Response to a review by Jeppe Kristensen of "Ideas and perspectives: Beyond Microbes—Integrating Termites into Global Soil Carbon Cycling Models"

We thank Jeppe Kristensen for his thorough review of our manuscript and for his constructive comments. We have carefully addressed all points raised, as detailed in our point-by-point responses below. Reviewer comments are in blue fonts, our responses in black, and revisions to the manuscript text are highlighted in orange fonts. All line numbers refer to the revised version of the manuscript.

I had the pleasure of reading Farooq et al.'s paper on termite effects on the global C cycle. It is an incredibly well-written article presenting a mechanistic framework for how termites can be incorporated in soil carbon models and eventually into earth system models. They also provide global estimates of termite-mediated C-fluxes, both into the atmosphere as GHG gasses, and into the soil as labile and stabilised C-pools. Impressively, the emergent estimate of global termite-driven CH4 emission is very consistent with estimates from the Global Carbon Budget.

The framework is clearly presented and logical. Proper and thorough sensitivity analyses are conducted and presented clearly. Relevant recommendations for future research are outlined.

I have no severe concerns with this manuscript, and recommend it for rapid publication in Biogeosciences. Below I suggest some minor comments that can hopefully help improve the manuscript further.

Thank you for the positive evaluation of our manuscript.

Title: consider getting rid of the double colon.

Thank you for this suggestion. To avoid the double-colon construction and improve readability, we have replaced the second colon with an em dash. The revised title now reads: "Ideas and Perspectives: Beyond Microbes—Integrating Termites into Global Soil Carbon Cycling Models".

L 77-78: may be worth relating this to the total annual CH4 emission, to make the estimate more immediately interpretable. If I remember correctly, it can be around 5% of total methane emissions, no?

We have added the relative contribution of termite CH_4 emissions to the global CH_4 budget to make their magnitude more readily interpretable. Based on the Global Methane Budget

estimate of 575 Tg CH_4 yr^{-1} for total global emissions during 2010–2019 (Saunois et al., 2025), the estimated termite contribution of 10.2 Tg CH_4 yr^{-1} corresponds to approximately 1.8% of total global CH_4 emissions. We have added this comparison to the revised manuscript (lines 79-80): "The Global Methane Budget estimates termite methane (CH_4) emissions of ~10.2 ± 6.2 Tg CH_4 yr^{-1}, equivalent to ~1.8% of the estimated total global CH_4 emissions for 2010–2019."

L 114-115: It is not clear exactly how you distinguish between these three litter pools. Can you give a short description of what each of them comprise?

We have revised the text to briefly distinguish the two litter pools, clarifying that metabolic litter (I_M) represents relatively labile, readily decomposable plant material, whereas structural litter (I_S) comprises more chemically resistant, lignocellulose-rich material that decomposes more slowly. The revision text reads as follows (lines 121-124): "In these models, litter inputs (I) are typically partitioned into metabolic (I_M) and structural (I_S) pools, where I_M represents relatively labile, readily decomposable plant material, whereas I_S comprises more chemically resistant, lignocellulose-rich plant material that decomposes more slowly."

L 158: Is the pronounced aggregate formation through soil particle ingestion and regurgitation during mound construction for Macrotermes contributing to the MAOC formation? I suppose they would feature as 'fungus-farmers' in your framework, as they do not really ingest soils for nutritional purposes?

Yes, *Macrotermes* would fall within the fungus-growing termite guild in our framework. We agree that the substantial soil processing associated with mound construction by *Macrotermes* can promote aggregate formation and potentially contribute to SOC stabilization. However, this physical engineering pathway is not explicitly represented as a separate MAOC formation process in the current framework; rather, termite contributions to MAOC are represented through the downstream processing of termite-derived residues. We have acknowledged this limitation in the revised manuscript (lines 151-154): "This representation necessarily simplifies the diversity of feeding pathways observed in natural systems. For example, TER_{FG} can also collect woody material and inoculate it *Termitomyces* before incorporation into fungus combs."

L 186-193: These simplifications seem fair to me, but I would still like a rough description of what the structural, metabolic and CWD pools comprise, perhaps just with a few examples at first mention - you do give examples for CWD, so that is less critical.

We have added brief descriptions of the metabolic (I_M) and structural (I_S) litter pools at their first mention, clarifying their composition and relative decomposability (lines 121-124). CWD is already described with representative examples in the Introduction.

L 252-253: I agree, but you could make this clearer by relating some of your numbers to total global annual fluxes or similar, i.e. X% of total annual CO2 emissions.

We agree that expressing the modeled flux relative to a global benchmark improves its interpretation. In Section 5, L301, we have therefore compared termite-associated CO_2 emissions with global soil respiration, which provides a process-relevant benchmark for this biologically mediated terrestrial CO_2 flux. Specifically, the modeled termite-associated CO_2 flux (3170.6 ± 1629.8 Tg CO_2 yr^{-1}) corresponds to approximately 3.2–4.7% of global soil respiration. We consider this comparison more directly relevant than comparison with total global CO_2 fluxes, which encompass multiple sources and sinks.

Table 2: I see the termite-driven turnover of structural litter in grasslands is 0, which again makes me curious what exactly this litter pool is exactly. If structural tissue is defined by molecular composition, there would be structural compounds in grasslands (e.g. cellulose, hemi-cellulose and lignin), but perhaps there are no termites eating those pools in grassland biomes?

