

Reviewer 1:

2. Does the paper present novel concepts, ideas, tools, or data? Highlight the importance of microbial communities for primary succession.

In the revised version we clarified that the focus of the review is the role of microbial communities for primary succession.

For example:

Title:

*“The role of microorganisms at different stages of ecosystem development for soil formation”
line 36:*

“The review focusses on the microbiology of major steps of soil formation.”

12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used? There are too many abbreviations (C, N, SOM, OM, SOC, BP, OC, BSC). Even though most of them well known for soil scientists, they still need to be spelled out when mentioned for the first time.

We reduced the number of abbreviations to the names of the elements (C, N, P, S) and biological soil crusts (BSC). All other abbreviations have been deleted in the revised version for means of clarification

13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated? Figures are nice, but not explored in the text.

We explored Figures in more detail in the revised version.

Example:

“As depicted in Figure 1 the glacier forefield is flanked by two lateral moraines, which emerged during the Little Ice Age around 1850. Two brief advancements of the glacier in 1928 and 1992 resulted in two further moraines, which divided the forefield in three parts: initial (6 – 13 yr), intermediate (50 – 80 yr) and developed sites (110 – 150 yr).”

“Decomposition and mineralization of this organic matter was suggested to be the dominant N transformation process in the initial soils at the Damma glacier (Brankatschk et al., 2011), which is declared as initial phase in Figure 2.”

“As shown in Figure 3 BSC development at the Damma glacier is very heterogeneous and strongly depends on the right equilibrium of water availability and water holding capacity of the substrate.”

“However, during incubation the N content of L. alpina grown in the 10-year soil strongly increased while plant and roos biomass stays stable as shown in Figure 4,...”

General comments:

This discussion papers deals with the role of microorganisms and plants during soil development, using the chronosequence found at Damma glacier as an example. The topic of this review is very interesting, as it highlights the key role of microorganisms already at the initial stages of development, before plants get established. There is however a mismatch between the title of this review and its contents, especially when it comes to plants. Plants and plant microbe interactions are very important for reaching the final stages of soil development, but these factors are not fully developed in the text. I would suggest to remove plants from the title, keep the major focus on microbes and discuss plants more in the plant-microbe interaction.

We changed the title to “The role of microorganisms at different stages of ecosystem development for soil formation” and also specified that in the abstract and introduction.

“The review focusses on the microbiology of major steps of soil formation.”...

“In this review we summarized our current knowledge about the role of microorganisms in soil development by using current data from the Damma glacier forefield chronosequence and how this improves our view of soils as the most important bioreactor on earth. “

I miss a general description of the stages of soil development, in terms of amount of biological crust, plant cover/types, nutrients, pH, etc. It could be added as a table, linked to figure 1. That would help illustrating many of the concepts/results presented in the review.

We provided in the revised version a table including dominant plant species, plant coverage, pH, maximum water holding capacity, microbial biomass carbon, total carbon, total nitrogen, dissolved organic nitrogen, dissolved organic carbon, nitrate, ammonium and phosphate.

	approximate soil age			
	6-13 yr	60-80 yr	110-150 yr	2000 yr
plant coverage	< 10%	> 70%	100%	100%
dominant vegetation	<i>Agrostis gigantea</i> , <i>Rumex scutatus</i> , <i>Cerastium uniflorum</i> , <i>Oxyria digyna</i>	<i>Agrostis gigantea</i> , <i>Salix</i> spp., <i>Deschampsia cespitosa</i> , <i>Athyrium alestre</i>	<i>Rhododendron ferrugieum</i> , <i>Salix</i> spp., <i>Agrostis gigantea</i> , <i>Festuca rubra</i>	<i>Agrostis gigantea</i>
pH _{CaCl2}	5.5	4.7	4.6	3.6
mWHC [%]	3.5	2.4	4.8	6.7
microbial biomass C	58	122	241	902
microbial biomass N	6	19	29	115
TC	700	4700	12000	39600
TN	70	250	730	2670
DOC	7	18	42	78
DON	0.3	0.9	3	12
NO ₃ ⁻	0.1	0.2	1.3	0.8
NH ₄ ⁺	0.03	0.2	7	13
NaHO ₃ extractable P	6.7	9.7	7.8	n.d.
S	0.25	1.25	870.7	1300

Another major comment relates to the figures, which are very nice but hardly explored in the text.

We explored Figures in more detail in the revised version. For details see comment above.

I would suggest sending it to a native English speaker. There are some very long or too short sentences, the use of English is not always correct (too many to be mentioned) and punctuation marks are not always properly used.

We gave the manuscript to a native speaker for proof-reading.

Specific comments:

P1868, L17-18: what do you mean by “the respectively set up of plant communities”?

With respect to the general comment about the plants we changed that sentence to point out the importance of plant-microbe interaction for the establishment of stable plant communities.

“The review focusses on the microbiology of major steps of soil formation. Special attention is given to the development of nutrient cycles, on the formation of biological soil crusts (BSCs) and the establishment of plant-microbe interactions.”

