Predicting the impact of spatial heterogeneity on microbial redox dynamics and nutrient cycling in the subsurface

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Response to RC1

We thank the reviewer for the constructive comments. We acknowledge that we have to provide an improved explanation of the aims of our study and of the used approach, and an improved discussion of our results and we address this in the revised version of our manuscript. With these revisions we address all the specific comments made by the reviewer. Besides this, we try to clarify that the aim of our study is to find general relationships between the spatial heterogeneity of the aquifer matrix and the dynamics of biogeochemical reactions. We do use data from our subject site as well as from the literature to constrain the model scenarios but it has not been our aim to provide a simulation of any specific part of the subject site. For the sake of generality we thus also consider higher initial reaction rates than those likely to be found at the site which allowed us to span a larger range of conditions. We are also fully aware of the uncertainties associated with the parameter values used in our simulations. However the parameter values we used are consistent in their relative magnitude to each other and with the range of experimental observations. We found independently of the compound and its specific reactivity in a given domain that the Damköhler number is a good predictor of the importance of spatial heterogeneities which allowed us to present and discuss our findings independently of the specific parameter values used. In the revised manuscript we expand our discussion of the uncertainties associated with our approach and the associate limitations.

Response to specific comments:

P1-L18: 'undertook'
Addressed:
"…
Therefore, we undertook a numerical modelling approach to evaluate the sensitivity of groundwater microbial biomass distribution and nutrient cycling to spatial heterogeneity in different scenarios accounting for various residence times.
…"

P1-L21: In biology we have a clear nomenclature. Conditions are either 'oxic' or 'anoxic', Organisms and processes are 'aerobic' or 'anaerobic'. I suggest to use this nomenclature concisely throughout the MS.
This is exactly how we intended to use it as well. Thus, oxic and anoxic zones refers to presence or absence of oxygen, while aerobic and anaerobic zones refer to the predominant respiration type that is

occurring at that location. We can clarify this wording further in the revised manuscript, and we have proof-read the manuscript to ensure that we do not misuse the terminology. Note that we have used the term "oxic/anoxic cell" when referring to grid cells of the numerical model. We replace this term in the revised manuscript to avoid any confusion: (revised to "mesh nodes").

P2-L37: Here and at many other spots

We assume that this comment pertains to the references shared by the referee. If not, could they please clarify the specific comment associated with this line?

P2-L49: Papers of potential interest for the authors: Zhou et al. (2012) FEMS Microbiol. Ecol. 81: 230-242, Hofmann et al. (2020) Front. Microbiol. 11: 543567

Both the papers are interesting and are now referred to in the Introduction section.

"…
Schwab et al. (2017);Zhou et al. (2012);Hofmann et al. (2020) linked changing diversity of microbial communities in groundwater with spatio-temporal variation of the groundwater 50 physico-chemical quality.
…"

P2-L50: Papers of potential interest for the authors: McGuire et al. (2000) Chem Geol 169: 471–485, McGuire et al. (2005) Ground Water 43: 518–530

These papers suitably display the point that physicochemical characteristics of and redox zones in groundwater vary in both space and time (although for contaminated sites and not for oligotrophic conditions as in our study) and are referred to now in the Introduction section.

"…
McGuire et al. (2000) and Benk et al. (2019);McGuire et al. (2000) linked changing composition of terminal acceptors and of dissolved organic matter (DOM) in groundwater with surficial events, respectively.
…"

In the Introduction section important issues such as the discrimination between 'active' and 'inactive' as well as 'mobile' and 'immobile' cells are not picked out as central points.

The central point of this work is to enhance understanding about how spatial heterogeneity controls access to nutrients and in turn shapes the microbial community in a system that provides feedback on carbon and nitrogen cycling. We thus did not focus on the discrimination between different types of microbial cell in the introduction. However, following the suggestion of the reviewer we now address this issue in the Introduction).