Thank you for raising this point. As clarified in the revised description (lines 121-124), structural litter (I_S) represents relatively resistant, lignocellulose-rich plant material and is present in grassland ecosystems. The zero termite-driven turnover of I_S in Table 2 therefore does not indicate an absence of structural litter. Rather, grasslands are represented by soil-feeding termites (TER_{SF}) in our guild parameterization (Table S3), which consume LMWC in the current framework. Consequently, termite-mediated consumption of both I_s and CWD is zero in grasslands, while these substrate pools remain available for processing through the microbial pathway.

L 273-274: Overall the sensitivity analysis seems quite robust to me. Yet, it may be helpful to suggest here towards the end what this means in terms of future research to constrain and reduce this uncertainty. It is not completely clear what research we need to reduce King uncertainty. It is better termite biomass (stocks and fluctuations) estimates, is it better grip around field metabolic requirements, feeding preferences or what is it?

Thank you for the suggestion. The implications of the sensitivity analysis for future empirical work are discussed in detail in Section 6, where we identify improved constraints on termite

biomass, ingestion rates, carbon partitioning between respiration and residue formation, and productivity–biomass scaling as key priorities for reducing model uncertainty. We have added a cross-reference at the end of the sensitivity analysis to make this connection clearer.

L 283-288: This is very interesting, and makes sense due to their role as physical ecosystem engineers able to optimise the environmental conditions of their surroundings (built structures) to their advantage. Reminds me of the ecosystem resilience arguments brought forward for drylands in the 2015 Science paper by Bonachela et al.: https://www.science.org/doi/10.1126/science.1261487 and for tropical rainforests in the 2019 Science paper by Ashton et al. https://doi.org/10.1126/science.aau9565 . Perhaps worth citing.

Thank you for suggesting these relevant studies. Both studies provide useful evidence that termite ecosystem engineering can sustain ecosystem functioning under water-limited conditions, including enhanced dryland resilience (Bonachela et al., 2015) and maintenance of decomposition and other ecosystem processes during drought in tropical rainforest (Ashton et al., 2019). We have added these references and briefly discussed this connection in the revised manuscript (lines 305-307): " These findings are consistent with previous studies showing that termite ecosystem engineering can enhance ecosystem resilience under water limitation, both in drylands and during droughts in tropical forests (Ashton et al., 2019; Bonachela et al., 2015)."

L 290-295: There is perhaps even more to it than just translocation into mounds. Macrotermes typically ingest and chew CWD together with spores from Termitomyces as a form of inoculation before they excrete both to form the fungus comb.

We agree that, in natural systems, fungus-growing termites such as *Macrotermes* can ingest and process woody material, including its inoculation with *Termitomyces* prior to incorporation into the fungus comb. This level of substrate overlap is not explicitly represented in our simplified guild structure. We have acknowledged this limitation in revised manuscript (lines 151-154): "This representation necessarily simplifies the diversity of feeding pathways observed in natural systems. For example, TER_{FG} can also collect woody material and inoculate it *Termitomyces* before incorporation into fungus combs (Otani et al., 2016). Nevertheless, through these simplified interactions, termites modify both the amounts and chemical forms of carbon entering soil microbial pathways."

L 311: Impressively consistent!

Thank you.

L 361: and as mentioned, it is not clear to me whether the ingested-regurgitated soil aggregates for mound construction is included, which has been reported to account for up to 30% of the soil matrix in areas with high termite activity.

Thank you for raising this point. Soil ingestion, regurgitation, and aggregate formation associated with mound construction are not explicitly represented in the current framework. The modeled termite-mediated MAOC flux represents carbon derived from frass and necromass and therefore does not include any additional SOC stabilization arising from mound-associated soil aggregation. We have clarified this explicitly in the revised manuscript (lines 263-266): "It is important to note that the modeled MAOC flux represents carbon derived from frass and necromass and does not include additional SOC stabilization associated with soil ingestion, regurgitation, or aggregate formation during mound construction."

Discussion

One aspect that hasn't really been touched on, but which could be an interesting aspect for future research to mention in the discussion is the interactive effects of termites and larger animals on C-processes. Some places to begin are:

- https://doi.org/10.1017/S0266467411000125
- https://doi.org/10.1016/j.tree.2021.09.006
- https://doi.org/10.1002/ece3.7445

Thank you for the suggestion. We have revised the Caveats and Priorities for Empirical Work section to discuss interactions between termites and larger animals, together with the potential complexity associated with incorporating additional soil-fauna groups and possible approaches for their representation in future global modelling frameworks. The following text has been added to Section 6 (lines 401-416):

"An additional challenge for future global implementation is representing termites within the broader faunal community without introducing excessive model complexity. Termite-mediated carbon cycling does not occur in isolation; interactions with larger animals, through effects on vegetation, litter inputs, soil disturbance, and termite activity, may indirectly modify termite-driven carbon processing (Buitenwerf et al., 2011; Charles et al., 2021; Kristensen et al., 2022). Explicitly representing these interactions alongside individual soil-fauna taxa and their functional subgroups would, however, increase model complexity. We therefore suggest that future frameworks prioritize process-based functional aggregation, whereby fauna sharing similar substrate use and effects on carbon transformations are represented collectively, while

distinct identities are retained where they introduce biogeochemical pathways that cannot readily be generalized. Termites may warrant such distinction because, in addition to their substantial processing of plant and soil organic matter, they represent a direct biological source of CH_4 (Law et al., 2024; Saunois et al., 2025) that cannot appropriately be assigned to a generic soil-fauna pool. Future model development should therefore test which faunal groups and associated processes can be aggregated without materially altering predicted carbon and GHG fluxes.”

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