Response to referees' comments on "Microbial dynamics in a High-Arctic glacier forefield: a combined field, laboratory, and modelling approach."

We would like to thank the reviewers for their extremely helpful and constructive comments and suggestions, which helped improve the manuscript significantly. In what follows, we addressed all concerns that were raised.

Reviewer: 1

1. The manuscript, "Microbial dynamics in a High-Arctic glacier forefield: a combined field, laboratory, and modelling approach" presents a novel study combining field sampling and numerical modeling (the previously described SHIMMER model) to characterize microbial decomposer dynamics and community composition along a soil chronosequence in a oligotrophic, glacial forefield soil system in Svalbard.

In general, I found the manuscript to be clearly written and the methods/results easy to interpret. Critically, I believe the manuscript could be significantly improved if there were specific hypotheses to guide the study. For example, rather than 'exploring' microbial community structure and C cycling dynamics in this recently exposed, High Arctic soil environment, how and why did the authors expect these dynamics to differ along the soil age chronosequence (0 – 113 years old)? While the integration of the field and modeling efforts are commendable, I was surprised that the work was not guided by more clearly defined hypotheses that the model then tested.

The reviewer raises a valuable point. We have modified the text for a revised version of the manuscript, where appropriate, such that it is more clearly hypothesis driven.

"*The integrated field-model investigation aims at testing the hypotheses that to microbial growth and microbially-induced organic matter transformations can drive the accumulation of microbial biomass and available soil nutrient pools over a century of soil development, as well as that that changes in soil geochemistry (e.g. accumulation of nutrients, decomposition of labile substrate) are driven by microbial processes, and that those changes in soil geochemistry are reflected in the microbial community composition. Laboratory experiments were specifically carried out to constrain the most sensitive model parameters that had been previously identified through comprehensive sensitivity studies. Together with the collected field data, these experimentally informed helped improve the confidence in our model predictions and understanding of soil development at the Midtre Lovénbreen forefield*."

"*Thirdly, high rates of substrate degradation encouraged by low BGE were responsible for rapid nutrient release, thus supporting the hypothesis that observed changes in soil geochemistry are driven by microbial processes*."

2. I was also interested in seeing a stronger discussion of how this study might compare to other arctic (high and low) and alpine glacial forefield systems.

For a revised manuscript, we have expanded on comparisons in section 4 (*Discussion*). We have added additional studies for comparison (from Alpine, Arctic and Antarctic forefields) and provided more detail on individual studies. However, for sake of being concise, the reader is also directed, in the revised manuscript, to Bradley et al. (2014) for a thorough review of microbial dynamics in Arctic, Alpine and Antarctic glacier forefields, in which heterogeneities between glacier forefields are

compared, contrasted and discussed in detail (rather than adding lengthy additional discussion to the manuscript).

3. L. 182, 189, 233, elsewhere. Why was the C content (TOC and inorganic carbonates) of 0 year old soil analyzed, but not the other samples in the chronosequence?

C content of year 0 soil was analysed primarily to constrain the initial value of TOC in SHIMMER. Initial values for all state-variables are a pre-requisite for modelling using SHIMMER (see Bradley et al. (2015)). During fieldwork, soil samples were collected from the entire glacier forefield for TOC analysis. This is the subject of ongoing analytical work and will be presented in a forthcoming publication alongside additional detailed geochemical profiles and weathering indices. Preliminary analyses indicate a range in TOC from 600-3000 μg C g^{-1} with high variability across the glacier forefield chronosequence. The range of values is in good agreement with model simulations.

4. Similarly, I was not convinced that by testing the microbial growth rate and respiration for the 113 year old sample only (L 191 – 192); why not explore the growth rate and respiration dynamics for the microbial biomass across the chronosequence, even if biomass is lower in those soil ages?

Laboratory incubations of soil samples were conducted in order to derive estimations for the most sensitive parameter values that had been previously identified through comprehensive sensitivity studies (Bradley et al., 2015). Many microbial or microbially-mediated processes such as microbial growth and organic matter decay are controlled by a complex interplay of different factors such as, for instance, light, temperature, thermodynamics, moisture availability and community structure. For modelling purposes, these semi-tangible biologically relevant expressions may be represented by parameters and determined empirically using well-designed experimental protocols. The design of laboratory experiments to inform model parameters must thus implicitly account for neglected factors from the model description (see e.g. Blagodatsky and Richter (1998), Blagodatsky et al. (1998)) however all other factors must be controlled - in order to isolate the effects of specific variables.

Thus, in order to mitigate variability in measurements derived from differences in soil properties between soil ages, laboratory experiments were conducted on a single soil age. A key assumption of the SHIMMER model (Bradley et al., 2015) is that the parameter values are defined as constants (i.e. fixed) thus do not vary with soil age or soil properties. Moreover, it is the changing environmental (temperature, light) and geochemical (carbon substrate, available nitrogen, available phosphorus) conditions that drive changes in microbial activity by mathematical formulations (e.g. Monod kinetics) in the model equations. In a laboratory set-up encompassing a range of soil ages, it would be extremely difficult to disentangle and quantify the interacting sources of variability in measured rates due to the interplay of various environmental and geochemical differences between sites. Thus, confidently isolating and quantifying the effect of a single variable on measurements would not be possible if parameter values were derived from multiple soil ages.

In order to quantify variability in parameter values attributed to experimental procedures and measurement techniques, replicate incubations and measurements were performed, and the variability is presented in the manuscript as confidence intervals. We also explored these ranges numerically in additional model runs (illustrated in yellow in Fig. 6 (a-c)).

Here, we present a meaningful integration of field and laboratory derived data with numerical modelling. The design of this study provided a simple means of deriving a plausible range for three key parameters, in order to refine model predictions.

We have revised the manuscript to briefly highlight this point:

"*The microbial activity was determined in 113 year old soil samples after they were thawed (in the dark at 5°C to mimic typical field temperature) for 168 hours. This age was chosen because these soil samples were assumed to be the ones with the highest microbial biomass and activity and thus the most appropriate for all laboratory measurements. In order to mitigate the effect of variability derived from differences in soil properties between soil ages (that will later be predicted by the model), laboratory experiments were conducted on a single soil age, with replicate incubations to assess the possible variability in rates (and thus parameter values) that can be attributed to experimental procedures and measurement techniques*."

