

Reviewer 1:

Response to a review by Omar Flores of “Ideas and perspectives: Beyond Microbes—Integrating Termites into Global Soil Carbon Cycling Models”

We thank Omar Flores 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.

The study by Farooq et al. presents a novel work that explicitly includes termites within Microbial Explicit Soil Carbon (MES-C), a process-based SOC model. The relevance of such work is well justified, particularly due to the key role of termites in regulating SOC sequestration and CO₂ and CH₄ emissions, which is missing in global SOC models.

The main technical weaknesses of the presented work (e.g. uncertainty in some assumptions, simplification of key soil processes, homogeneous spatial representation of termites despite their highly heterogeneous distribution) are reasonable taking into account issues in the availability of data, the novelty of the approach, and common limitations in model structure. Moreover, they have been also properly addressed by the authors.

Nevertheless, there is one issue with the perspective of a detailed representation of termites into global models. The authors have divided termites in three feeding guilds, with their own parameters and specialized interactions with litter and SOC pools. Such level of detail is very reasonable for ecosystem-scale models, but it might be excessive for global models, which is the claimed goal of the authors. Despite it can be done, as shown by the authors, a question remains: should we really add all that complexity in global models? There is no doubt that termites are an important biota group with high impact, but the same can be said for several other groups, like ants, earthworms, nematodes, etc. Global models normally do not represent any of them, and if they were to include them, it would not be feasible to add each taxon separately (let alone with several guilds or subgroups per taxon). While the specific framework developed by the authors can be interesting for specific simulations related to termites, or as reference for future model developments, its future integration into global models seeking to improve the representation of soil fauna will probably need a simplification. After reading this study, I see right now two possibilities (for future developments):

1) Justify (if that is the case) that termites must remain separately from any other biota due to unique roles, but perhaps combining all guilds into one pool, and parameterize the different roles of each guild within that common pool. For example, equations S7-S9 could be modified using one single TER pool, but adding in each case a multiplier with the fraction of the TER pool that corresponds to the fraction of biomass of each feeding guild (at each time step). Some processes could retain the specialized effects of each guild that way, while other processes should be simplified with an average effect of the entire termite biomass across guilds, which would reduce the number of parameters (together with reduced interactions and fluxes) and therefore reduce complexity.

2) Discuss if termites could be mixed with other fauna groups, splitting if needed their guilds into different functional groups of soil fauna, in the same way that for example in some soil food web models nematodes are divided into different functional groups depending on their body size and/or feeding roles (e.g. microbivores, herbivores, predators). Maybe the way to go could be to modify generic functional groups (once they are added to global models) to account for the specific roles played by termites, as for example including the role of TER_{SF} within microbivores, and the roles of TER_{FG} and TER_{XP} within detritivores, taking into account that termites will only be a fraction of such pools.

I don't think there is any need to modify the study for that reason, the presented perspectives (and all equations, results, etc.) can stay as they are, but I would suggest to add to the discussion also those challenges related to adding termites to global models while keeping complexity as low as possible. Despite this work has merit on its own and can certainly help to improve models, I would like the authors to address, from their expertise on modelling termites, what would be the best option to deal with future global modelling frameworks including termites along with other soil fauna groups.

Overall, the manuscript is interesting, well written, it represents a first step towards a potentially relevant improvement of global SOC models, and it should be suitable for publication after a minor revision.

We agree with the broader point that the explicit representation of multiple soil-fauna taxa and their respective functional groups could rapidly increase the complexity of global soil carbon models. We also agree that future global frameworks incorporating multiple faunal groups will require careful consideration of the minimum level of biological detail needed to retain the relevant biogeochemical processes. We have therefore expanded the Discussion to address this trade-off between functional realism and model complexity.

