



Plant-microbe interactions modulate the effect of soil respiration to P fertilization in a mature Eucalyptus woodland

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Abstract. The activity of vegetation and soil microbiota are key drivers of soil respiration and thereby exert a strong control of an ecosystem's net carbon balance. Plant productivity and soil microbial activity are among others dependent on phosphorus (P) availability; however, P fertilization experiments show ambiguous responses in soil respiration and underlying mechanism are difficult to identify. In the Eucalyptus Free Air CO₂ enrichment experiment (EucFACE), which is situated in a mature, P-limited *Eucalyptus tereticornis* woodland, P fertilization decreased soil respiration, but it is unclear to what extent plant-microbe interactions, specifically plant C allocation to fine root growth, root exudation and microbial activity, contributed to this response. Here we used the terrestrial biosphere model QUINCY-JSM, which comprises an implementation of a root exudation flux dynamically dependent on plant nutrient status, as well as an explicit representation of soil microbial controls on soil organic matter decomposition to investigate how plant-microbe interactions may control the soil respiration response to P fertilization in EucFACE. Simulations suggest that reduced root exudation and increased microbial carbon-use efficiency are major drivers of reduced soil respiration under P addition. Model results further suggest microbial P demand, soil P availability and treatment duration as mediating factors in this response. The model further shows that P addition only marginally influenced the response in soil respiration to CO₂ fertilization. Our results indicate soil microbial responses to reduced root exudation and microbial P demands as major drivers, highlighting the need for additional measurements in plant belowground allocation and microbial community traits to improve our understanding of the nutrient-dependence of soil respiration.



1 Introduction

Model-data synthesis, which combines observations with terrestrial biosphere models (TBMs), provides an established framework for disentangling the mechanisms linking ecosystem carbon (C) cycling to nutrient availability, and has been widely used to identify the main drivers of ecosystem responses, such as soil respiration, in Free Air CO₂ enrichment (FACE) experiments (Zaehle et al., 2014; Jiang et al., 2024b; Medlyn et al., 2016). At the Eucalyptus FACE (EucFACE) experiment, the first FACE experiment in a subtropical, phosphorus-limited forest, model-data synthesis has been used to identify the key drivers of soil respiration under CO₂ fertilization (Jiang et al., 2024b; Schufft et al., accepted) and, now ongoing, P addition (Wang et al., 2026). Models predicted an increase in soil respiration under P addition (Wang et al., 2026), while measurements in other Eucalyptus forests suggested a decrease (Keith et al., 1997a). However, the models used in these studies neglected the role of root exudation and plant-microbial interactions as key modulators for ecosystem C cycling at this site (Jiang et al., 2024a, 2020b; Pihlblad et al., 2023; Jiang et al., 2024b), leaving it unclear how plant-microbial driven processes contributed to the response of soil respiration (R_s) in this FACE experiment under increased nutrient availability.

Soil respiration is composed of autotrophic root respiration (R_{ar}) and heterotrophic microbial respiration (R_h) (Bond-Lamberty et al., 2024), which are both influenced by CO₂ fertilization and nutrient availability. Elevated atmospheric CO₂ concentrations (eCO₂) can enhance plant productivity, including root growth, and increase belowground C allocation through litter production or root exudation, thereby increasing microbial activity (Walker et al., 2019). However, nutrient availability modulates such responses by potentially limiting plant growth, altering plant C allocation, and further influencing microbial growth and soil organic matter decomposition (Jiang et al., 2020b; Drake et al., 2011). To improve predictions of future ecosystem C balance under eCO₂, it is essential to understand how nutrient availability controls the underlying mechanisms of R_s . While a lot of emphasis has been put on the impacts nitrogen (N) availability (Finzi et al., 2007), much less is known about the impact of phosphorus (P), which is a strongly limiting nutrient for plant and microbial growth particularly in older, highly weathered soils (Vitousek et al., 2010; Elser et al., 2007).

Nutrient addition generally increases aboveground biomass (Crous et al., 2015; Keith et al., 1997b; Feng et al., 2023) in nutrient-limited systems. However, the consequences for microbial activity and R_s are less clear (Camenzind et al., 2018; Wu et al., 2022; Liu et al., 2012; Zhang et al., 2018). Observations show that nutrient addition can have stimulating Cleveland and Townsend (2006); Wei et al. (2020); Zhou et al. (2014) or reducing (Keith et al., 1997a; Janssens et al., 2010; Zhang et al., 2021) effects. In a recent meta-analysis, Feng and Zhu (2019) concluded that the response of R_s to P addition is influenced by ecosystem type, with grasslands and temperate forests showing both stimulating and reducing effects, while tropical, often P-limited, forests show positive responses (Feng and Zhu, 2019). This aligns with a meta study from Zheng et al. (2023) identifying a negative correlation between the R_s response to P addition and total soil P at the global scale. However, responses at the site-level may differ from global patterns Zhang et al. (2021); Keith et al. (1997a) and depend on the effect of P addition on underlying drivers.



50 In ecosystems where P limits plant productivity and microbial activity, P addition generally alters R_s through shifts in micro-
bial activity and plant productivity, as well as changes in plant belowground C allocation (Fig. 1). Increased P supply typically
alleviates microbial growth limitation imposed by stoichiometric constraints, and increases microbial carbon-use efficiency of
growth (CUE), thereby decreasing R_h (Fig. 1 (1)) (Manzoni et al., 2012; Duan et al., 2025). In addition, increased P supply can
55 increase decomposition for N acquisition (Fig. 1 (2)) (Spohn et al., 2013; Mehnaz and Dijkstra, 2016; Cui et al., 2022).