5. Paragraph beginning L. 231. For the soil respiration study, why not include a range of temperatures (not just 5 and 25C, which may be beyond the peak metabolic tolerance for this community)? Do you have any data to support these temperature choices?

The SHIMMER model is designed such that temperature dependency of microbial growth is described by a Q_{10} formulation: effectively slowing down or speeding up all life processes with soil temperature change.

Q10 is commonly calculated by the equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$$

Where R_1 and R_2 represent the measured reaction rates at temperatures T_1 and T_2.

During the process of model development, testing, sensitivity assessment and validation, the reference temperature (T_2) for which rates (I_{max} and α) are described was chosen to be 25˚C - which is commonly used for measurements of microbial growth in soils (Mur et al., 1999; Ingwersen et al., 2008; Frey et al., 2010; Knapp et al., 1983; Zelenev et al., 2000; Darrah, 1991; Blagodatsky et al., 1998; Vandewerf and Verstraete, 1987; Foereid and Yearsley, 2004; Toal et al., 2000; Scott et al., 1995), including in glacier forefields (Frey et al., 2010) and Svalbard tundra soils (Stapleton et al., 2005). Thus, we were able to derive appropriate parameter values, and in the present study, were easily able to compare our maximum growth rates with the previously identified plausible range (as illustrated in Fig. 5). Since the Q_{10} formulation describes a relationship between two temperatures, we chose a second temperature value that is typical for Svalbard soils (5˚C, see Fig. S3, Supplementary Information) in order to derive the Q_{10} value.

We have revised the manuscript to reflect this:

"*Samples were incubated at 25°C (in keeping with the design of SHIMMER and for comparison with previous plausible range (Bradley et al., 2015))…*"

6. Paragraph beginning L. 428 This information should be folded into the Results section.

Agreed. Manuscript has been edited accordingly.

7. Paragraph beginning L 448. Do you expect the Q 10 to vary seasonally (see Mikan et al. 2002). If so, how would this affect the model interpretation?

The referee raises a valuable point about the potential variability of Q_{10} over a temperature (or temporal) range, as discussed in Mikan et al. (2002).

The Q_{10} (Arrhenius) model is derived from the fundamental relationship between temperature and the reaction rate of an elemental chemical reaction formulated by van t'Hoff, whereby:

ln Q10 = ln (k2/k1) = Ea / r*(1/T1-1/T2)

Where *k1* and *k2* are the rate constants at temperatures *T1* and *T2*. *Ea* is the activation energy and *R* the gas constant. Q_{10} is thus not a constant property of a reaction, but decreases as temperature decreases.

The Arrhenius equation is a semi-empirical formulation commonly used to describe the temperature dependency of the complex multi-step biogeochemical reactions involving a multitude of different organisms and intermediate products. The apparent values for *A* and *Ea* are generally calculated from rate measurements (although the Arrhenius equation relates the reaction rate constant, k, and not the rate to temperature). As a consequence, apparent values are an integrative measure of the activation energies of all the elementary reactions that comprise the overall reaction and thus, are appropriate for encapsulating the temperature response of the total microbial ecosystem and the organic matter degradability/availability. Therefore, apparent *Eas* show large variabilities between different environments and/or increase/decrease with for instance temperature, substrate bioavailability etc.

Although temperature co-efficients are known to change depending on environmental conditions, we decided that a fixed-value Q_{10} model was the most appropriate for SHIMMER. We did so for the following reasons:

- **It represents an ecosystem response.** The typical response of an individual organism to temperature is an increase in metabolic activity to a clearly defined optimum, after which rates decrease. However, the Q_{10} is more representative of a community response (see below) (Soetaert and Herman, 2009). SHIMMER is not an individual-based model, and groups multiple individuals and species together into six functional groups ($A_{1\text{-}3}$ & $H_{1\text{-}3}$). Thus, the Q_{10} model is appropriate for representing the response of the grouping.

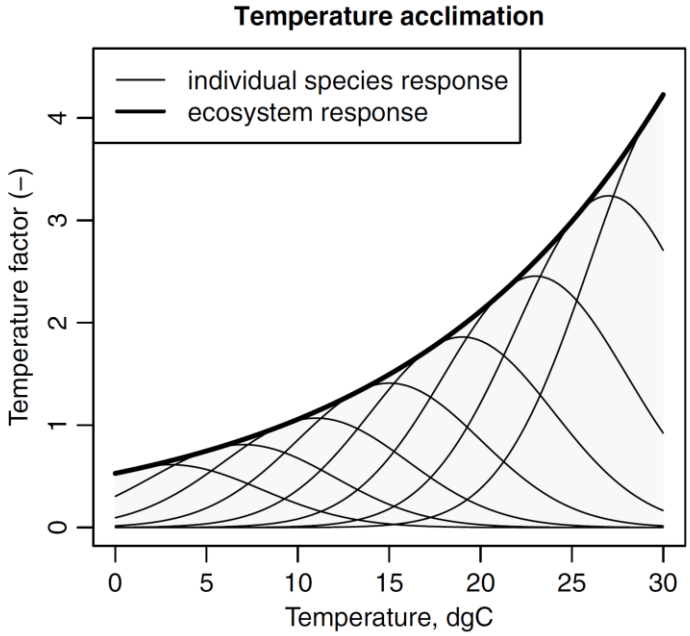

Figure 1. Response of an ecosystem for individuals (thin lines) and for groups of organisms/ecosystem (thick line) (from Soetaert and Herman (2009))

- **Q_{10} is a typical measure for soil respiration,** both in field or lab analyses (e.g. Uchida et al. (2002), Tang et al. (2005), Zhou et al. (2013), Zheng et al. (2009)) and in models (e.g. Zhou et al. (2009)). Therefore, it is more familiar among this field of research.
- Whilst it is known that the Q_{10} value varies depending on the environmental characteristics of the system of interest (Xu and Qi, 2001; Zhou et al., 2009), **we can constrain the Q_{10} value from previous studies, and compare it with our own lab-derived value**.
- **It is appropriate for the level of detail resolved by the model.** If the model resolved finer detail (molecular and chemical processes), then an intrinsic temperature sensitivity (i.e. theoretic rates determined by molecular structure e.g. Gibbs free energy), or varying Q_{10} model, may be appropriate. However, for the current SHIMMER model formulation, based on the current level of understanding of glacier forefield systems, the apparent temperature sensitivity (with appropriate environmental constraints caused by heterogeneous soil properties) formulated with a Q_{10} function over a typical temperature range is sufficient.
- **The Q10 formulation is simple** enough that it could be fully tested in the sensitivity and uncertainty evaluation (Bradley et al., 2015).

