Reviewer #1 (Citation: https://doi.org/10.5194/egusphere-2026-1571-RC1)

This manuscript presents a novel theoretical framework for positive and negative priming effects, grounded in microbial growth traits (copiotrophs versus oligotrophs), dynamic metabolic regulation, and interactions between degraders and non-degraders. The use of cybernetic modelling to capture resource-allocation trade-offs is a major strength. To this reviewer's knowledge, the combination of optimal-control-derived cybernetic laws with Monte Carlo ensembles across community configurations is new in the priming literature. The work explores multiple functional-group setups, generates clear testable hypotheses (most notably that <10% labile organic matter [OM] addition triggers near-maximal positive priming), and offers a substantial advance for biogeochemical modelling. The manuscript is well-written logically structured and moves the field beyond correlative trait–priming links toward a process-based regulatory mechanism. This reviewer has no major scientific concerns and recommends publication after revisions. The points below are intended to stimulate constructive discussion.

We sincerely appreciate the reviewer's positive assessment of our work and the constructive feedback provided, which have significantly contributed to improving the clarity and quality of both the manuscript and the research. We address the specific comments individually below and highlight the corresponding changes in the manuscript in red.

First, the balance between generalisation and oversimplification in the representation of microbial traits warrants discussion. Although the copiotroph-oligotroph distinction provides a useful conceptual scaffold, real soil communities occupy a continuum and exhibit substantial metabolic flexibility. In the model (page 7), these traits are enforced by fixing the kinetic parameters governing labile-OM uptake (maximum rate $k_{S,i}$ and saturation constant $K_{S,i}$) and by imposing a binary exoenzyme-synthesis rule (degraders: $dE_i/dt \neq 0$; non-degraders: $dE_i/dt = 0$). While this simplifies interpretation, it also raises the question of whether such predefined boundaries might artificially constrain the emergence of negative priming, particularly given that some copiotrophs can exhibit slow growth under stressful conditions. The authors should thus discuss the sensitivity of their results to the specific threshold values chosen for $k_{S,i}$ and $K_{S,i}$, and whether relaxing these contrasts (e.g. allowing partial overlap or condition-dependent shifts) would alter the qualitative patterns. Relatedly, Section 4.6 correctly highlights the omission of nutrient stoichiometry, nitrogen limitation and mineral protection, factors known to modulate microbial strategies and priming responses (page 17). A short additional paragraph, or ideally a supplementary sensitivity test exploring how relaxing the fixed complex OM parameters (k_Z, K_Z, Y_S) or introducing a simple nitrogen co-limitation term affects the copiotroph/oligotroph contrast, would substantially strengthen the manuscript. Such an analysis would directly address a common critique of purely carbon-centric priming models and help clarify whether the observed trait-based patterns are robust to broader biogeochemical constraints.

1. We acknowledge that microbial trophic strategies likely exist along a continuum and can shift with environmental conditions, whereas our model represents copiotrophs and oligotrophs as distinct end-member strategies through fixed values of $k_{S,i}$ and $K_{S,i}$. We intentionally adopted this simplification to isolate the effects of contrasting trophic strategies and degradation abilities on priming outcomes. By fixing these parameters, we can more directly attribute differences in priming responses to microbial trait contrasts rather than to parameter variability. In the main text, we have clarified our model definition and how it differs from microbial ecological reality in Section 2.1. Please also refer to our response to comments from Reviewer #2: https://doi.org/10.5194/egusphere-2026-1571-RC2.
2. We agree that varying $k_{S,i}$ and $K_{S,i}$ parameter values (especially if the variation leads to overlap between the two trophic strategies) may alter the qualitative priming responses. Following the reviewer's suggestion, we have therefore performed a comprehensive local sensitivity analysis using the method of Brun et al. (2001). The sensitivity analysis indicates that our main findings remain valid, including the prevalence of positive priming over negative priming, stronger