On the one hand, P addition generally increases plant biomass production (BP) and autotrophic respiration, including root
respiration (3). Increased leaf and root growth increases litter input (4) and root exudation (5), leading to increased microbial
growth and R_h (6). On the other hand, if provided with a sufficient P supply, plants can alter nutrient acquisition strategies,
possibly reducing C investment in root growth (3), mycorrhizal associations or root exudation (5), and thus reducing microbial
60 C supply (Prescott et al., 2020; Song et al., 2022; Han et al., 2026). Consequently, microbes may increase their CUE (1) to
sustain growth, resulting in decreased R_h from root zones. Although microbial growth, plant growth, and plant C allocation
determine the R_s response to P addition, their individual responses can be modulated by microbial P demand and soil P avail-
ability.

65 Phosphorus demand is tightly linked to plant and microbe stoichiometry. A lower C:P ratio implies a higher P demand per
unit of biomass C and potentially stronger competition with plants for soluble PO_4 . Plant C:P ratios show strong plasticity and
are generally higher than microbial C:P ratios (Serner and Elser, 2002). While microbial C:P ratios are considered homeostatic
on a global level (Cleveland and Liptzin, 2007; Xu et al., 2013), studies indicate wide differences between individual sites, with
the C:P ratio additionally depending on soil depth or ecosystem characteristics (Tischer et al., 2014; Gao et al., 2022; Pihlblad
70 et al., 2023; Yu et al., 2020b). P availability is controlled by the amount of soil organic P and soluble PO_4 in the soil and their
availability for microbial and plant acquisition strategies. Both characteristics - P demand for growth and availability - likely
control the effect of P addition on plant and microbial growth and plant C allocation, and therefore modulate the response of
 R_s . However, exploring the interactions between individual processes and their dependence on microbial and plant P require-
ments remains challenging and is often limited by observational constraints.

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In this study, we focus on P addition in the EucFACE experiment in order to investigate the responses in mechanism along the
plant-microbe interface to clarify the underlying drivers of R_s responses. We use the microbial-explicit TBM QUINCY-JSM,
with an implementation of plant-nutrient-dependent root exudation (Schufft et al., accepted), to (a) explore potential reasons
for the responses observed to date and (b) suggest directions for further fieldwork to increase our understanding (Medlyn et al.,
80 2016; Norby et al., 2016; Leuzinger and Medlyn, 2026). The research questions of this study are as follows:

1. (Q1) Could decreased root exudation, as an underlying mechanism, explain the R_s response to P addition in EucFACE?
2. (Q2) How do microbial P demand and soil organic matter P availability modulate the simulated response of R_s to P
addition?



To further guide experimental work, we

- 85 3. (Q3) assess whether CO_2 fertilization and P addition show an interaction effect on R_s and its underlying processes, and
4. (Q4) assess whether responses in R_s to P addition will change over a longer treatment period.

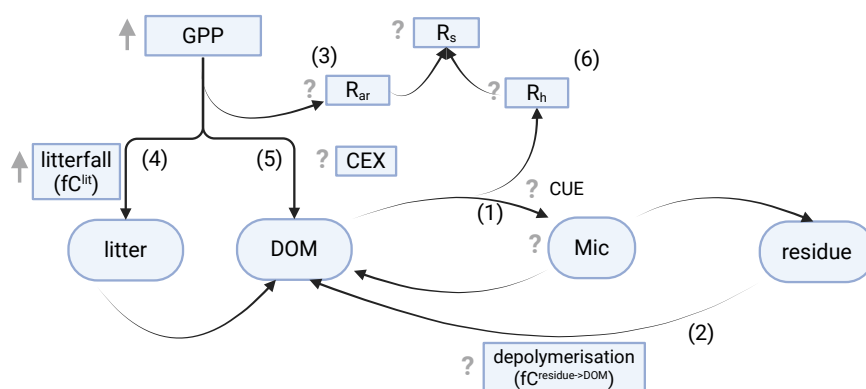


Figure 1. Conceptual representation of underlying mechanisms driving soil respiration responses to P addition in a P-limited system. Grey arrows indicate possible response directions to P addition. P addition generally increases gross primary productivity (GPP) and total litterfall (fC^{lit}), the effects on root respiration (R_{ar}), root exudation (CEX), microbial biomass (Mic), microbial carbon-use efficiency in first soil layer ($CUE_{Mic,L1}$), necromass depolymerisation flux ($fC^{necro \rightarrow DOM}$), heterotrophic soil respiration (R_h), and soil respiration ($R_s = R_{ar} + R_h$) be ambiguous. Created in BioRender. Schufft, K. (2026) <https://BioRender.com/ofj4d3v>



2 Methods

2.1 Model description

QUINCY-JSM (Thum et al., 2019; Yu et al., 2020a) (A1) is a terrestrial biosphere model simulating fluxes and interactions in energy, water, carbon (C), nitrogen (N) and phosphorus (P) in vegetation (QUINCY) and soils (JSM), which has been previously used in FACE model intercomparison studies (Jiang et al., 2024b; Wang et al., 2026). All calculations run on a half-hourly timestep.