This has previously been discussed in Bradley et al. (2015) and elsewhere, and further discussion is beyond the scope of this paper.

In order to address concerns about variable parameters, we have included the following additional text in the manuscript:

"*A major assumption of SHIMMER is that parameter values remain constant throughout the duration of the simulation. Empirical evidence suggests that parameters defined as fixed in SHIMMER (e.g. Q_{10}) may be variable over time, however in SHIMMER, like many numerical modelling formulations, changing environmental (temperature, light) and geochemical (carbon substrate, available nitrogen, available phosphorus) conditions drive subsequent variability in microbial activity via mathematical formulations (e.g. Monod kinetics, see Bradley et al. (2015)) affixed to parameter values. A second major assumption is the assignment of measured rates to parameters for all microbial functional groups. Rather than taxonomic based classification, SHIMMER distinguishes and classifies microbial communities based on functional traits. These mathematical formulations assigned to, for example, microbial growth, between these groups are different to represent distinct functional traits associated with that group. Whilst actual rates may be different between different organisms and functional groups, for the level of model complexity and outputs required, a community measurement of those parameters is sufficient, particularly considering that the differences are accounted for in the mathematical formulation of SHIMMER (see Bradley et al. (2015))*."

8. L. 538 – 540, elsewhere in the discussion. How would the authors propose to improve our understanding of allochthonous nutrient inputs in this system? Is there plant or lichen biomass at the older sites in the chronosequence? How does this compare to other glacial forefield sites?

The importance of allochthonous nutrient contributions is one of the major unknowns, and thus sources of uncertainty, in investigations into microbial dynamics in glacier forefields (Bradley et al., 2014). Current attempts to measure allochthonous inputs in the Midtre Lovénbreen catchment have relied on geochemical analyses of snow and rainfall, modelling, and constraining hydrological and budgets (Hodson et al., 2010; Hodson et al., 2005; Bjorkman et al., 2013; Kuhnel et al., 2013; Kuhnel et al., 2011). Improving the understanding of allochthonous nutrient inputs to the Midtre Lovénbreen forefield system is the subject of ongoing research. We are currently investigating the importance of allochthonous nutrient inputs with additional modelling simulations that explore a range of allochthonous nutrient input scenarios (as well as temperature, precipitation and snow cover

scenarios). Preliminary results show that microbial biomass is highly sensitive to allochthonous nutrient input. Each functional group responds uniquely to allochthonous inputs. Similarly, soil of different ages responds with varying sensitivity to allochthonous inputs. We are preparing a manuscript for publication of these results since it is beyond the scope of the present study. Fungi, lichen and plant biomass is present at the older sites in the Midtre Lovénbreen forefield, as explored by Moreau and others (Moreau et al., 2005; Moreau et al., 2008). However, the initial young stages of the Midtre Lovénbreen forfield soils are characterized by microbes with almost a complete absence of plants, making this system an ideal location to study the interactions between microbes and rock during soil formation.

9. L 183. 'as-collected' is not phrased correctly.

Agreed. Manuscript has been edited accordingly.

10. Instead of reporting P > 0.05 for non-significant results, report the actual P-value.

Agreed. Manuscript has been edited accordingly.

11. L 345. Please report error around mean respiration values presented.

Agreed and included in revised manuscript.

12. L 351. Do you mean P > 0.05?

Yes. P-values included in revised manuscript.

Reviewer: 2

1. This combined laboratory and modeling study of microbial community development in glacier forefields was well designed and well written, but narrowly limited to a very specialized environment. In addition, although the Midtre Lovenbreen forefield seems ideal for the study of soil microbial community succession in an extreme oligotrophic system, it also seems to be an outlier among such systems, by having no vegetation. Thus, the results are interesting with respect to potential microbial succession without the influence of plants, but may have little relationship to any natural system. It would have more general appeal if the authors try to relate their work to more common soil microbial communities or, alternatively, to those in other extreme environments, like Antarctic soils, desert microbial crusts, cryptoendoliths, etc.

Most of the non-ice-covered surface land area of Antarctica and the high Arctic has very little plant coverage. Thus, the system investigated in this study in fact represents a major ecosystem, experiencing extremely rapid climatological changes, that is presently under-investigated. This study aims to identify and characterize the process of soil development before the influence of plants. Thus, as the reviewer mentions, the Midtre Lovénbreen forefield is an ideal location to study these processes, since the forefield of this glacier provides one of the best ways to understand the interactions between microbes and rock during soil formation. Thus, this study focusses in detail on this catchment to tackle this specific problem rather than arctic and desert soils more generally. However, the design of SHIMMER is kept as general as possible, and thus is easily transferable to other microbial ecosystems such as desert soils, ice surfaces (e.g. cryoconite), microbial mats and the

built environment (e.g. fuel and chemical storage). Thus, we anticipate future research integrating modelling with empirical data in a variety of environments.

2. For similar reasons, the argument that these communities might make important contributions to atmospheric CO2 requires more information about the total amount of land involved over a defined time frame and thus the quantities of CO2 likely to be emitted. If microbial communities actually drive the net accumulation of organic matter and nutrients in the centuries after glacial retreat, this argues for net C-sequestration rather than release. The authors make their best case for this study with regard to uncertainties in the sources and fates of organic matter and nutrients in these systems, rather than extrapolations to global C cycling.

The importance of glacier forefield soils to atmospheric CO_2 concentrations and global C cycling is not well understood. There has so far been no effort to quantify the effect of soil development on atmospheric CO_2 concentrations. Here, we do not present data to support or reject such claims that glacier forefields are important to atmospheric CO_2 or global C cycling. Thus, we are careful in this manuscript to not make unjust statements and do not attempt to make extrapolations or upscalings. We have edited the manuscript replacing "CO_2 efflux" with "net ecosystem production" to avoid confusion and misinterpretation of the results presented here.