"…
Spatial heterogeneity influences subsurface microbial and nutrient dynamics by limiting access to nutrients and electron acceptors (Murphy et al., 1997), thereby influencing the distribution of active, dormant, suspended and attached microbes as well (Grösbacher et al., 2018; Couradeau et al. 2019). Dormant microbes were found to vary between 60% to 80% of total microbial biomass in soil (Lennon and Jones, 2011), and attached microbes commonly form the majority of microbial biomass fraction in the subsurface (Griebler and Lueders, 2009; Grösbacher et al., 2018). However, data on these fractions for groundwater systems are still scarce.
…"

Methods

As highlighted in the first paragraph, the conceptual model is simplistic. While the focus is to test for spatial heterogeneity and flow velocity as steering factors with respect to carbon, nutrient and microbial dynamics, frame conditions for the model simulations are non-dynamic with steady-state flow and constant inflow concentrations of dissolved

species. In this respect, I would expect an in-depth discussion of the model output. Are the set frame conditions sensitive factors? How may the results change with respect to transient input concentrations of carbon and nutrients.

We fully realise that we are not exploring all the factors that govern microbial activity and nutrient cycling in a system. The study is limited to studying the impact of spatial heterogeneity and how it controls access to carbon substrate and electron donors and acceptors. We compensate for the lack of exploring other factors (such as varying concentrations of chemical inputs) by varying the flow regime. For example, a higher substrate input at the inlet in a slow flow regime will result in a reaction dominant regime (recall that the slow flow regime is already reaction dominant). With the consideration of a variety of electron acceptors in varying flow regimes we do cover a comprehensive set of conditions for the research question that is explored in the manuscript. As suggested by the referee, the impact of temporal dynamics, or transient conditions, is an interesting and pertinent question in the field. But it results in more confounding factors, and thus we believe that we won't be able to do justice to the question at hand, i.e., how does spatial heterogeneity impact microbial activity and nutrient cycling in a system? We now clarify the aim of our approach at several locations in the Introduction:

"…
Since preferential flow paths have been established to control access to nutrients, electron acceptors and thus influence the emergence of microbial hotspots (Franklin et al., 2019), we focus on investigating spatial heterogeneity alone.
…"

"…
Simulated scenarios are informed by data from the literature and from a subject site to describe realistic although generic conditions, which allows us to combine these conditions with different types of subsurface heterogeneities to determine the resulting biogeochemical potential of the subsurface system.
…"

And in the Methods sections:

"…
It is however not the aim to explicitly simulate and specific part of the subject site. For some model input we rather considered values at the extreme end of possible conditions to enlarge the range of conditions covered by our model scenarios.
…"

We also discuss its limitation and suggest further research steps building upon the result of our study in the Discussion section:

"…
The reaction network was formulated using literature knowledge and geomicrobial activity identified at the subject site. At the same time, it captures varying respiration and microbial regimes, from aerobic autotrophy to aerobic heterotrophy and anaerobic heterotrophy. The activity of geomicrobial reactive systems is dependent on a variety of factors, such as nutrient availability, access to energy gradients, pH, pore size, hydraulic conductivity, particle size distribution (Smith et al., 2018). The limited information on 490 microbial activity applicable to oligotrophic conditions in the subsurface does challenge the parameterization of the reaction network, which is a priori a potential major source of uncertainty for the obtained model results. Given this limitation, we calibrated the parameters of the reaction network to ensure that it covers a sufficiently large range of Da values and that it does not violate the established redox hierarchy in any of the flow regimes considered (see Appendix A and the base case results). Additionally, 495 we consistently used our parameter set in all scenarios and used results of the homogeneous base cases as internal reference to which we compared results of the individual heterogeneous scenarios as we aimed to study the impact of spatial heterogeneity on microbial activity and subsurficial nutrient dynamics.
Lastly, consideration of varying flow regimes in combination with the reaction network provides a view on both reaction dominant systems and flow dominant systems, indicated by the use of Da. This approach 500 compensates for our approach wherein we do not explore additional scenarios varying concentrations

of chemical species and their influence on microbial growth and distribution. By treating the analysis of results in terms of Da, we condense the discussion to effective rates of microbial activity given presence of spatial heterogeneity of hydraulic conductivity.
…"

"…
We expect additional studies exploring the impact of varying concentrations of chemical species, parameters relevant to other ecosystems or subject sites to add to the evidence generated by our study that the impact of spatial heterogeneity on subsurficial reactive systems may be predicted using field estimated indicators such as breakthrough time, Pe and Da.
…"

The authors mention the 'use of geochemical and geomicrobial observations from a common study site' as basis of the conceptual model. However, I could not find any sources (papers cited) with respect to 'values'. The concentrations of TOC, DOC, NH4, NO3, O2, prokaryotic cells (active and inactive) have been selected and based on which studies and sites.).