QUINCY represents vegetation as average individual representatives of 8 distinct plant functional types. For the purpose of this study, the parameters for the plant functional type dry broad-leaved evergreen vegetation are used for the simulations. In QUINCY, vegetation is described by 5 structural (leaf, fine roots, sapwood, heartwood and coarse roots) and 2 non-structural pools (labile pool, reserve). All incoming fluxes in C, N, and P, through photosynthesis and plant nutrient uptake, first enter a labile pool and are then partitioned to different plant organs, or—in the case of C and N—released via root exudation, or consumed as respiration. Photosynthesis of sunlit and shaded leaves is calculated for a multi-layer canopy (Kull and Kruijt, 1998), taking into account vertical gradients of foliar chlorophyll and photosynthetic N (Friend, 2010; Zaehle et al., 2010; Medlyn et al., 2011). Nitrogen and P are acquired via fine-root uptake from soils, based on fine-root biomass, substrate availability, and plant nutrient demand. Internally, leaf and sapwood N and P are partially resorbed during tissue senescence (Sophia et al., 2026). Carbon is partitioned from the labile pool in decreasing priority to respiration, root exudation and plant growth. Respiration is calculated as the sum of tissue-specific maintenance respiration based on tissue-N content, growth respiration and nutrient uptake respiration. Root exudation is calculated based on fine-root respiration and labile pool C surplus and stoichiometry as proxies for plant growth nutrient limitation (Schufft et al., accepted). The C:N ratio of root exudation follows that of the labile pool. Allocation of growth to different tissues follows the pipe-model theory, with the additional assumption that the ratio of fine root to leaf mass does not vary with time. Nitrogen and P growth allocation follows C allocation with flexible, tissue-specific C:N:P ratios. Tissue turnover times are fixed.

JSM is the Jena-Soil-Model (A1), a microbial-explicit soil biogeochemical model that explicitly represents microbial decomposition of soil organic matter (SOM) and litter, microbial nutrient uptake and mineral sorption processes (Yu et al., 2020a). All pools and processes are calculated for 15 soil layers with increasing layer thickness with depth up to a total depth of 9.5 m. All processes are influenced by soil moisture and temperature (Yu et al., 2020a). JSM is fully coupled to QUINCY: transpiration by vegetation influences soil moisture and albedo of the vegetation affects soil temperatures. Microbes recycle and grow on vegetation inputs such as litterfall and root exudation, and vegetation and microbes compete for available inorganic nutrients.

JSM simulates five different soil organic matter pools: dissolved organic matter (DOM), mineral-associated DOM, microbial biomass (Mic), microbial necromass and mineral-associated necromass. Organic matter is moved between soil layers via bioturbation. Plant material enters soils via three plant litter pools: woody litter, polymeric litter, and soluble litter. Root exudation enters soils as DOM following the root distribution (Schufft et al., accepted).

Microbial enzymes decompose polymeric litter and microbial necromass into DOM, which is then taken up by microbial biomass. Enzymes are represented implicitly, while enzymatic activity is modeled following Michaelis-Menten or reverse



Michaelis-Menten kinetics with enzyme allocation following microbial demands for C, N, and P (Schimel and Weintraub, 2003; Wutzler et al., 2022). Mineral-associated pools are protected from decomposition but are in Langmuir equilibrium with their non-mineral-associated counterparts (Ahrens et al., 2015). Microbes take up DOM and turn it over into microbial biomass following a flexible carbon-use efficiency (CUE) (0.3–0.5) and fixed nitrogen-use efficiency (0.8) and phosphorus-use efficiency (0.8). Carbon, N, and P contained in DOM that is not used for microbial growth (i.e., $1 - \text{use-efficiency}$, but accounting for the imbalance between microbial and DOM stoichiometry) is mineralized as CO_2 , NH_4 or PO_4 . Additionally, biochemical mineralization, based on microbial and vegetation phosphatase production, allows for direct mineralization of P from soil organic matter pools without direct microbial uptake (Yu et al., 2020a). Upon decay microbial biomass is partly mineralized (N only) and transferred to DOM and necromass, simulating microbial grazing and different fates of microbial cytoplasm and cell walls (Schimel and Weintraub, 2003). Microbes are in competition with plants and soil sorption sites (P only) for free inorganic nutrients. Uptake kinetics are based on Michaelis-Menten equations and are calculated using the ECA approach (Tang and Riley, 2013; Zhu et al., 2016).

Nitrogen enters the system via atmospheric deposition, as well as symbiotic and asymbiotic (soil-bound) N fixation and leaves the system via leaching and gaseous emissions, including N_2O . Inorganic P is further divided into primary P, solute PO_4 , adsorbed PO_4 , and occluded PO_4 . Only solute PO_4 can be taken up by microbes and roots. Solute phosphate is described to be in Langmuir equilibrium with adsorbed phosphate (Barrow, 1978; Yu et al., 2023). The latter one is slowly transferred to occluded PO_4 , where it is bound and cannot be regained (Yu et al., 2020a). Newly available PO_4 enters the system via weathering of primary material and P deposition. P leaves active cycling via leaching and occlusion.

2.2 Site description and soil respiration measurements

The EucFACE experiment was established in 2012 to study the effect of increasing atmospheric CO_2 concentrations in a P-limited forest. The overstorey is dominated by *Eucalyptus tereticornis*, while the understorey is dominated by *Microlaena stipoides*. The soil is characterized as alluvial Spodosol with low P content (Ross et al., 2020; Jiang et al., 2020b). The experiment has been conducted in two phases. In phase one, six plots were established with FACE infrastructure, three of which were exposed to elevated CO_2 concentrations, while the remaining three served as control under ambient atmospheric CO_2 concentrations. Fumigation with CO_2 started at the end of 2012 with a 3 month ramp-up to 150 ppm above ambient in February 2013. In phase two of the experiment, commencing 2023, two of the original rings (one ambient, one elevated) were closed down, and the remaining four plots (two ambient, two elevated) were fertilized with triple superphosphate. Fertilizer was applied in two doses, in April 2023 and July 2023, with a rate of 1.5 g m^{-2} for each application. Two additional rings (ambient CO_2 , no FACE infrastructure) were established as control plots for the P addition experiment. Further details of the experimental design are given by Zhao et al. (in review).