positive priming associated with copiotrophs and more frequent negative priming and slightly weaker positive priming associated with oligotrophs, and the presence of an approximately <10% labile OM threshold, where the priming response increases approximately linearly before transitioning to nonlinear saturation. Briefly, for the single functional group models of either CDG or ODG, the relative sensitivities remain largely consistent across all labile-complex OM mixing fractions (i.e., they do not substantially switch between positive and negative values), indicating that parameter perturbations primarily amplify or diminish the response without altering the qualitative trends. In contrast, the binary consortia models (CDG-OND and ODG-CND), particularly the former, exhibit greater variation in relative sensitivities. This is likely because parameter perturbations increase the overlap between the trophic strategies of the two microbial groups, resulting in more pronounced changes in the priming response.We have briefly discussed the sensitivity analysis results in Section 4.3, with results presented in the Supplementary Fig. S4.

3. We agree that assumptions such as fixed degradation parameters (k_Z, K_Z, Y_S), the omission of OM stoichiometry, and the lack of nitrogen limitation may influence priming responses, including the relatively infrequent occurrence of negative priming in our simulations. While exploring these factors through sensitivity analyses would be valuable, doing so would complicate the interpretation of the results, especially when conflated with effects of the uptake kinetic parameters $k_{S,i}$ and $K_{S,i}$. In the present study, we intentionally held these parameters constant to isolate the effects of microbial trophic strategies and interactions on priming outcomes. Moreover, we are currently exploring the explicit representation of complex OM properties as a natural extension of this work by using population balance models to account for the distribution of polymeric properties (e.g., degree of polymerisation). In this case, degradation kinetics would be explicitly governed by the polymeric structure rather than by degradation parameter variability. We have expanded the discussion in Sections 4.1 and 4.6 to clarify these limitations, their potential implications for priming predictions, and their importance for future model development.

Second, the definition of non-degraders and the treatment of metabolic "cheating" require clarification. Non-degraders are implemented as completely unable to synthesise exoenzymes ("non-degraders ($dE_i/dt = 0$)", page 7). In nature, many microbes produce low baseline levels or can switch strategies. This simplification is acceptable for tractability but becomes relevant given for the counterintuitive result (page 10) that oligotrophic non-degraders (OND) promote positive priming when paired with copiotrophic degraders (CDG). The R* explanation (page 14) is plausible, but establishing a more explicit mechanistic link between OND's slow substrate uptake and increased exoenzyme investment by CDG would provide a clearer explanation of the feedback. In addition, the model assumes a well-mixed batch system, while many cited empirical contexts (e.g. hyporheic zones, rhizosphere; pages 3, 13) are transport-limited. A brief discussion of how advective/diffusive constraints might shift the ~10 % threshold or temporal dynamics would improve translation to field conditions. A supplementary figure showing example time series of E (exoenzyme), e (endoenzyme), S (labile substrate) and Z (complex OM) for one representative parameter set would nicely illustrate the regulatory loop.

1. We have highlighted in Section 2.1 the distinction between the metabolic flexibility of microbes in nature, which are capable of shifting degradative strategies, and the model assumption of fixed degradation ability, which is necessary to maintain tractability of the modelling framework. We have now provided a more mechanistic explanation of the synergy between CDG and OND based on their inherent trophic traits and R* theory in Section 4.3.
2. It is true that much of the literature cited in the manuscript to draw parallels with our model results involves transport-limited systems such as soils, hyporheic zones, and the rhizosphere, whereas our model assumes a well-mixed batch system. We agree that it would be an interesting investigation of how transport limitation could affect the ~10% threshold identified here.

However, determining the direction and magnitude of such changes would require explicit reactive transport modelling that accounts for transport processes and microbial spatial organization, which is beyond the scope of the present study. We emphasize that the magnitude of the threshold in this study is not the primary focus, but rather the emergence of a threshold at relatively low labile OM additions, highlighting nonlinear microbial regulatory feedback and saturation of microbial energy demand. We expect this qualitative behaviour to remain robust even in transport-limited systems, along with the qualitative mechanisms and directional patterns of priming identified in this study. We have now clarified these points in Section 4.5.