3. The key terms for model sensitivity, i.e., heterotrophic growth rate, bacterial growth efficiency and temperature response, are generally the parameters that are important to other models. That these terms were assumed to be the same for all microbial groups is problematic, as many other field, laboratory and modeling studies have reported otherwise. For example, it is unlikely that the maximum growth rate is so high and yet BGE is so low and both are the same for all autotrophs and heterotrophs.

In Bradley et al. (2015) we identified heterotrophic growth rate, bacterial growth efficiency and temperature response to be highly sensitive and poorly constrained parameters. In that paper, we derived the plausible ranges for these parameters based on other models and other lab experiments. The number and the range of estimations for these key parameters was reasonably large due to their importance in quantitative assessments of ecosystem properties and numerical modelling. Whereas it is not novel to measure growth rate, bacterial growth efficiency and temperature response, we did so in order to reduce the plausible range, derive a value that is appropriate for the system specifically of interest here (soil bacteria from the forefield of the Midtre Lovénbreen glacier), and, most novel, significantly refine model predictions. The low measured BGE is not uncommon for glacial environments (Anesio et al., 2010; Hodson et al., 2007)

We know that growth and BGE are different for the different organisms resolved in SHIMMER, however, for the level of model complexity and outputs required, a community measurement of those parameters is sufficient, particularly considering that the differences are accounted for in the mathematical formulation of SHIMMER (see Bradley et al. (2015)).

For a revised version of the manuscript, we have included text in the discussion to reflect on the assignment of parameter values to microbial groups:

"*A second major assumption is the assignment of measured rates to parameters for all microbial functional groups. Rather than taxonomic based classification, SHIMMER distinguishes and classifies microbial communities based on functional traits. These mathematical formulations assigned to, for example, microbial growth, between these groups are different to represent distinct functional traits*

associated with that group. Whilst actual rates may be different between different organisms and functional groups, for the level of model complexity and outputs required, a community measurement of those parameters is sufficient, particularly considering that the differences are accounted for in the mathematical formulation of SHIMMER (see Bradley et al. (2015))."

Please also see response to Reviewer 1, point 7.

4. Moreover, citing Allison 2005 for exudation rates, given that his earlier work was based on Hawaiian sites, seems a strange match to this study.

During the design, testing and validation phases of SHIMMER (Bradley et al., 2015), plausible parameter values were derived from appropriate literature, including empirically based studies on soil microbial communities and numerical modelling investigations. Allison (2005) is a helpful study for a numerical investigation into exudation and this work provides a useful framework for examining microbes that control the degradation of organic matter. The Allison (2005) is intended to simulate a microbial ecosystem whereby co-existence and scarcity of resources (e.g. substrate) are major important factors – which is appropriate for glacier forefield systems (Schulz et al., 2013; Bradley et al., 2014). For SHIMMER, we therefore adapted and simplified this study such that it is suitable for the Arctic environment and the data availability for this study site. We explored the plausible range for exudation (and the plausible range of other parameters) through sensitivity and uncertainty testing. The exudation parameter was found to be extremely insensitive (compared to other more poorly constrained and sensitive parameters); thus model results do not depend strongly on this value and hence confidence in model results does not rely on deriving an exact value. Accordingly, the original value for exudation rate (derived in Bradley et al. (2015)), whilst not entirely perfect, nor exact, is reasonable for the purpose of the present study.

5. Model: despite the supplemental information, I needed to read Bradley et al. 2015 for the details of SHIMMER. I'm not certain that anyone could easily decipher the manuscript without doing so.

The description of SHIMMER in the present study is relatively brief for sake of manuscript length and because the *Geoscientific Model Development* paper (Bradley et al., 2015) already provides a very comprehensive and detailed model description, sensitivity tests and model case studies. Here, we sought to include the appropriate level of detail necessary for the reader to gain a critical understanding of SHIMMER by presenting the central components and key processes. For a full description of SHIMMER, the reader is directed to Bradley et al. (2015). Nevertheless, we have edited the description of the model (**2.5. Microbial Model: SHIMMER**) such that the description is more comprehensive and laid out more clearly, as well as including a conceptual diagram of the model (as presented in Bradley et al. (2015)) in the Supplementary Information (Fig. S2).

6. Line 192: SOC quality might reasonably select community composition. If empirical data suggest otherwise, please show these results. Are changes in SOC quality characteristics over time (labile/refractory) known from field sites?

Empirical evidence suggests that organic substrate resource quality influences microbial community composition in glacier forefield soils (Zumsteg et al., 2013). Unfortunately we do not currently have empirical data on SOC quality. However, the model is part of an iterative approach and this is point will guide future research to test model results and interpretation with regard to changes in SOC quality. Several studies from Alpine glacier forefields have suggested the overall decline in quality of organic substrates in older soils compared to younger soils (Goransson et al., 2011; Insam and

Haselwandter, 1989). A detailed assessment of glacier forefield geochemistry (including organic carbon characterisation using quantification and stable isotope methods) is the subject of current work and will be published in a separate study.

7. Line 289: What is the quality of allochthonous inputs? Is it the same as initial materials? Perhaps I missed that information. The SHIMMER model description appears to conflate factors controlling the utilization rates of the labile and refractory substrates, so the dynamics aren't easy to anticipate.

The SHIMMER model distinguishes between two pools of organic matter: a reactive pool (S_1) comprising highly available and fresh organic compounds that are preferentially degraded by microorganisms, and a less reactive pool (S_2) represents the bulk of substrate present in the non-living organic component of soil. There is interest among the geomicrobiological community in characterising changes in bioavailability of organic substrate with soil age. Thus, we divide substrate into two pools. In order to express a preference of labile substrate, the parameters JS_1 and JS_2 (with $JS_1 > JS_2$) represent factors that scale the maximum rate at which labile carbon substrate (S1) and refractory substrate (S_2) are utilised, respectively. A two pool representation is the simplest way to simulate organic matter quality changes. We chose this simplistic approach because any further complexity is not possible to constrain. Presently, there is nor the understanding nor the data to justify resolving organic carbon compounds in any more detail than this. This is useful for a first attempt at modelling the processes that control carbon utilization in order to provide insight into the changing substrate dynamics with soil age in this High-Arctic forefield. The bioavailability of allochthonous inputs are assumed to be the same as initial materials and microbial necromass. For the revised manuscript, we have added a sentence to clarify this:

"*The bioavailability of allochthonous material is assumed to be the same as initial material and microbial necromass*."