In P6-L176, we refer to Kuesel et al. (2016) that presents concentrations of DOC, TOC, nitrate, DO (Figure 6) observed in the groundwater at the subject site. We used the upper limits of observations made for the reactive species at the site, as clarified in the Methods section:

"…
It is however not the aim to explicitly simulate and specific part of the subject site. For some model input we rather considered values at the extreme end of possible conditions to enlarge the range of conditions covered by our model scenarios.
…"

The paper also mentions the geomicrobial activity that has been identified at the site: aerobic and anaerobic heterotrophy as well as autotrophy, and we duly noted them and included them in the process network. At the same time, we made sure to calibrate the process network so that it adheres to redox hierarchy (see Appendix A for details on the process network). This also enabled us to generalize the findings.

In P6-L182 you say: 'The concentrations of the reactive species mimicked conditions observed in the subject site'. However, in the discussion it is mentioned that there were two orders of magnitude difference in prokaryotic cell numbers. I ask the authors to carefully consider input values. Is it true that a prokaryotic concentration of mobile prokaryotic cells in groundwater of 10^9 have been found in the field? Seems very high to me.

It looks like there is confusion with respect to the use of reactive species. By reactive species, we refer to DOC, ammonium, nitrate etc. (not the microbial species). Naturally, having used data collected at the site, we drew a comparison between the microbial biomass present at the site and in our domain. However, it must be kept in mind that our scenarios are not meant to resemble exactly the conditions at specific locations of the subject site. We defined our input concentrations by the upper limits of the concentrations having been measured at the subject site which rather represent conditions close to the groundwater table. This allowed us to consider a wider range of Damköhler numbers including high reactivities. This explains that also the bacterial number are higher than observed at the well of the subject side with travel times of years to decades needed for the recharged groundwater to reach them. If we would have considered conditions of low reactivity/Damköhler numbers, matching conditions around the observation wells, a better match of the observed bacterial cell numbers would have been possible. But answering the question of the study, how spatial heterogeneities affect the dynamics of biogeochemical transformations at a variety of conditions found in groundwater, would not have been possible. This was the motivation to also bring into perspective findings from other studies and sites and we included the above points into the discussion of the revised manuscript:

"…
However, the simulated values of mobile biomass are in the range derived in both lab scale and field scale studies (Holm et al., 1992;Griebler and Lueders, 2009;Grösbacher et al., 2018). Also, the mobile biomass concentration is in the range of particulate organic carbon concentration observed to be exported in the seepage at the subject site (Lehmann et al., 2021). The relatively high biomass values obtained in the 515 simulations are attributed to the relatively high inflow concentrations as well as to the relatively high microbial reactivity we considered in the simulations to allow them to cover also high Da ranges. We note that while the total biomass may not be matching the observations at the subject site, the relative composition of the microbial species fractions (that is, immobile, mobile, active and dormant) follow established findings. For example, immobile microbial biomass indeed forms the majority biomass in the 520 subsurface (as well as in our study), with its ratio with mobile biomass changing based on nutrient and other environmental conditions (Griebler et al., 2002; Grösbacher et al., 2018). It is proposed that the ratio of immobile and mobile biomass in (Griebler et al., 2002; Grösbacher et al., 2018) varies per nutrient availability, with higher ratios observed in oligotrophic conditions and lower ratios in nutrient rich conditions. We extend this further in our study, by observing that the ratio depends on the Damköhler 525 number, with higher ratios in in low Da systems, and lower ratios in high Da (reaction dominant) systems. It is further estimated that 60%-80% of microbial biomass in soil may be inactive (Lennon and Jones, 2012). In our study, we observe these ranges in the slow flow and medium flow regimes, but not in the fast flow regime. With newer technologies equipped to better characterise activity of microbes in environmental samples (Couradeau et al. 2019), we expect that it will be easier to draw the comparison in the future.
…"

Having said that, we acknowledge that the gene count in Opitz et al. (2014) is actually 10^6 to 10^8, we have corrected this in the revised version:

"…
Opitz et al. (2014) measured the total bacterial biomass in groundwater of the subject site to vary from 10_6 to 10_8 gene copies L^{-1} (depending on 510 location, tapped aquifer and season of measurement), which is lower than the simulated mobile values.
…."

The concept of the reaction network is simplistic, which is ok. But it should be as realistic as possible. Does all NH4 originate from DOM? Isn't there direct input of NH4 from the surface?