3. As requested by the reviewer, we have now included sample model results showing the transient profiles of complex OM, labile OM, biomass, exoenzymes, and endoenzymes for a single run with randomly sampled parameters from the Monte Carlo simulations in Supplementary Fig. S3, and are referenced in the main text in Section 4.1. These results clearly illustrate the microbial regulatory response underlying complex OM degradation dynamics. We thank the reviewer for this suggestion, which we believe has made our work more comprehensible to readers and has significantly improved the manuscript.

Third, the temporal dynamics of priming warrant closer examination. Figures 2–4 are clear, but adding a small inset or secondary y-axis to show the fractional contribution of each functional group to total priming (CDG–OND versus ODG–CND) would make interaction effects even more intuitive. Specifically, Figure 4 shows negative instantaneous priming emerging late and at high n (labile fraction). The authors attribute this to a switch toward accumulated labile-OM consumption (page 13). It would be helpful to comment on whether explicit maintenance respiration, cell death or necromass recycling would shift the timing or magnitude of this transition, as the current model lacks these terms.

We appreciate the suggestion to show the distinct contribution of each microbial group to priming, which would certainly improve interpretability of our results. However, in our formulation, priming is defined based on the amount of complex OM degraded over a fixed time interval between a control (without exogenous labile OM addition) and an amended case (with exogenous labile OM addition). Within this framework, we are not able to resolve the fractional contribution of each microbial group to the overall priming effect. Moreover, while we can infer that degraders implicitly contribute to priming through exoenzyme synthesis, the contribution of non-degraders is indirect and not directly quantifiable. In addition, our model focuses on complex OM degradation dynamics and its implications for priming effects, hence, metabolic processes such as cell maintenance, cell death, and necromass recycling have not been considered in this work.

Fourth, the apparent threshold behaviour deserves additional sensitivity analysis. The saturation of positive priming beyond ~10% labile OM is striking and empirically testable. However, the threshold depends on the fixed assumptions Y_S>1 ("Y_S must be greater than 1", page 7) and fixed complex-OM kinetics ("the complex OM degradation kinetic parameters … were also fixed", page 7). Although limitations are acknowledged, a brief sensitivity analysis, e.g. varying Y_S from 2 to 10, would confirm that the ~10% threshold is a general feature rather than a model artefact. For clarity, "less than 10 %" should be explicitly defined as the proportion of labile OM within the total OM mixture on pages 2 and 12.

Following the reviewer's suggestion, we included the yield parameter Y_S in the sensitivity analysis. The analysis reveals that this parameter has no effect on model outputs in the binary consortia models (CDG-OND and ODG-CND). In the single functional group model of ODG, increasing Y_S by 20% produces a consistently positive effect on the priming response from 0% to approximately 70% mixing fraction, whereas in CDG the effect is negligible from 0% to approximately 40% mixing fraction. Overall, these results indicate that in single functional group models, the parameter primarily affects the magnitude of priming without altering directional patterns or other qualitative trend. Therefore, the approximate less than 10% threshold remains robust under variations in Y_S, although the priming magnitude at which this

threshold occurs may vary. We have briefly discussed these sensitivity analysis results in Section 4.3, with results presented in the Supplementary Fig. S4.

Nevertheless, we acknowledge the importance of explicitly considering complex OM properties and quality in controlling priming effects, which represents a natural extension of this work currently being explored. In particular, accounting for the full distribution of polymeric properties such as degree of polymerisation through population balance models would allow a more explicit representation of OM quality via its recalcitrance to degradation (e.g., more or less depolymerizable substrates). In such a framework, Y_S becomes irrelevant, as yield would instead be determined explicitly by the distributed polymeric structure. We have now briefly explained this in Section 4.6.

Minor comments include equation formatting, clarity, missing parameter tables and typographical issues:

- It would be helpful to state explicitly whether the cybernetic time horizon in Eq. (9) (Δt) is fixed or state-dependent, and to indicate how sensitive the results are to this value.