8. The lab results show high variability for low means, which provided no resolution of treatment effects. Clearly, the methods employed to determine BGE were too insensitive for these systems. The extraordinarily low BGE values in this system are fascinating, and contrast with other soil systems. This deserves more discussion and justification for remaining constant across groups and time.

The purpose of measuring growth and respiration rates, as well as deriving BGE, was to reduce the plausible range of model parameters that is appropriate for the Midtre Lovénbreen glacier forefield community, and refine model predictions. Whilst variability in rates was high, we cross-correlated all measurements with quadruplicate measurements of biomass from each treatment in order to meaningfully quantify variability. We then explored a 95% confidence range for our measurements using SHIMMER. The variability resulting from laboratory experiments was minimal compared to the plausible range for parameter values prior to laboratory experiments. The referee suggests that additional discussion and justification of parameter fixing is deserved. We have discussed this in detail in response to Reviewer 1 (please see point 7). In order to address these concerns in the manuscript, we have included the following:

"*A major assumption of SHIMMER is that parameter values remain constant throughout the duration of the simulation. Empirical evidence suggests that parameters defined as fixed in SHIMMER (e.g. Q_{10}) may be variable over time. However in SHIMMER, like many numerical modelling formulations, changing environmental (temperature, light) and geochemical (carbon substrate, availability of nitrogen and phosphorus) conditions drive subsequent variability in microbial activity via mathematical formulations (e.g. Monod kinetics, see Bradley et al. (2015)) affixed to parameter values. A second*

major assumption is the assignment of measured rates to parameters for all microbial functional groups. Rather than taxonomic based classification, SHIMMER distinguishes and classifies microbial communities based on functional traits. These mathematical formulations assigned to, for example, microbial growth, between these groups are different to represent distinct functional traits associated with that group. Whilst actual rates may be different between different organisms and functional groups, for the level of model complexity and outputs required, a community measurement of those parameters is sufficient, particularly considering that the differences are accounted for in the mathematical formulation of SHIMMER (see Bradley et al. (2015))."

The extraordinarily low BGE is not uncommon for glacial environments (Anesio et al., 2010; Hodson et al., 2007) however is contrasting with many other soil systems (Blagodatsky et al., 1998). We are presently conducting additional modelling studies to examine BGE and its effect on soil microbial dynamics in greater detail.

9. Line 352: I assume that respiration rate was ug C/ g day?

The units for maximum heterotrophic growth rate (represented by parameter I_{maxH}) are in fact per day (day^{-1}) since this parameter represents the relative growth rate – that is, the growth rate relative to the size of the population, defined on the basis of doubling rate. Thus, the unit day-1 as written in the manuscript is appropriate for the parameter I_{maxH}.

10. Lines 465-467: "Recycled" may not be the best term for the mineralization of C, N and P. In other microbial literature, this term refers to the reincorporation C, N and P into biomass from dead organisms.

Agreed. Manuscript has been edited accordingly.

11. Lines 510-512: The large difference in community structure between 16S and microscopy data deserves more discussion. This is a big departure from expectations (and simulations). What's the reasoning? The same is true later (lines 536-538), although the spatial heterogeneity of Nostoc colonies provides a potential explanation: are observations available to contrast the N-characteristics of Nostoc +/- locations?

The reviewer raises an important point about the apparent differences in microbial community structure between 16S, microscopy, and model simulations. 16S data is an exciting resource of information that is rarely (or never) used to test models. However, the environment (difficulty to extract DNA), the presentation (percentages of low concentration and thus easy to shift) and model uncertainties make comparisons challenging. This first attempt at comparison is will spark discussion and further development of approaches that compare 16S data with model results. It is clear from the results presented in this paper that standard analytical techniques encounter problems and limitations in this harsh biomass- and nutrient-poor Arctic soil environment, as shown by discrepancies in the microscopy, 16S data and model output, particularly in the later stages of soil development (illustrated in Fig. 8 by years 50 and 113). In the field, we observed patchy coverage of microbial mat coverage. Due to the random sampling approach, it is very possible that these (likely Nostoc colonies) were missed. It is also important to note that the model is not a tool to solely reproduce data. Discrepancies, such as in our data, show that further attention is required to the empirical methods of data generation and/or the model formulation. We have included additional discussion in the revised manuscript as appropriate:

"*Microscopic analyses indicated low total biomass in recently exposed soils (up to 1.7 µg C* g^{-1} *in soil exposed for 50 years) that was comprised predominantly of autotrophic bacteria. Model simulations*

agreed well with microscopy derived data. Overall, the 16S data, when categorised into functional groups as defined by the model, agreed well with the microscopy and model output in the very early stages of soil development. However, in later stages of soil development (50 years and older), microscopy and modelling suggested a continuation of predominantly autotrophic soil microbial communities whereas 16S sequence data notably indicated a predominantly heterotrophic community. With extremely low biomass, cell counts derived from microscopy, as well as representation of relative abundance by 16S extraction and amplification, can be largely skewed by relatively small variability in the soil microbial community. Furthermore, the comparative difficulty to lyse autotrophic bacteria (such as some groups of cyanobacteria) from an environmental sample compared to heterotrophic bacteria, and thus successfully amplify the 16S gene during the PCR process, may skew 16S sequence data in favour of heterotrophic sequence reads. Additionally, SHIMMER is an ambitious model in that it attempts to simulate, predict and constrain multiple functional types of bacteria species in a numerical framework. Numerical models containing multiple species or multiple microbial functional groups are often extremely challenging to constrain (Servedio et al., 2014; Hellweger and Bucci, 2009; Jessup et al., 2004; Larsen et al., 2012), and as such, the majority of microbial soil models often only resolve one or two living biomass pool that represents the bulk activity and function of the entire community (see e.g. Manzoni et al. (2004), Manzoni and Porporato (2007), Blagodatsky and Richter (1998), Ingwersen et al. (2008), Wang et al. (2014) and others. Our rationale for resolving six distinct functional groups was to quantitatively assess, using modelling, the relative importance of and role of each functional group at different stages of soil development. Regardless of discrepancies in older soils (over 50 years since exposure), both the 16S and microscopy data indicated that there was a mixed community of autotrophs and heterotrophs in soils of all ages, which was supported by modelling, since no functional groups were extirpated over simulations representing 120 years of soil development. Thus, SHIMMER is able to represent the diversity of the sample well over 120 years of soil development, but the detailed community composition requires further investigation. 16S data is an exciting resource of information that is rarely (or never) used to test models. However, the environment (difficulty to extract DNA), the presentation (percentages of low concentration and thus easy to shift relative abundance) and model uncertainties make comparisons challenging. This first attempt at comparison is will spark discussion and further development of approaches that compare 16S data with model results.