As clarified earlier, we used the concentration values across the entire site to be the input at the inlet. The concentration of ammonium at the inlet is not attributable solely to the depolymerisation of organic matter (POM), but also attributable to incoming flux from the upstream zones.

As mentioned in Table A.4.2. there is a constant input of 60µM of NH4 (about 1mg/L) that cannot originate from the 10mg of DOC (800 µM). I recall that the studied Hainich Critical Zone sites are partially located in areas with agriculture. To which of the Hainich sites does the conceptual model refer to?

The referee understands correctly that the input into soil will be different in different land use areas. At the same time, soil and the vadose zone are good buffer zones. Additionally, the groundwater in the agricultural area lies in a confined aquifer with more limited interaction with the surface. It must be noted that considering the size of our domain, this modelling exercise is not intended to replicate the processes in the entire study site but to understand if there is an impact on how we predict the nutrient cycling in the subsurface were we to neglect spatial heterogeneity. Thus, all results and associated discussions are carried out with respect to the homogeneous domain (a common assumption) being the base case.

I know that it is hard to collect reliable information from the literature with respect to

microbial features in shallow aquifers. Having this in mind, one need to carefully select values for 'rate constants', 'yield coefficients', … The values summarized in Table A.4.1 originate from field studies and lab studies very different in nature, i.e. values derived from lab experiments with pure bacterial cultures. Are the chosen values sufficiently representative for the Critical Zone in Hainich and shallow aquifers in general? This at least needs to be critically discussed.

We agree that different literature source have been used for the parameter values used in this study we also agree that there is a large uncertainty regarding these values and to which extent they are representative for our subject site. However, we took care that the parameter values are in reasonable relation to each other (i.e. aerobic processes taking place faster and providing higher yields than anaerobic processes etc.). Since rate parameter for DOC degradation are also highly depending on the composition/reactivity of DOC which is highly variable in the subsurface even the use of field derived rate parameters from the subject site or any other field site would not have been representative for shallow aquifers in general. As pointed out above in the context of the bacterial numbers the maximum reaction rates we consider in our study might be at the higher end of the range of rates one would potentially observe at the subject site but this allowed us to cover a larger range of Damköhler numbers when investigating the impact of spatial heterogeneities on biogeochemical transformations, which was our focus in this study. In the revised version we expanded our discussion to address these issues:

"…

The reaction network was formulated using literature knowledge and geomicrobial activity identified at the subject site. At the same time, it captures varying respiration and microbial regimes, from aerobic autotrophy to aerobic heterotrophy and anaerobic heterotrophy. The activity of geomicrobial reactive systems is dependent on a variety of factors, such as nutrient availability, access to energy gradients, pH, pore size, hydraulic conductivity, particle size distribution (Smith et al., 2018). The limited information on 490 microbial activity applicable to oligotrophic conditions in the subsurface does challenge the parameterization of the reaction network, which is a priori a potential major source of uncertainty for the obtained model results. Given this limitation, we calibrated the parameters of the reaction network to ensure that it covers a sufficiently large range of Da values and that it does not violate the established redox hierarchy in any of the flow regimes considered (see Appendix A and the base case results). Additionally, 495 we consistently used our parameter set in all scenarios and used results of the homogeneous base cases as internal reference to which we compared results of the individual heterogeneous scenarios as we aimed to study the impact of spatial heterogeneity on microbial activity and subsurficial nutrient dynamics.

Lastly, consideration of varying flow regimes in combination with the reaction network provides a view on both reaction dominant systems and flow dominant systems, indicated by the use of Da.

…"

With respect to DOC, an contstant input concentration of 800µM has been chosen. DOC degradation in soil and in groundwater is determined not only by its concentration but more likely by its quality (degradability). Has this been considered.

There is dynamics in many aspects, including flow velocity, water retention time, activity and biomass of microbes, DOM concentration and transformation, N transformation, …

Only a subset of parameters, i.e. spatial heterogeneity and flow velocity (related to residence time) has been tested. This needs to be clearly mentioned already in the Introduction section.

Clarification added in the introduction section of the revised manuscript:

"…

Since preferential flow paths have been established to control access to nutrients, electron acceptors and thus influence the emergence of microbial hotspots (Franklin et al., 2019), we focus on investigating spatial heterogeneity alone.