Soil respiration data was manually measured every fortnight for 8 collars in each of the ambient CO_2 rings from September 2023 to July 2024 as described in Zhao et al. (in review). Manual measurements were made using infrared gas analysers (IR-GAs; 20-cm-diameter chamber, model Li-8100-103, Licor Environmental, Lincoln, NE, USA). There are eight soil respiration collars inserted at random locations in each plot, giving a total of 32 collars. The 20-cm-diameter PVC collars were inserted



155 into the soil to 7 cm depth to eliminate lateral diffusion of CO₂ beneath the collars in the sandy soil at the site. These collars
were left in place to reduce soil disturbance by repeated measurement and to ensure that the same soil was measured over time
(King et al., 2004). In each survey, measurements of all collars were made fortnightly between 9 am and 3 pm. After each mea-
surement, any visible grass was removed to ensure that newly emerged vegetation was cleared regularly and did not contribute
to dark respiration. We calculated mean (R_s) for ambient and elevated P based on the 16 collars placed in the respective plots,
160 for each survey. We then calculated response ratio of soil respiration to P addition for each survey to derive a range of response
ratios over the measurement period.

2.3 Modeling protocol and forcing

We used the QUINCY-JSM model to simulate P and CO₂ fertilization at the EucFACE experiment. We followed the modeling
protocol used in previous modeling studies for this site (Jiang et al., 2024b; Wang et al., 2026) and used site-specific parameters
165 for QUINCY-JSM as described in Schufft et al. (accepted). Meteorological observations from 2013–2018 were randomized
and repeated to create forcing before 2013. This data were used for a spin-up of 1000 years to reach quasi-equilibrium in soil
and vegetation pools (Yu et al., 2020a). We further ran the model for another 312 years with atmospheric CO₂ concentrations,
as well as N and P deposition following transient historic concentrations (Jiang et al., 2024b). We fixed climate forcing from
2013 onward, repeating the forcing of the year 2015, a relatively wet year, to reduce the effect of climate variability in the
170 model. To simulate the FACE experiment, we increased atmospheric CO₂ forcing in simulations (eCO₂) to 150 ppm above
ambient CO₂ (aCO₂) conditions, following the concentrations of the EucFACE experiment. We simulated P addition for
both CO₂ treatments by increasing daily deposition for three years from 2020–2022 to 3 g m⁻² yr⁻¹ (Crous et al., 2015). To
analyze long-term effects of P addition, we additionally simulated a continuous addition of 10 years from 2020 to 2029 with
3 g m⁻² yr⁻¹, under continued ambient and elevated CO₂ treatments.

175 2.4 Effect sizes

We analyzed our simulations as a two-factor experiment with the factors CO₂ fertilization and P addition, where C_a and C_e
represent ambient and elevated CO₂ treatments and P_a and P_e represent ambient and elevated P treatments (Table 1).

Table 1. Setup for the simulated two-factorial experiment

	P ambient	P elevated
CO ₂ ambient	$C_a P_a$	$C_a P_e$
CO ₂ elevated	$C_e P_a$	$C_e P_e$

Following Jiang et al. (2020a) and Hawkes and Sullivan (2001), we calculated response ratios for modeled vegetation and
soil fluxes (X) for 1-year and 3-year P addition as:



$$\begin{aligned}
 (1) \quad r_P^{aCO_2} &= X_{C_a P_e} / X_{C_a P_a} && \text{response ratio of P addition under aCO}_2 && (1) \\
 (2) \quad r_P^{eCO_2} &= X_{C_e P_e} / X_{C_e P_a} && \text{response ratio of P addition under eCO}_2 && (2) \\
 (3) \quad r_{eCO_2}^{aP} &= X_{C_e P_a} / X_{C_a P_a} && \text{response ratio of CO}_2 \text{ fertilization under ambient P} && (3) \\
 (4) \quad r_{aCO_2}^{eP} &= X_{C_e P_e} / X_{C_a P_e} && \text{response ratio of CO}_2 \text{ fertilization under P addition} && (4) \\
 &&&&& (5)
 \end{aligned}$$

185 We further calculated the response ratio of the interaction effects, which can be interpreted as the effect of CO₂ treatment on P addition response (Jiang et al., 2020a). We linearized the effects as described in Morris et al. (2007):

$$\begin{aligned}
 (5) \quad r^{interaction} &= [\ln(X_{C_e P_e}) - \ln(X_{C_e P_a})] - [\ln(X_{C_a P_e}) - \ln(X_{C_a P_a})] && \text{response ratio of interaction effect} && (6) \\
 &&&&& (7)
 \end{aligned}$$

2.5 Parameter sensitivity

190 We expected that the simulated response of R_s to P would change depending on our assumptions about microbial P demand for growth and available soil P (Q2). To test the strength of this dependence, we performed a parameter sensitivity analysis for the target parameters: microbial stoichiometry and background soil organic matter P pool size (background SOM-P) (Table 2). We fixed the microbial C:N ratio to 4.3 g N⁻¹ (Pihlblad et al., 2023) and varied the microbial N:P ratio, thereby representing microbial C:P ratios from 12.9 to 38.7. Pihlblad et al. (2023) measured microbial C:P ratios between 9.8 and 13.4 at EucFACE, 195 while estimations based on measured microbial C and P pools described in Jiang et al. (2020b) and Jiang et al. (2024a) range between 13.2 and 24.8.

To generate alternative scenarios of background SOM-P, we altered the C:P ratio of the microbial necromass pool (12.9, 21.5) with which the model is initialized, but kept the size of the microbial necromass pool in terms of its C content constant. Since ecosystem loss of P during the simulation is very small, this value determines the overall amount of P in the system in 200 equilibrium. We report background SOM-P as 10-year mean before treatment application (2002–2011). Background SOM-P values were also influenced by prescribed microbial C:P ratio, which determined initial microbial biomass P, and influenced weathering, occlusion, and soil P distribution throughout the soil profile. (Fig. A2). Simulated 10-year annual mean values for gross primary productivity (GPP), vegetation C, R_s and R_h are shown in Fig. A3 and Fig. A4. We removed three simulations from further analysis in which a combination of low SOM-P and a low microbial C:P ratio of 12.9 caused a strong decrease in 205 microbial biomass under the applied meteorological forcing (Fig. A5). Overall, our simulations cover a range of 83 g m⁻² to 190 g m⁻² in the top 50 cm, background SOM-P, and are therefore still higher than the reported 25.1 ± 4.8 g m⁻² Jiang et al. (2024a).