Nitrogen-fixing bacteria were prevalent in recently exposed soils but declined in relative abundance with soil age. By fixing N_2 instead of assimilating DIN, the model predicted that nitrogen-fixers were able to grow rapidly in the early stages relative to other organisms (Fig. 4a, 4b). The model prediction supports findings by previous studies demonstrating the importance of nitrogen fixation in Alpine (Duc et al., 2009; Schmidt et al., 2008) and Antarctic (Strauss et al., 2012) glacier forefields and other High-Arctic (Svalbard, Greenland) glacial ecosystems (Telling et al., 2011; Telling et al., 2012). However, there was poor agreement on the relative abundance of nitrogen fixers between the model and the 16S data in the later stages of soil development (years 50 to 120), particularly between autotrophs and heterotrophs. The model over-predicted the relative abundance of nitrogen fixing organisms (Fig. 8). The majority of the biomass of the autotrophic nitrogen fixers was composed of sequences belonging to the cyanobacterium from the genus Nostoc. Nostoc forms macroscopically visible colonies that grow on the surface of the soils. Its distribution in the Arctic soils is thus extremely patchy and therefore, part of the discrepancy between the 16S data and the model regarding the relative distribution of the A_3 group in the older soils could be due to under-sampling of the Nostoc colonies as a consequence of a random sampling approach. Furthermore, allochthonous inputs of nitrogen to the Arctic (e.g. aerial deposition (Geng et al., 2014)) strongly affect the productivity of microbial ecosystems and the requirement of nitrogen fixation for microbes (Bjorkman et al., 2013; Kuhnel et al., 2013; Kuhnel et al., 2011; Hodson et al., 2010; Telling et al., 2012; Galloway et al., 2008). Thus, uncertainty in the allochthonous availability of nitrogen strongly affects nitrogen fixation rates. In attempting to replicate a qualitative understanding of the nitrogen cycle in a quantitative mathematical modelling framework, the predicted importance of nitrogen-fixing organisms may be

over-estimated. The poor agreement in the relative abundance of nitrogen-fixers between the model and the 16S data indicates an incomplete understanding of allochthonous versus autochthonous nutrient availability. Allochthonous nutrient availability is a known source of uncertainty (Bradley et al., 2014; Schulz et al., 2013; Schmidt et al., 2008), and addressing this concern is the subject of future work."

12. Line 602: I'm not convinced that it is possible to evaluate key processes independently of one another, as they occur simultaneously and interactively. So, I'm not certain what the authors are trying to say with this statement. Throughout, the relationships between allochthonous inputs, microbial production and necromass are uncertain. More clarity is needed in tracing the dynamics and interactions of these C pools.

The reviewer has commented on the following statement:

"*This exercise shows how an integrated model-data approach can improve understanding and predictions of microbial dynamics in forefield soils and disentangle complex processes interactions to ascertain the relative importance of each process independently*"

With this statement, we refer to the budget of carbon fluxes derived from the modelling exercise; in particular illustrated by Fig 4 (original manuscript). We show here that via modelling, daily carbon fluxes can be derived which allows us to compare and contrast processes and fluxes at individual time-points (e.g. summer versus winter, young soil versus developed soil). This type of analysis is exactly the power of a modelling approach.

We have edited this section so that it reads:

"*This exercise shows how an integrated model-data approach can improve understanding and predictions of microbial dynamics in forefield soils and disentangle complex processes interactions to ascertain the relative importance of each process independently (a process that would, for annual budgets, be extremely challenging with a purely empirical approach). Nevertheless, more clarity is needed in tracing the dynamics and interactions of these carbon pools to improve confidence, mostly as empirical data for model validation*."

References

Allison, S. D.: Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments, Ecol Lett, 8, 626-635, DOI 10.1111/j.1461-0248.2005.00756.x, 2005.

Anesio, A. M., Sattler, B., Foreman, C., Telling, J., Hodson, A., Tranter, M., and Psenner, R.: Carbon fluxes through bacterial communities on glacier surfaces, Ann Glaciol, 51, 32-40, 2010.

Bjorkman, M. P., Kuhnel, R., Partridge, D. G., Roberts, T. J., Aas, W., Mazzola, M., Viola, A., Hodson, A., Strom, J., and Isaksson, E.: Nitrate dry deposition in Svalbard, Tellus B, 65, Artn 19071

Doi 10.3402/Tellusb.V65i0.19071, 2013.

Blagodatsky, S. A., and Richter, O.: Microbial growth in soil and nitrogen turnover: A theoretical model considering the activity state of microorganisms, Soil Biol Biochem, 30, 1743-1755, Doi 10.1016/S0038-0717(98)00028-5, 1998.