…"

Captions of Tables are generally on top of the tables, not below. See all tables.
Noted, corrected in the revised version.

P11-L297: Is there evidence for a parallel reduction of nitrate and oxidation of ammonium?
Both ammonia oxidation and nitrate reduction have been found to be active in sub-oxic conditions: (De Brabandere et al., 2014; Kalvelage et al., 2013; Seitzinger et al., 2006.) In our simulations these processes thus take place sequentially and not in parallel. In particular, in the base cases in our study, the overlap of nitrate removal and ammonium removal zones (i.e. the local co-occurrence of both processes) is very small, ranging from ~1cm in the base case of the slow flow regime to ~8cm in the base case of the fast flow regime, and characterized by relatively low rates for both processes.

P12-L321: Is there any evidence that the portions of active and inactive cells/species are realistic? In particular when these ratios are calculated for individual physiological guilds (nitrate reducers, ammonium oxidizers, …). See also table 4.
To the best of our knowledge '…little is known about the relevance and extent of dormancy in groundwater systems' (review of Ruiz-Gonzales et al., 2021) but it is assumed that dormancy is a crucial factor for groundwater bacterial communities. For soil systems up to 96% of the bacterial cells we found to be inactive (review of Lennon and Jones, 2011) which implies that the numbers obtained in our model scenarios are realistic. In the revised manuscript we added a few word on this issue to the Discussion:
"…
It is further estimated that 60%-80% of microbial biomass in soil may be inactive (Lennon and Jones, 2012). In our study, we observe these ranges in the slow flow and medium flow regimes, but not in the fast flow regime.
…"

P15-L386: log10Da?
Correct. Thank you for pointing it out. Addressed in the revised version.

P15-L394: Dissolved oxygen (DO) is not a nutrient.
Correct. Thank you for pointing it out. Phrase replaced with "chemical species" in the revised version.

P16-L411: Provide a citation that supports this statement.
Addressed:
"…
This may be due to the presence of DO at reduced concentrations in the downgradient region of the domain. DO at these concentrations and low DO/Ammonium ratios can be 425 preferentially taken up by ammonia oxidizers compared to aerobic degraders (Gu et al., 2006).
…"

Discussion

P19-L459: The 'available' process knowledge, does it refer to the Hainich study site?
This phrase refers to knowledge from literature from deep subsurface studies (groundwater, marine sediments), and thus includes but is not limited to the Hainich study site. We clarified this in the revised manuscript:
"…
In this study we synthesized available process knowledge and observations from our subject site on geomicrobial activity in the deep subsurface, both terrestrial and marine, into a set of in silico scenarios on 475 the fate of biogeochemically reactive compounds in heterogeneous subsurface settings.

…”

P19-L474: from carbon concentration and carbon content per cell one will not end up with gene copies per volume but cells per volume.
Correct. Thank you for pointing it out, addressed in the revised version of the manuscript:
“…
Microbial abundance can be derived from carbon content in the biomass using available conversion factors varying from 5 - 39 femtogram (fg) C/cell (Fukuda et al., 1998;Vrede et al., 2002). This resulted in median values of total mobile biomass in the domain of 10^9 to 10^11 cells/L.
…”

Quantification of cell numbers in
groundwater and aquifers by means of molecular tools quantifying 16S rDNA gene copies is only a rough estimation of cell abundance.
Absolutely, we agree. This contributes to the general uncertainty when comparing the model derived biomass data with experimental data. See also our comment above.

P19-L474: Does 100times less cells equal 100times less microbial activity and 100times less transformation of C and N? Please comment on that.
The overall activity is the product of the number of active cells and the rate per cell at the given conditions. Since the in situ rates per cell are not known for the subject site it is difficult to speculate how much less activity comes with the reduced cell numbers. As discussed above and in the revised manuscript the conditions we imposed in the model are more representative for conditions close to the groundwater table and allow (on purpose) a higher reactivity than in deeper groundwater regions next to the observation wells.