To clarify how parameter changes are reflected in plant P limitation and plant-microbial competition for PO₄, we assess the ecosystem P-state by ranking simulations in a space of two variables: the long-term average plant labile C:P ratio and the ratio 210 of plant PO₄ uptake to microbial PO₄ uptake, hereafter the plant-microbial PO₄ uptake ratio. The higher the labile C:P ratio,



Table 2. Simulated parameter space for parameter sensitivity analysis. Alterations in target parameters microbial C:P ratio and background SOM-P were derived from internal model calculations based on the model parameters microbial N:P ratio (under fixed microbial C:N ratio) and N:P ratio of microbial necromass. Values in brackets refer to standard values used for this site (Schufft et al., accepted).

target parameter	explanation	range	model parameter	explanation	range
microbial_cp	Microbial C:P ratio [g g^{-1}]	12.9–38.7 (17.63)	microbial_np	Microbial N:P ratio [g g^{-1}]	3–9 (4.1)
SOM-P	Soil organic matter P content (top 50 cm) [g m^{-2}]	83–200 (100)	k_som_np_init	initial N:P of microbial necromass [g g^{-1}]	7–35 (21)

the stronger the P constraint on growth given the stoichiometric imbalance between the labile pool and the P required to build new tissue, and the higher the plant P demand. Low values of the plant-microbial PO_4 uptake ratio indicate that PO_4 uptake is strongly dominated by microbes, while higher values indicate that plants are not directly outcompeted by microbes.



3 Results

215 First, we examine the simulated response of plant-microbial processes to P addition and how these are modified by microbial P demand and soil P availability. Then we examine the effect of P addition on the CO₂ response and investigate the effect of long-term P addition.

3.1 Reduced root exudation following P addition drives decline in soil respiration

220 Soil respiration was observed to be lower in elevated P plots than in ambient P plots (Fig. 2). The model reproduced the direction of this response, although it underestimated the magnitude of this effect (absolute response: Fig. B1). Observation based responses ranged from 34 % decrease to 7 % increase, with a median response of 19 % decrease (median $r_P^{aCO_2} = 0.81$, $r_P^{aCO_2} = 0.66 - 1.07$). Simulated R_s decreased by 3 % ($r_P^{aCO_2} = 0.97$). In our simulations, and under standard parameter configuration used in Schufft et al. (accepted), decreased root exudation was the primary driver of this response. During three years of P addition, GPP increased by 8 %. Additionally, the model simulated a shift in plant C allocation: P addition increased 225 biomass production by 39 % (Fig. B2). While the majority of C was allocated towards sapwood growth, leaf and fine root production increased by 7 % (Fig. B2), causing a 3 % increase in litter fall and R_{ar} (Fig. 2). At the same time, root exudation decreased by 19 %, due to an alleviation of P limitation. The reduced input of labile C through reduced root exudation increased microbial C limitation for growth such that microbial carbon-use efficiency (CUE) increased by 15 %. Nevertheless, microbial biomass C remained unchanged as increased CUE compensated for the reduced plant C input to the soil. Microbial necromass 230 decomposition remained stable as this flux is primarily controlled by microbial biomass and microbial N demand in the model. The combination of reduced labile C input and enhanced microbial CUE caused a 7 % decrease in heterotrophic respiration. The decline outweighed the increase in R_{ar} , resulting in an overall 3 % reduction in R_s (Fig. 2). Sensitivity analyses of microbial P demand and available SOM-P showed that parameter variation substantially altered the response ratios, with simulated R_s responses ranging from a 7 % decrease to a 2 % increase.

235 3.2 Microbial P demand modulates plant response to P addition

In the model, high microbial P demand for growth suppressed the decline of root exudation and R_s in response to P addition (3). When prescribing a small microbial C:P ratio of 12.9, reflecting a high microbial P demand, P addition increased plant PO₄ uptake by 4 %, while PO₄ microbial uptake increased by 8 %, as microbes out-competed plants for additional PO₄ (3a)). Consequently, simulated plant fluxes such as R_{ar} or root exudation remained stable following P addition. Instead, 240 simulated microbial growth enhanced heterotrophic respiration slightly by 3 %. Increasing the prescribed microbial C:P ratio, thus reflecting a lowered microbial P demand, allowed for a stronger response in plant PO₄ uptake. In simulations with a prescribed microbial C:P ratio equal to or higher than 17.2, plant uptake increased by more than 175 %. As a consequence of high plant P uptake, simulated root exudation declined between 18 % and 39 % and R_h decreased between 6 % and 15 %. The model limits microbial CUE. In simulations with higher microbial C:P ratio, CUE under ambient P was closer 245 to that limit, effectively lowering the theoretical maximum response of microbial CUE to P addition (Fig. 3b)). Regardless