P1869, L3-12: please rephrase these sentences, they are too long and hard to read.

We rephrased and condensed the sentences.

“Due to the complex interactions it is not surprising that the formation of soils with a high level of fertility is a result of more than 1000 years of soil “evolution” (Harrison and Strahm, 2008). As a result of global change in general and the loss of soil quality in particular many soils are threatened. Thus, there is a huge need to develop strategies for a sustainable protection of soils for future generations. In this respect the knowledge gained from soil chronosequences might help to improve our understanding about the development of biotic-abiotic interplays and to identify factors that drive the formation of soils (Doran, 2002).“

P1869, L29: delete “as”

Has been deleted.

P1870, L12-16: please rephrase these sentences

We rephrased and condensed the sentences.

“Forefields of receding glaciers are ideal field sites to study the initial steps of soil formation as in a close area of some square kilometres a chronosequence of soils of different development stages can be found. As time is substituted by space a simultaneous comparison of the formation of organismic interactions and of abiotic – biotic interfaces at different development stages is possible.”

P1871, L3-5: replace “picture on” by “view of”. Delete “approaches”

Has been replaced.

P1872, L23: delete “and can be considered as important C456 contributors” which is a repetition of what you said earlier in this sentence.

Has been deleted.

P1873, L2-5: replace “a predicting” by “the prediction”.

Has been replaced.

If this field observations are rare, why not providing more details about what Tamburini et al 2010 found?

We included a brief description about the outcome of the mentioned study.

“Direct field observations are rare and include for example a study on the role of microorganisms in phosphate cycling in the Damma glacier forefield (Tamburini et al., 2010), which revealed a shift from substrate derived P at initial sites to internal P turnover at more developed sites.”

P1874, L1: what do you mean by in abiotic initial soils?

As this part duplicates the chapter before we deleted the first paragraph. The chapter now starts with:

“At the Damma glacier important macronutrients, such as phosphorus (P) and sulfur (S) are part of the mineral composition....”

P1874, L19: delete C

Has been deleted.

P1874, L22: I don’t think “we” is appropriated here, since the authors from the cited paper are not the same as the those writing these review.

Indeed the author of the cited article is a co-author of that review as well, but of course it is better to use passive.

“In contrast to small changes in clay mineralogy, pronounced shifts of soil organic matter quality with increasing age of the clay fractions at the Damma glacier were found.”

P1875, L25: What do you mean by carboxyl C?

We clarified the sentence in the revised version.

“Clay-bound OM from the 15-year-old soils was mainly inherited organic C rich in aromatic compounds and compounds carrying carboxyl groups.”

P1876, L9: delete N after “contribute”

Has been deleted.

P1876, L14-16: Is 6×10^6 copies of nifH low? Compared to what?

Here we wanted to compare nitrogen fixation activity and abundance along the chronosequence. We changed the sentence according to that purpose.

“Lowest N fixation activity was accompanied by lowest abundance of the N fixation marker gene nifH (2×10^6 copies g^{-1}) at initial sites confirming the presence of few microorganisms capable of the N fixation process.”

P1877, L1-2: delete or rephrase this sentence, which has been already mentioned before.

Sentences were partly deleted or moved to the “carbon chapter”.

“Within the study period of three summer months $33 g C m^{-2}$ were released via respiration and $2 g C m^{-2}$ leached from the soil. Taking into consideration the total C stocks of $90 g C m^{-2}$ these data indicate a highly active microbial community degrading the soil organic matter. Similarly, Bardgett and Walker (2004) described a heterotrophic stage of C decomposition at Ödenwinkelkees glacier, Austria.”

P1877, L7-10: Same as previous comment on nifH gene copy number, what kind of comparisons are you making to infer that this amount of amoA gene copies are too high?

This was meant in comparison to the abundance of ammonia oxidizing archaea. In most cases AOA are more abundant than AOB. We pointed that out more clearly in the revised manuscript.

“The abundance of the marker gene for nitrification amoA of ammonia oxidizing bacteria (AOB) was two orders of magnitude higher (2×10^6 copies g^{-1}) than for ammonia oxidizing archaea (AOA) (Brankatschk et al., 2011), what is in contrast to many other studies (Leininger et al, 2006; Schauß et al., 2009). It might be that the conditions in the initial soils are more ideal for AOB. On the one hand ammonium is supplied from atmospheric deposition and mineralization of organic matter, while competition about ammonium with plants is low. On the other hand the low pH of the soil is more favorable for AOB than AOA (Gubry-Rangin et al., 2011).”

P1877, L13- 15: How do you explain that?

At the glacier forefield we have very harsh conditions, low nutrient contents and rather low pH. During the measurement of potential enzyme activities in the lab, conditions are completely different and AOB from the glacier forefield are not adapted to lab conditions. Thus they might be less active than in the field.