Blagodatsky, S. A., Yevdokimov, I. V., Larionova, A. A., and Richter, J.: Microbial growth in soil and nitrogen turnover: Model calibration with laboratory data, Soil Biol Biochem, 30, 1757-1764, Doi 10.1016/S0038-0717(98)00029-7, 1998.
Bradley, J. A., Singarayer, J. S., and Anesio, A. M.: Microbial community dynamics in the forefield of glaciers, Proceedings. Biological sciences / The Royal Society, 281, 2793-2802, 10.1098/rspb.2014.0882, 2014.
Bradley, J. A., Anesio, A. M., Singarayer, J. S., Heath, M. R., and Arndt, S.: SHIMMER (1.0): a novel mathematical model for microbial and biogeochemical dynamics in glacier forefield ecosystems, Geosci. Model Dev., 8, 3441-3470, 10.5194/gmd-8-3441-2015, 2015.
Darrah, P. R.: Models of the Rhizosphere .1. Microbial-Population Dynamics around a Root Releasing Soluble and Insoluble Carbon, Plant Soil, 133, 187-199, Doi 10.1007/Bf00009191, 1991.
Duc, L., Noll, M., Meier, B. E., Burgmann, H., and Zeyer, J.: High Diversity of Diazotrophs in the Forefield of a Receding Alpine Glacier, Microbial Ecol, 57, 179-190, DOI 10.1007/s00248-008-9408-5, 2009.
Foereid, B., and Yearsley, J. M.: Modelling the impact of microbial grazers on soluble rhizodeposit turnover, Plant Soil, 267, 329-342, DOI 10.1007/s11104-005-0139-9, 2004.
Frey, B., Rieder, S. R., Brunner, I., Plotze, M., Koetzsch, S., Lapanje, A., Brandl, H., and Furrer, G.: Weathering-Associated Bacteria from the Damma Glacier Forefield: Physiological Capabilities and Impact on Granite Dissolution, Appl Environ Microb, 76, 4788-4796, Doi 10.1128/Aem.00657-10, 2010.
Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z. C., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., and Sutton, M. A.: Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions, Science, 320, 889-892, 10.1126/science.1136674, 2008.
Geng, L., Alexander, B., Cole-Dai, J., Steig, E. J., Savarino, J., Sofen, E. D., and Schauer, A. J.: Nitrogen isotopes in ice core nitrate linked to anthropogenic atmospheric acidity change, P Natl Acad Sci USA, 111, 5808-5812, 10.1073/pnas.1319441111, 2014.
Goransson, H., Venterink, H. O., and Baath, E.: Soil bacterial growth and nutrient limitation along a chronosequence from a glacier forefield, Soil Biol Biochem, 43, 1333-1340, DOI 10.1016/j.soilbio.2011.03.006, 2011.
Hellweger, F. L., and Bucci, V.: A bunch of tiny individuals-Individual-based modeling for microbes, Ecol Model, 220, 8-22, DOI 10.1016/j.ecolmodel.2008.09.004, 2009.
Hodson, A., Anesio, A. M., Ng, F., Watson, R., Quirk, J., Irvine-Fynn, T., Dye, A., Clark, C., McCloy, P., Kohler, J., and Sattler, B.: A glacier respires: Quantifying the distribution and respiration CO2 flux of cryoconite across an entire Arctic supraglacial ecosystem, J Geophys Res-Biogeo, 112, Artn G04s36

Doi 10.1029/2007jg000452, 2007.
Hodson, A., Roberts, T. J., Engvall, A. C., Holmen, K., and Mumford, P.: Glacier ecosystem response to episodic nitrogen enrichment in Svalbard, European High Arctic, Biogeochemistry, 98, 171-184, DOI 10.1007/s10533-009-9384-y, 2010.
Hodson, A. J., Mumford, P. N., Kohler, J., and Wynn, P. M.: The High Arctic glacial ecosystem: new insights from nutrient budgets, Biogeochemistry, 72, 233-256, DOI 10.1007/s10533-004-0362-0, 2005.
Ingwersen, J., Poll, C., Streck, T., and Kandeler, E.: Micro-scale modelling of carbon turnover driven by microbial succession at a biogeochemical interface, Soil Biol Biochem, 40, 864-878, DOI 10.1016/j.soilbio.2007.10.018, 2008.

Insam, H., and Haselwandter, K.: Metabolic Quotient of the Soil Microflora in Relation to Plant Succession, Oecologia, 79, 174-178, Doi 10.1007/Bf00388474, 1989.
Jessup, C. M., Kassen, R., Forde, S. E., Kerr, B., Buckling, A., Rainey, P. B., and Bohannan, B. J. M.: Big questions, small worlds: microbial model systems in ecology, Trends Ecol Evol, 19, 189-197, 10.1016/j.tree.2004.01.008, 2004.
Knapp, E. B., Elliott, L. F., and Campbell, G. S.: Carbon, Nitrogen and Microbial Biomass Interrelationships during the Decomposition of Wheat Straw - a Mechanistic Simulation-Model, Soil Biol Biochem, 15, 455-461, Doi 10.1016/0038-0717(83)90011-1, 1983.
Kuhnel, R., Roberts, T. J., Bjorkman, M. P., Isaksson, E., Aas, W., Holmen, K., and Strom, J.: 20-Year Climatology of NO3- and NH4+ Wet Deposition at Ny-Alesund, Svalbard, Adv Meteorol, Artn 406508

Doi 10.1155/2011/406508, 2011.
Kuhnel, R., Bjorkman, M. P., Vega, C. P., Hodson, A., Isaksson, E., and Strom, J.: Reactive nitrogen and sulphate wet deposition at Zeppelin Station, Ny-Alesund, Svalbard, Polar Res, 32, Unsp 19136

Doi 10.3402/Polar.V32i0.19136, 2013.
Larsen, P., Hamada, Y., and Gilbert, J.: Modeling microbial communities: Current, developing, and future technologies for predicting microbial community interaction, J Biotechnol, 160, 17-24, 10.1016/j.jbiotec.2012.03.009, 2012.
Manzoni, S., Porporato, A., D'Odorico, P., Laio, F., and Rodriguez-Iturbe, I.: Soil nutrient cycles as a nonlinear dynamical system, Nonlinear Proc Geoph, 11, 589-598, 2004.
Manzoni, S., and Porporato, A.: A theoretical analysis of nonlinearities and feedbacks in soil carbon and nitrogen cycles, Soil Biol Biochem, 39, 1542-1556, 10.1016/j.soilbio.2007.01.006, 2007.
Mikan, C. J., Schimel, J. P., and Doyle, A. P.: Temperature controls of microbial respiration in arctic tundra soils above and below freezing, Soil Biol Biochem, 34, 1785-1795, Pii S0038-0717(02)00168-2