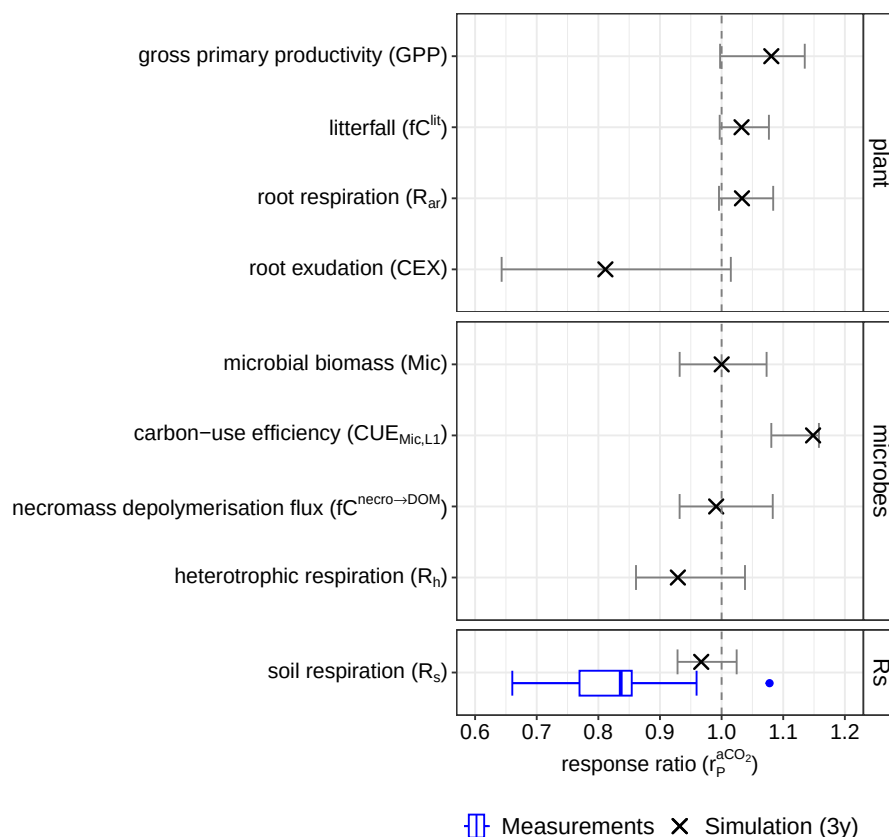


Figure 2. Response ratio ($r_P^{aCO_2}$) of plant and microbial processes, and R_s to P addition. Simulated response during 3 years of P addition under ambient CO_2 and wet meteorological forcing, using model default parameters ('x') for EucFACE configuration (Schufft et al., accepted) is given for gross primary productivity (GPP), total litterfall (fC^{lit}), root respiration (R_{ar}), root exudation (CEX), microbial biomass (Mic), microbial carbon-use efficiency in first soil layer ($CUE_{Mic,L1}$), necromass depolymerisation flux ($fC^{necro→DOM}$), heterotrophic respiration (R_h), and soil respiration ($R_s = R_{ar} + R_h$). Grey error bars represent the range of response ratios in the simulated parameter space from parameter sensitivity analysis (prescribed microbial C:P: 12.9 - 38.7 [$g\ g^{-1}$], SOM-P: 83–200 [$g\ m^{-2}$]). The measured response ratio in R_s , refers to response ratios in fortnightly measurements over one year and are represented by a blue boxplot, where the middle bar represents median, notches represent inter-quartile range (IQR), and whiskers represent the highest/lowest value in 1.5 times IQR. Values smaller than one describe a decrease, while values above one describe an increase in the respective variable.

of prescribed microbial C:P ratio, P addition increased microbial CUE in the first soil layer due to an alleviation of nutrient limitation ($r_P^{aCO_2} = 1.08–1.16$). However, responses were closer to their theoretical maximum with lower microbial P demand, especially for simulations with prescribed microbial C:P ratio equal to or higher than 17.2, indicating that both increased P supply and reduced root exudation increase microbial CUE in these simulations.

250 Simulated plant labile C:P ratio declined when prescribed microbial C:P ratio increased, indicating that plant P-limitation



declined when microbial P demand for growth lowered (Fig. 3c)). At the same time, uptake ratio, defined as the quotient of plant uptake divided by microbial uptake, increased with microbial C:P ratio, indicating that microbes were less competitive for P. Overall, the results suggest that under a low microbial C:P ratio, plants may be P limited but are not able to profit from P addition as microbes out-compete plants for P uptake.