“This can be explained by two scenarios: (i) The AOB community at the initial sites of the glacier forefield is inactive per se or (ii) the AOB community is adapted to the harsh conditions at the initial sites and is not able to adapt to laboratory conditions, thus turnover rates during potential nitrification measurements are low.”

P1878, L9-10: I miss a general description of the sites (see general comment)

We provided a table including dominant plant species, plant coverage, pH, maximum water holding capacity, microbial biomass carbon, total carbon, total nitrogen, dissolved organic nitrogen, dissolved organic carbon, nitrate, ammonium and phosphate. For details see comment above.

P1879, L6: replace “plant available” by “available for plants”

Has been replaced.

P1880, L5: delete anyhow (same in P1883, L21)

Has been deleted.

P1880, L9-11: please elaborate more on how they differ

We replaced that figure by a picture, which illustrates crust development at the Damma glacier more precise.

“As shown in Figure 2 BSC development at the Damma glacier is very heterogeneous and strongly depends on the right equilibrium of water availability and water holding capacity of the substrate.”

P1881, L6: delete comma after although (same in P1882, L14 and L27)

Has been deleted.

P1881, L14-15: How can these crusts be associated with vegetation patches and at the same time be absent in the sites (same page, line 7)?

In this part we wanted to address two types of crusts, on the one hand bacteria dominated ones (mostly Cyanobacteria) and on the other hand moss and lichen dominated crusts. Regarding the first, studies showed that Cyanobacteria, which are able to form crusts, exist, but no Cyanobacteria-driven crust formation was observed. In contrast the formation of moss-lichen patches were observed in protected areas of initial sites of the glacier. We restructured that part to make the distinction between the two types of crusts clear.

“Although crust forming bacteria have been detected at initial sites of the Damma glacier, the formation of Cyanobacteria-dominated crusts at the sampling site was not observed (Duc et al., 2009). This might be mainly attributed to the exposed position of some parts of the initial sites to the glacier tongue, which leads to regular disturbances of the surface by the glacial stream. However, as soon as sites are more protected against erosion, because of the moraines or they are located in hydrologic islands, moss and lichen dominated crusts develop (Bernasconi et al., 2011; Figure 3), which is in accordance with observations in the Negev desert (Israel) (Zaady et al., 2000). Interestingly, these types of crusts are often associated with vegetation patches (Duc et al., 2009)....”

P1881, L20-25: How can crusted soils have 200% more N than uncrusted soils and at the same time be N limited? Do you mean that they have higher demand for N? In that case you should find lower N concentrations in the crusted soil.

We rephrased the sentence to make that more clear and to remove the confusion.

“Regarding soil fertility, data from different BSCs indicated that crusts comprise 200% higher N contents than uncrusted soils from the same site (Harper and Belnap, 2001; Rogers and Burns, 1994; Pointing and Belnap, 2012). However due to increased microbial activities and leaching of N to deeper soil layers (Johnson et al., 2007), nitrogen is still one of the limiting factors in BSCs.”

P1885, L18: connect the word “fingerprinting”

Has been connected.

Fig 2: how does that connect to fig 1? How come mineralization of biomass is bigger at initial than transient stages?

We changed Figure 1 and 2 so that terminologies were similar.

Regarding your second question, all underlying data were normalized against biomass so that the relative abundance of the different processes is shown and the effect of the increasing biomass is excluded. Thus, it is possible that the group of mineralizers is relatively more important in the initial than the transient stage. We included that information in the figure legend.

“Figure 1:

The Damma glacier forefield (Switzerland) as it developed in response to the continuous retreat of the glacier. The numbers mark important corner points of the forefield: (1) the glacier terminus, (2) the glacier stream, (3) morain from 1992, (4) morain from 1928, (5) the south flanking moraine and (6) the north flanking moraine, which both originate from the Little Ice Age in 1850. The small pictures are closeups from 10, 50, 70 and 120 yr ice free soils, where the 10 yr site is situated in the initial part of the glacier forefield (6 – 13 yr), 50 and 70 yr sites in the intermediately developed sites (50 – 80 yr) and the 120 yr site in the most developed part of the forefield (110 – 160 yr).

Figure 2:

“The development of the microbial nitrogen cycle during soil formation. To exclude the strong influence of the increasing biomass along the glacier forefield, underlying data were related to ng DNA to be able to compare results from different development stages.”

Reviewer 2:

I am not an expert in soil biota and mainly familiar with soil chronosequences on much longer timescales. However I have some experience with soil chronosequences in the Alps (Morteratsch & Val Mulix region). Ans so I note that there are a few references that might be incorporated into this review that might make the final summation more robust: those of Mavris et al (2010), *Geoderma* 155:359; Mavris et al., (2011) *Geoderma* 165:106; Egli et al., (2011) *Geoderma* 164:11; Mavris et al. (2012) *sedimentary Geology*, doi:10.1016/j.sedgeo.2012.04.008 I read the comments of anonymous reviewer #1 and strongly agree with 95% of them. Thus, please consider my review as very much in concert with review #1.

We included the mentioned references in the respective passages in the text.