Doi 10.1016/S0038-0717(02)00168-2, 2002.
Moreau, M., Laffly, D., Joly, D., and Brossard, T.: Analysis of plant colonization on an arctic moraine since the end of the Little Ice Age using remotely sensed data and a Bayesian approach, Remote Sens Environ, 99, 244-253, DOI 10.1016/j.rse.2005.03.017, 2005.
Moreau, M., Mercier, D., Laffly, D., and Roussel, E.: Impacts of recent paraglacial dynamics on plant colonization: A case study on Midtre Lovenbreen foreland, Spitsbergen (79 degrees N), Geomorphology, 95, 48-60, DOI 10.1016/j.geomorph.2006.07.031, 2008.
Mur, L., Skulberg, O., and Utkilen, H.: Cyanobacteria in the environment, in: Toxic Cyanobacteria in Water: A guide to their public health consequences, monitoring and management, edited by: Chorus, I., and Bartram, J., 1999.
Schmidt, S. K., Reed, S. C., Nemergut, D. R., Grandy, A. S., Cleveland, C. C., Weintraub, M. N., Hill, A. W., Costello, E. K., Meyer, A. F., Neff, J. C., and Martin, A. M.: The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils, P Roy Soc B-Biol Sci, 275, 2793-2802, DOI 10.1098/rspb.2008.0808, 2008.
Schulz, S., Brankatschk, R., Dumig, A., Kogel-Knabner, I., Schloter, M., and Zeyer, J.: The role of microorganisms at different stages of ecosystem development for soil formation, Biogeosciences, 10, 3983-3996, DOI 10.5194/bg-10-3983-2013, 2013.
Scott, E. M., Rattray, E. A. S., Prosser, J. I., Killham, K., Glover, L. A., Lynch, J. M., and Bazin, M. J.: A Mathematical-Model for Dispersal of Bacterial Inoculants Colonizing the Wheat Rhizosphere, Soil Biol Biochem, 27, 1307-1318, Doi 10.1016/0038-0717(95)00050-O, 1995.

Servedio, M. R., Brandvain, Y., Dhole, S., Fitzpatrick, C. L., Goldberg, E. E., Stern, C. A., Van Cleve, J., and Yeh, D. J.: Not just a theory--the utility of mathematical models in evolutionary biology, Plos Biol, 12, e1002017, 10.1371/journal.pbio.1002017, 2014.
Soetaert, K., and Herman, P.: A Practical Guide to Ecological Modelling: Using R as a Simulation Platform, Springer, UK, 2009.
Stapleton, L. M., Crout, N. M. J., Sawstrom, C., Marshall, W. A., Poulton, P. R., Tye, A. M., and Laybourn-Parry, J.: Microbial carbon dynamics in nitrogen amended Arctic tundra soil: Measurement and model testing, Soil Biol Biochem, 37, 2088-2098, DOI 10.1016/j.soilbio.2005.03.016, 2005.
Strauss, S. L., Garcia-Pichel, F., and Day, T. A.: Soil microbial carbon and nitrogen transformations at a glacial foreland on Anvers Island, Antarctic Peninsula, Polar Biol, 35, 1459-1471, DOI 10.1007/s00300-012-1184-5, 2012.
Tang, J. W., Misson, L., Gershenson, A., Cheng, W. X., and Goldstein, A. H.: Continuous measurements of soil respiration with and without roots in a ponderosa pine plantation in the Sierra Nevada Mountains, Agr Forest Meteorol, 132, 212-227, 10.1016/j.agrformet.2005.07.011, 2005.
Telling, J., Anesio, A. M., Tranter, M., Irvine-Fynn, T., Hodson, A., Butler, C., and Wadham, J.: Nitrogen fixation on Arctic glaciers, Svalbard, J Geophys Res-Biogeo, 116, Artn G03039

Doi 10.1029/2010jg001632, 2011.
Telling, J., Stibal, M., Anesio, A. M., Tranter, M., Nias, I., Cook, J., Bellas, C., Lis, G., Wadham, J. L., Sole, A., Nienow, P., and Hodson, A.: Microbial nitrogen cycling on the Greenland Ice Sheet, Biogeosciences, 9, 2431-2442, 10.5194/bg-9-2431-2012, 2012.
Toal, M. E., Yeomans, C., Killham, K., and Meharg, A. A.: A review of rhizosphere carbon flow modelling, Plant Soil, 222, 263-281, Doi 10.1023/A:1004736021965, 2000.
Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H.: Net photosynthesis, respiration, and production of the moss Sanionia uncinata on a glacier foreland in the High Arctic, Ny-Alesund, Svalbard, Arct Antarct Alp Res, 34, 287-292, Doi 10.2307/1552486, 2002.
Vandewerf, H., and Verstraete, W.: Estimation of Active Soil Microbial Biomass by Mathematical-Analysis of Respiration Curves - Calibration of the Test Procedure, Soil Biol Biochem, 19, 261-265, Doi 10.1016/0038-0717(87)90007-1, 1987.
Wang, Y. P., Chen, B. C., Wieder, W. R., Leite, M., Medlyn, B. E., Rasmussen, M., Smith, M. J., Agusto, F. B., Hoffman, F., and Luo, Y. Q.: Oscillatory behavior of two nonlinear microbial models of soil carbon decomposition, Biogeosciences, 11, 1817-1831, 10.5194/bg-11-1817-2014, 2014.
Xu, M., and Qi, Y.: Spatial and seasonal variations of Q(10) determined by soil respiration measurements at a Sierra Nevadan forest, Global Biogeochem Cy, 15, 687-696, Doi 10.1029/2000gb001365, 2001.
Zelenev, V. V., van Bruggen, A. H. C., and Semenov, A. M.: "BACWAVE," a spatial-temporal model for traveling waves of bacterial populations in response to a moving carbon source in soil, Microbial Ecol, 40, 260-272, 2000.
Zheng, Z. M., Yu, G. R., Fu, Y. L., Wang, Y. S., Sun, X. M., and Wang, Y. H.: Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: A trans-China based case study, Soil Biol Biochem, 41, 1531-1540, 10.1016/j.soilbio.2009.04.013, 2009.
Zhou, T., Shi, P. J., Hui, D. F., and Luo, Y. Q.: Global pattern of temperature sensitivity of soil heterotrophic respiration (Q(10)) and its implications for carbon-climate feedback, J Geophys Res-Biogeo, 114, Artn G02016

10.1029/2008jg000850, 2009.
Zhou, Z. Y., Guo, C., and Meng, H.: Temperature Sensitivity and Basal Rate of Soil Respiration and Their Determinants in Temperate Forests of North China, Plos One, 8, ARTN e81793

10.1371/journal.pone.0081793, 2013.
Zumsteg, A., Schmutz, S., and Frey, B.: Identification of biomass utilizing bacteria in a carbon-depleted glacier forefield soil by the use of 13C DNA stable isotope probing, Env Microbiol Rep, 5, 424-437, Doi 10.1111/1758-2229.12027, 2013.