The future finite time horizon, Δt, is a state-dependent variable that is automatically determined at every time instant in the cybernetic model by the smallest time scale (i.e., the magnitude of the first eigenvalue of Jacobian matrix of the model equations) and updated throughout the simulation. This provides a balance between adequately capturing future returns and limiting the influence of disturbances on control decisions (Young and Ramkrishna, 2007). Priming outcomes are indeed highly sensitive to Δt, where a non-zero future time horizon is essential for their emergence. Setting $\Delta t = 0$ prevents the anticipation of future benefits and restricts microbial control decisions to instantaneous returns, which are practically absent for complex OM degradation. This has now been briefly clarified in Section 2.4, which we believe further strengthens our modelling framework for priming.

- For Eq. (11) and following, defining ΔZ explicitly as the mass or amount of carbon (or OM) mineralised would help readers distinguish between changes in mineralisation fluxes and changes in substrate pools. In terms of terminology, the use of "amended" (page 11) and "control" (at various instances throughout the text) is consistent. However, to avoid ambiguity regarding the mineralisation of added labile organic matter (OM), it would be better to specify that "degraded complex OM" (page 9) refers exclusively to the organic matter that occurs naturally in soil. This would strengthen the clarity of the priming interpretation.

We agree that Z should be explicitly defined as the complex OM naturally present in the ecosystem, distinct from the exogenously added labile OM, to avoid ambiguity. The manuscript has been revised accordingly for clarity.

- The authors may consider rephrasing the text of Eq. (12), "The threshold above is low enough that it will no longer drive priming", to "… low enough that priming becomes negligible".

We concur with the suggestion, and we have now revised the text accordingly in the manuscript.

- In Eqs. (13) and (14), the index j=2, 3, … and the summation should explicitly state the time discretisation used (e.g. the timestep Δt or the discrete time grid) to improve clarity and reproducibility.

A discrete time grid with a one-hour interval was used with the MATLAB ode15s solver, corresponding to the time points in Eqs. (13) and (14). This has now been clarified in the manuscript for improved clarity.

- The caption of Figure 3 states that "markers are individual runs with an overall negative priming effect". The top panel of Figure 3A displays markers with negative relative priming (P_{rel}). The authors should clarify whether all markers shown correspond to simulations with an overall negative priming effect, or only a subset of runs. This would avoid ambiguity in interpreting the patterns displayed.

All markers shown in Figures 2 and 3 indeed correspond to every simulation runs that resulted in an overall negative priming effect, evaluated across different mixing fractions. The confusion likely stems from the apparent overlap of some markers with the zero line in the top panel of Fig. 2A, which actually reflects cases of very weak negative priming, where the values are close to zero and therefore visually indistinguishable from zero or positive values. This has now been clarified in the caption of Figures 2 and 3 for improved clarity.

- The long sentence on page 15, “This is because ODG is at a greater disadvantage in a labile OM-rich environment compared to OND because although both are unable to competitively utilize the surplus labile OM, ODG must continue synthesizing exoenzymes to maintain the labile OM level in the environment, incurring additional metabolic costs”, would benefit from splitting or rephrasing for readibility.

We have revised the sentence accordingly.

- The authors may consider revising the phrase on page 5, “degraders and non-degraders, each with either copiotrophic or oligotrophic growth traits”, which repeats the abstract wording almost *verbatim* (“degraders and non-degraders with either oligotrophic or copiotrophic growth traits” on page 2).

We have revised the phrase accordingly.

- Tables S1 (parameter ranges) and S2 (summary of outcomes) are referenced, but this reviewer failed to find them attached to the preprint. To facilitate public discussion, either these tables should be provided, or the key randomised ranges and outcomes should be listed in the main text together with the random sampling procedure and seed to ensure reproducibility.

Tables S1 and S2 are provided in the Supplementary Materials accompanying the main manuscript and are referenced at appropriate points in the main text.

References

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