P20-L490 & L516: There is techniques and reports available on high-resolution sampling in aquifers. The ready should not get the impression one cannot get spatially more resolved in sampling. E.g. Ronen et al. 1987 J. Hydrol. 92, 173–178, Báez-Cazull et al. 2007 Appl. Geochem. 22, 2664–2683, Smith et al. 1991Contam. Hydrol. 7, 285–300, Anneser et al. 2008 Appl Geochem 23:1715–1730.
*Absolutely, as we also mention, we have **some** capability to resolve the heterogeneity and obtain higher resolution samples, especially in groundwater. But it must be recognised that there will always be sub-sampling scale heterogeneities that the sampling technique will not be able to resolve. In the revised manuscript we modified our wording to clarify this point and expanded the references to do the same.*

“…
The requirement of vertically discretized sampling has already been recognized (Ronen et al., 1987; Smith et al., 2018) and addressed by various sampling methodologies such as low flow sampling techniques, passive samplers, point and discrete interval samplers (Ronen et al., 1987;Smith et al., 1991;Powell and Puls, 1993;Báez-Cazull et al., 2007;Anneser et al., 2008) even though sub-sampling scale heterogeneities will not be resolved. Our results support the usefulness of such spatially resolved 575 sampling techniques for analysis of microbial activity in the groundwater.
…”

P20-L501: Have the authors considered that there is different growth rates with different physiological groups within the microbes, i.e. aerobes may grow faster that nitrate reducers and sulfate reduces are extremely slow. Did I miss this information?
The parameterisation of the reaction network addresses this aspect (among many others) of low respiration rates, low yield coefficients etc (see Table A.4.1). Thus, we see aerobic degraders (heterotrophs) outcompeting other species in presence of DOC and DO, while nitrate reducers become active only at much lower concentrations of DO (see figures S1-S4).

P20-Fig. 6: What do you mean with ‘oxic cells’. Please change.
Apologies for the confusion. We refer to the grid cells (0.01mx0.01m) that are oxic at a particular cross-section along the predominant flow path (P20-L495). We replaced this phrase with “mesh nodes” in the revised manuscript to avoid such confusion.

P21-L528: Consider the review paper of Smith et al. 2018 FEMS Microb. Ecol. 94: fiy191
Thank you the suggestion. We make reference to this paper in the revised manuscript at several locations including here:
“…
Immobile microbes account for more microbial activity compared to mobile microbes. However, groundwater samples represent mobile microbial biomass, termed as planktonic biomass (Smith et al., 2018). Estimates of microbial respiration 585 are thereafter made based on the abundance of mobile microbes in the obtained groundwater samples.
…”

P22-L565: I fully agree with this statement. In many cases the contribution of the mobile fraction of microbes can be neglected in terms of ‘transformation processes’.
Findings from other studies (like the one already cited Grösbacher et al. 2018) are not discussed in comparison to the model outcome.
We added some reference to the revised manuscript and discuss our findings in the context of these references:
“…
The relatively high biomass values obtained in the 515 simulations are attributed to the relatively high inflow concentrations as well as to the relatively high microbial reactivity we considered in the simulations to allow them to cover also high Da ranges. We note that while the total biomass may not be matching the observations at the subject site, the relative composition of the microbial species fractions (that is, immobile, mobile, active and dormant) follow established findings. For example, immobile microbial biomass indeed forms the majority biomass in the 520 subsurface (as well as in our study), with its ratio with mobile biomass changing based on nutrient and other environmental conditions (Griebler et al., 2002; Grösbacher et al., 2018). It is proposed that the ratio of immobile and mobile biomass in (Griebler et al., 2002; Grösbacher et al., 2018) varies per nutrient availability, with higher ratios observed in oligotrophic conditions and lower ratios in nutrient rich conditions. We extend this further in our study, by observing that the ratio depends on the Damköhler 525 number, with higher ratios in in low Da systems, and lower ratios in high Da (reaction dominant) systems.
…”
“…
This indicates that the mobile microbial abundance detected in groundwater samples must be used with care as a proxy for effective microbial activity and nutrient cycling (also confirmed by Alfreider et al. (1997), Murphy et al., (1997), Griebler et al. (2002) and Grösbacher et al. (2018) as mentioned earlier).
…”

Summary and conclusion

P24-L630: mention at which spatial scale.
Addressed in the revised manuscript:
“…
In this study, we investigated the impact of spatial heterogeneity on biomass persistence, distribution, and nutrient cycling at the sub-meter scale in the subsurface.
…”

P24-L640: Can this be visualized?

We display this in select heterogeneous scenarios in Fig S2 (1D spatially averaged concentration of different microbial species) and Fig S4 (2D concentration heatmaps of different microbial species). In addition, we display how predominantly anaerobic cross-sections in the domain may still contain oxic niches in Fig 6.