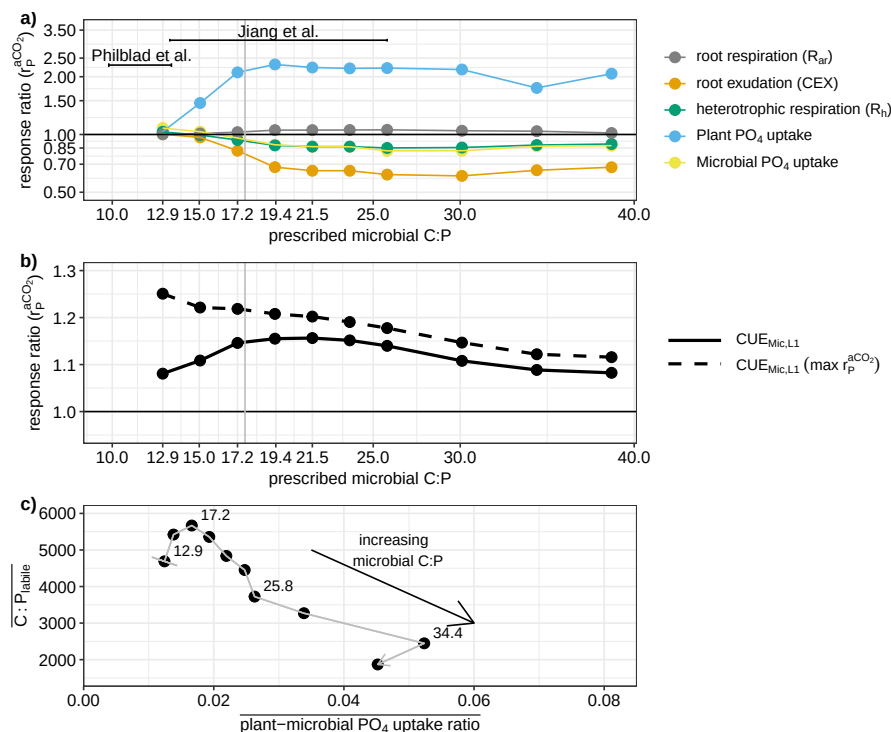


Figure 3. Microbial stoichiometry modulates modeled response in exudation and heterotrophic respiration to P addition. a) Simulated response ratios for 3 years of P addition under ambient CO_2 in heterotrophic respiration (R_h), root respiration (R_w), root exudation (CEX), plant and microbial PO_4 uptake ($f_{up_{\text{PO}_4}}^{\text{plant}}$ and $f_{up_{\text{PO}_4}}^{\text{mic}}$, respectively), given a range of predetermined a microbial C:P ratio ($C : P_{\text{mic}}$) (see Methods). Values below one describe a decrease, while values above one describe an increase in the respective variable. Grey vertical bars represent results used for standard C:P ratio of 4.1 (2). Horizontal bars indicate measured ranges from Pihlblad et al. (2023) and observation-based ranges based on the comprehensive C Jiang et al. (2020b) and P Jiang et al. (2024a) budgets. b) simulated ($CUE_{\text{Mic},L1}$) and theoretically possible maximum simulated response ratio ($\max CUE_{\text{Mic},L1}$) of microbial CUE in the first soil layer to 3 years of P addition for different microbial C:P ratios. c) Characterization of the long-term ecosystem P-state, defined by 10-year average plant labile C:P ratio, as an indicator for plant P limitation and 10-year average plant-microbial PO_4 uptake ratio ($\frac{\text{plant } \text{PO}_4 \text{ uptake}}{\text{microbe } \text{PO}_4 \text{ uptake}}$), as an indicator for microbial competitiveness. Values calculated based on the simulated 10-year annual mean before the start of treatment. The arrow direction indicates increasing microbial C:P ratio.



255 3.3 Background SOM-P modulates plant response to P addition

Background SOM-P modulated simulated responses in root exudation and R_h to P addition (Fig. 4) as a shift from an ecosystem state of high to low P limitation (Fig. 5). Under low background SOM-P and a microbial C:P ratio of 12.9, microbial competition suppressed responses in plant fluxes (Fig. 5 (1)). Only in simulations with $\text{SOM-P} \geq 121 \text{ g m}^{-2}$, root exudation and R_h declined up to 10 % and 4 %, respectively, in response to P addition (Fig. 4 a), Fig. 5(2)), as elevated P availability reduced microbial competitiveness (4c).

Under a microbial C:P ratio of 21.5 and a background $\text{SOM-P} < 137 \text{ g m}^{-2}$, microbial competitiveness was low, such that plant PO_4 uptake increased under P addition (Fig. 4c), Fig. 5(2)), which led to a substantial reduction in root exudation (up to 3.7%) and R_h (up to 14 %) (Fig. 4 a, b)). The reduced root exudation led to increased C allocation to growth, thereby increasing GPP, litterfall, and finally root growth and R_{ar} . However, the overall effect on R_s remained negative as reduced R_h outweighed increased R_{ar} (Fig. B3).

Under a microbial C:P ratio of 21.5 and a high background SOM-P ($\text{SOM-P} = 170 \text{ g m}^{-2}$), responses in plant C fluxes and R_s remained neutral, because neither microbes nor plants were strongly P limited (Fig. 4, Fig. 5(3)). Responses under assumed microbial C:P ratios higher than 21.5 followed the same trend as for the microbial C:P ratio of 21.5, with neutral responses in root exudation and R_h at lower background SOM-P (Fig. B4), underlining the importance of SOM-P availability in modulating R_s response.

3.4 Effect of P addition on the CO_2 fertilization effect

In the model, P addition did not modify the positive effect of eCO_2 on R_s , but enhanced its effect on root exudation (Fig. 6). Under ambient P conditions, eCO_2 increased R_s ($r_{\text{CO}_2}^{\text{aP}} = 1.13 - 1.18$) via increased R_h ($r_{\text{CO}_2}^{\text{aP}} = 1.12 - 1.19$) and R_{ar} ($r_{\text{CO}_2}^{\text{aP}} = 1.11 - 1.19$), for all tested parameter combinations. Elevated CO_2 also increased GPP and litterfall (Fig. B5), regardless of background SOM-P, as in QUINCY-JSM leaf P concentration does not directly control photosynthesis. Elevated CO_2 did increase root exudation ($r_{\text{CO}_2}^{\text{aP}} = 1.16 - 1.47$), with a higher response under high background SOM-P. In the model, root exudation depends on plant P demand but is limited by a maximum exudation rate. Higher background SOM-P values reduced initial P limitation, allowing for greater exudation responses under CO_2 -induced P limitation. Under P addition, the simulated effect of eCO_2 on R_s ($r_{\text{CO}_2}^{\text{eP}} = 1.14 - 1.20$) was marginally higher than under ambient P treatment. Differences were mainly induced by a stronger effect of eCO_2 on R_h ($r_{\text{CO}_2}^{\text{eP}} = 1.13 - 1.24$), then on R_{ar} ($r_{\text{CO}_2}^{\text{eP}} = 1.12 - 1.18$). This was caused by a stronger effect of eCO_2 on root exudation under P addition ($r_{\text{CO}_2}^{\text{eP}} = 1.18 - 1.86$), as—similar to increased SOM-P—P addition lowered P limitation, allowing for a stronger limitation effect through CO_2 . In general, interaction effects were close to neutral for most variables and parameter combinations (Fig. B6), with the exception of root exudation.