Importantly, our current implementation is already conceptually close to the reviewer's first proposed approach. The three termite feeding guilds are not represented as three independently constrained termite populations with separate ecosystem carrying capacities. At

each model time step, the total termite biomass that can be supported by the ecosystem is first calculated. This total biomass is subsequently partitioned among the three feeding guilds using prescribed guild fractions. Thus, the guild representation does not independently predict three termite biomass pools; rather, it provides a computationally inexpensive means of allocating a single ecosystem-level termite biomass among functionally distinct carbon-processing pathways. We retain guild-specific pathways because termites interact with fundamentally different substrates depending on feeding strategy. Xylophagous, fungus-growing, and soil-feeding termites process coarse woody debris, plant litter, and more decomposed soil organic matter, respectively. Representing these pathways separately preserves mechanistically important carbon flows while adding little computational complexity and avoiding the need to independently constrain three termite populations. A formulation based on a single termite pool with guild-fraction multipliers applied directly to substrate-consumption fluxes, as suggested by the reviewer, would be mathematically very similar and would require the same information on guild composition. We have clarified this point in the revised manuscript.

We also agree that future frameworks incorporating multiple soil-fauna groups may favour broader functional classifications rather than explicit taxonomic representation. However, we consider retaining termites as an identifiable component within such a framework to be important because some termite-mediated processes cannot readily be generalized to a broader soil-fauna pool. Most notably, termites are major macrofaunal processors of CWD, particularly in tropical and subtropical ecosystems, and xylophagous termites provide a direct pathway through which CWD-derived carbon is fragmented, transformed, and transferred to downstream soil carbon pools. By physically fragmenting and biochemically transforming lignified plant material, termites accelerate the transfer of CWD-derived carbon into smaller particulate and dissolved pools that can then enter microbial SOC formation pathways. In addition, termites represent a direct biological source of CH₄, and our framework explicitly links termite CH₄ production with atmospheric emissions, methanotrophic oxidation, methanotroph biomass production, and associated CO₂ release. Assigning these processes to a generic detritivore or soil-fauna pool containing organisms that do not share this metabolic pathway would be difficult to interpret mechanistically and could introduce inappropriate CH₄ production from the broader fauna pool. Together, the unique capacity of termites to process CWD and their distinct role in greenhouse-gas production provide a process-based rationale for maintaining termite identity even where other soil fauna may eventually be represented at a more aggregated functional level.

We have added the following text in Section 6 (lines 401-416) to address the trade-off between functional representation and model parsimony, including the potential integration of termites with other soil-fauna functional groups in future global modelling frameworks: “An additional

consideration for future global implementation is how to represent 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 CH₄ (Law et al., 2024; Saunio 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.”

Table 2 – The total Area was apparently calculated as the sum of all the areas by vegetation type. If I understand the represented concept correctly, termites occupy 17.3 m/km² of tropical evergreen, 5.9 m/km² of tropical deciduous, etc. Then what you are suggesting with that total is that, in general over all vegetation types, termites occupy 72.3 m/km², right? I don't think that is correct. You should calculate an average instead of a sum for such variable, or even a weighted average considering the different total areas of each vegetation type. If my interpretation is not correct, please explain better what exactly are you showing there.

The values reported in the Area column represent absolute termite-occupied area expressed in million km² within each vegetation type. Therefore, these values are additive, and the total value (72.3 million km²) represents the global termite-occupied area. We have revised the unit to “million km²” to avoid confusion.

You explain in the manuscript (L210) that GPP was smoothed using a 7-day running mean, while in the supplementary (L58) you also mention that you obtained GPP from MODIS 8-day productivity product, and that you constructed daily climatological time series. Can you explain in more detail how did you process the 8-day data? In particular, for generating the daily data; the use of a 7-day running mean from daily data is more obvious and should not require more details, but it would be better to explain the method used to go from 8-day to daily.

The MODIS GPP and NPP product provides GPP values over 8-day composites. To construct the daily forcing, we divided the value for each composite period by the number of days in that period and assigned the resulting daily value to each corresponding day. We have revised the Supplementary Methods (lines 67-69) to explicitly describe this procedure.

Supplementary:

L44 – the symbols ω and δ determine the fractions of decomposed carbon entering the LMWC pool for frass and necromass, respectively, with their complementary fractions determining what goes to MAOC in each case; the text wrongly describes them as if they refer to the different SOC pools, when they refer to different output fluxes from termite biomass.

Thanks for pointing this out. We have revised the text (lines 46-48) to clarify that ω determines the fraction of decomposed frass carbon entering the LMWC pool, with the complementary fraction ($1 - \omega$) entering MAOC, while δ determines the corresponding partitioning of decomposed necromass carbon between LMWC and MAOC.

