flow of aerial transported carbon (plant litter and invertebrate prey). The possible use of ancient carbon by terrestrial microbial communities is from the literature[18].

seven years (Supplementary S3), predatory larvae and adults of a diving beetle had a radiocarbon age of 1200 and 1130 years, respectively (Supplementary S1). We suspect they ate Chironomidae larvae. Because the fully grown beetle larvae leave the water in order to pupate on land, they may also transport ancient carbon to terrestrial predators.

The guts of Arthropleona Collembola, where *Agrenia bidenticulata* and *Desoria olivacea* dominated, did not contain fungal hyphae, as would be expected if they were decomposers of inblown organic material. Instead, they had transparent gut content with a high density of tiny mineral particles. Surprisingly, diatom algae with characteristic silica cell walls could be seen among the mineral particles in several guts (Fig. 3a–b). Diatoms were observed in 14% of the guts of 372 specimens of *Agrenia bidenticulata*, and in 5% of 127 guts in *Desoria olivacea*. These percentages are probably underestimated, since high density of mineral particles can mask the diatoms. On moist surfaces of sand and silt, terrestrial diatoms have the ability to establish a slimy biofilm by producing large quantities of extracellular polymeric substances. In this "microbial mat", they live together with other one-celled organisms and perform photosynthesis[26–28]. We assume that *Agrenia* and *Desoria* Collembola have eaten this biofilm, which is rich in proteins and carbohydrates, explaining the occurrence of transparent gut content with diatoms. When eating the biofilm, it is probably unavoidable to ingest tiny mineral particles at the same time. Guts of the large Collembola species *Bourletiella hortensis*, however, contained various species of mosses, including nutrient-rich diaspore bulbils (Fig. 3c–d), and sometimes a few fungal hyphae. Also adults of a pioneer beetle *Simplocaria metallica*, contained moss in the gut. Few insects are moss eaters, but beetles of the family Byrrhidae is an exception. Pitfall traps documented that moss fragments often were blown onto the pioneer ground, and tiny moss plants, barely visible by eye, established before higher plants[4,11]. We thus conclude that chlorophyll-based food chains start almost immediately on pioneer ground, but biofilm, moss diasporas and pioneer moss plants avoid the observer's eye.

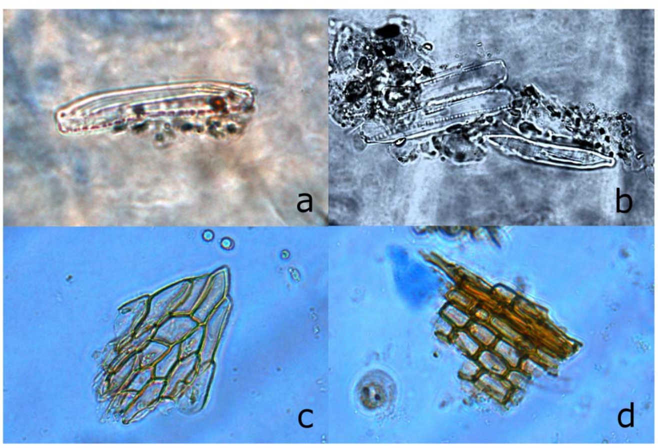

Figure 3 | Gut contents of pioneer Collembola. (a–b): Pennate diatom algae in guts of *Agrenia bidenticulata* (in b seen from different sides), (c–d): Moss fragments in the gut of *Bourletiella hortensis*. c = Tip of small leaf from the end of a dispersal unit (bulbil) of *Pohlia filum*. d = Leaf fragment of *Ceratodon purpureus*.

Discussion

Our pioneer glacier foreland community could be called "the invisible carbon source community", being driven to a large degree by a combination of ancient carbon from the glacier and unnoticed algae and mosses. We explain the paradox of pioneer terrestrial predators by their feeding on locally produced chironomid midges, which transport significant amounts of ancient carbon from aquatic habitats. The paradox of pioneer "decomposing" Collembola is explained by their herbivore habits in the glacier foreland, feeding partly on terrestrial biofilm with diatom algae, and partly on small and hardly visible pioneer mosses and their diaspores. In contrast to earlier theory, chlorophyll-based food chains start almost immediately by grazing Collembola, but they are unimportant for the predators. These observations shed a new light on pioneer food webs and early succession. Because ancient carbon from the glacier matters as an energy source, the term "primary succession" should be used with care. Finally, there is an increasing awareness of the importance of interactions between terrestrial and freshwater ecosystems regarding energy flow and element cycling[29–31] and our result adds a further dimension to the functional importance of interactions between different types of biota.

Methods

Sampling. Samples of soil for radiocarbon dating were collected in September 2010 a few weeks after the soil was deglaciated and about 20 m from the lower end of the glacier. The organic matter content in the soil samples was 0.49–0.65% (dry mass) when stones above 2 mm had been removed. Terrestrial invertebrates for radiocarbon dating and gut content analyses were pitfall-trapped on the 2005 moraine after 3–7 years (Fig. 1). Adults and larvae of diving beetles were collected by a sieve in a meltwater dam, about 50 × 20 m, less than seven years old, in August 2012 (Supplentary S3).

Radiocarbon analyses. Radiocarbon dating of soil samples and animals (Supplementary S1) was done by Beta Analytic, which is an ISO 17025-accredited radiocarbon dating laboratory in Miami, Florida.

Gut content analyses. Gut contents of predators (Supplementary S2) were carefully dissected and examined by a microscope at 400–1000 × magnification in a mixture of glycerol and lactic acid. Chironomids were identified by characteristic fragments of antenna and other body parts. Fragments of Diptera compound eyes were easy to identify and count, and were assumed to belong mainly to Chironomidae. Collembola remains were identified by species-specific, nondigestible chitionous part like jaws, claws and furca. Gut contents of Collembola were observed on ordinary slides, where gut content could be seen through a bleached body wall. Animals were sometimes squashed to spread compact gut contents. Diatom algae in Collembola guts were identified by their unique cell wall made of silica, and their form.

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Author contributions

S.H. and M.O. cooperated in designing the research and in writing the main manuscript text. S.H. organized the field work and radiocarbon dating, and performed the gut analyses.

Additional information

Supplementary information accompanies this paper at http://www.nature.com/scientificreports

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