Table S3 – the values shown for fractions of total termite biomass for Asia and Africa not always add up to 1. In particular, the first two rows for tropical vegetation (evergreen and deciduous) sum in total 0.91, and savanna and dense shrubland only have 0.33. Please explain why is that. Conversely, for grassland, there is already 1 for soil-feeding termites (SF), but also shows a zero for xylophagous termites (XP), while other cases in which one guild has 1 the others show a hyphen instead of a zero. Is that because the shown values for grassland are rounded, but SF guild is actually lower than 1, and XP higher than 0?

Thank you for identifying these inconsistencies. These were typographical errors in Table S3. For tropical vegetation, the fraction of fungus-growing termites should be 0.19 rather than 0.10, and for savanna, the FG fraction should be 0.67 rather than 0. For grassland, the value of 0 for xylophagous termites has been replaced with a hyphen for consistency with the notation used elsewhere in the table. We have corrected Table S3 accordingly.

Equation S14 – add an explanation of why the denominator is the square root of 12.

The factor 12 is not specific to the model but arises from the variance of a continuous uniform distribution. Since parameters were assumed to be independently and uniformly distributed within the bounds reported in Table 1, their standard deviations were calculated using the standard uniform-distribution relationship. We have revised the Supplementary Methods (lines 127-129) to make this assumption clear.

Technical corrections

The manuscript title is not very fluent to read, with the double colon. I would suggest to remove “Ideas and perspectives:” entirely, or if not, then at least remove the first colon, or rewrite the title in a more fluent way (not a correction, just a suggestion).

The phrase “Ideas and perspectives:” is a journal requirement for manuscript submitted under the *Ideas and Perspectives* article category and therefore cannot be removed. To improve the title’s 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”.

L17 – “their contributions ... remain” (instead of “remains”).

Corrected. Thanks!

L198 – “carbon biomass” instead of “biomass carbon”.

Thank you for this suggestion. We have retained the term “biomass carbon” because it is the standard terminology used in ecology and biogeochemical modelling to describe biomass expressed in carbon units (g C m^{-2}). We believe this term is clearer and more consistent with the broader carbon-cycling literature (e.g., Abramoff et al., 2018). We therefore prefer to retain this terminology in the manuscript.

L256 – In Fig. 2 caption, better make a clearer reference to the latitudinal mean representation, e.g. “The subset in each plot (blue line) shows...”. The same applies for Fig. S2.

We have revised the captions of Figs. 2 and S2 to explicitly identify the blue line as the latitudinal mean. The revised captions read: “The inset in each plot (blue line) shows...”.

L407 – “is available” instead of “are available”

Corrected.

Supplementary:

L21 – missing space in “times(Wang et al., 2010)”.

Corrected.

L26 – missing space in “underwentmicrobial”

Corrected.

Equations S13 – k_B should be k_n

Thanks for pointing this out. We have corrected the typo in Equation S13.

Table S3 – “from Sanderson (1996)”, the author name is explicitly referenced, so it should not be inside the parenthesis.

Corrected.

L68 – “carbon” instead of “substrates”, within the full name of LMWC.

Corrected. Thanks!

Reviewer 2:

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 CH₄ emissions to the global CH₄ budget to make their magnitude more readily interpretable. Based on the Global Methane Budget estimate of 575 Tg CH₄ yr⁻¹ for total global emissions during 2010–2019 (Saunois et al., 2025), the estimated termite contribution of 10.2 Tg CH₄ yr⁻¹ corresponds to approximately 1.8% of total global CH₄ emissions. We have added this comparison to the revised manuscript (lines 79–80): “The Global Methane Budget estimates termite methane (CH₄) emissions of $\sim 10.2 \pm 6.2$ Tg CH₄ yr⁻¹, equivalent to $\sim 1.8\%$ of the estimated total global CH₄ 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 with *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 CO₂ emissions with global soil respiration, which provides a process-relevant benchmark for this biologically mediated terrestrial CO₂ flux. Specifically, the modeled termite-associated CO₂ flux ($3170.6 \pm 1629.8 \text{ Tg CO}_2 \text{ yr}^{-1}$) corresponds to approximately 3.2–4.7% of global soil respiration. We consider this comparison more directly relevant than comparison with total global CO₂ 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 consideration for future global implementation is how to represent 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 CH₄ (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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