3.5 Long-term P addition changes responses in underlying drivers

Simulation of 10-year long P addition treatment caused shifts in microbial P demand, plant C allocation, and R_s compared to three years of P addition and caused accumulation of available PO_4 (Fig. 7). In a simulation with a prescribed microbial C:P

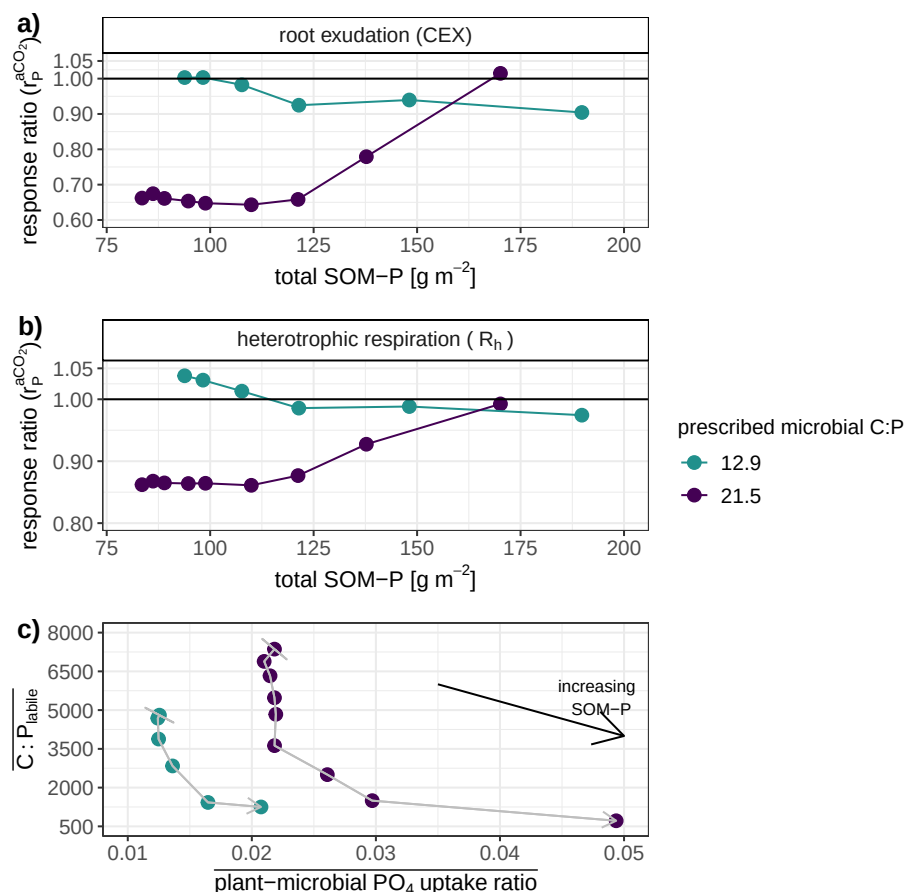


Figure 4. Influence of SOM-P on the response to P addition for distinct assumed microbial C:P ratios, achieved by different assumptions about the initial organic soil P at the beginning of the simulation. Simulated response ratios to 3 years of P addition under ambient CO_2 in a) root exudation (CEX) and b) heterotrophic respiration (R_h) for two distinct fixed microbial C:P ratios ($C : P_{Mic}$) settings along an artificial gradient of increasing SOM-P (g m^{-2}). Values below one describe a decrease, while values above one describe an increase in the respective variable. c) Characterization of the long-term ecosystem P-state, defined by plant labile C:P ratio, as an indicator for plant P limitation and plant-microbial PO_4 uptake ratio ($\frac{\text{plant } \text{PO}_4 \text{ uptake}}{\text{microbe } \text{PO}_4 \text{ uptake}}$), as an indicator for microbial competitiveness. Values calculated for two fixed microbial C:P ratios based on simulated 10-year annual mean the start of treatment. Arrow direction indicates increasing SOM-P.

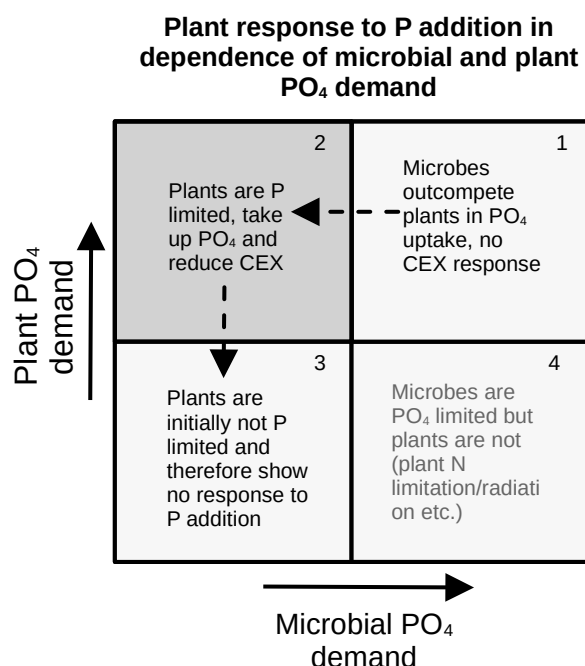


Figure 5. Conceptual representation of simulated ecosystem states and their responses to PO₄ addition based on plant and microbial demand for P. Dashed arrows represent directions of increased background P availability. The model suggests that in ecosystems with high microbial P demand and high plant P demand (1) microbes will out-compete plants for additional available PO₄, binding most of the P in soils and suppressing plant response in root exudation (CEX) to P addition. (2) In systems where plants are P limited but microbes are limited by other factors, microbial competitiveness will be lower, allowing increased plant PO₄ uptake under PO₄ addition. Consequently, plants will reduce CEX. (3) In systems with high P abundance, P addition will have no effect or only a minimal effect on plants and microbes. (4) For the studied conditions, the model did not simulate an ecosystem where microbial growth is PO₄ limited while plant growth is limited by other factors.

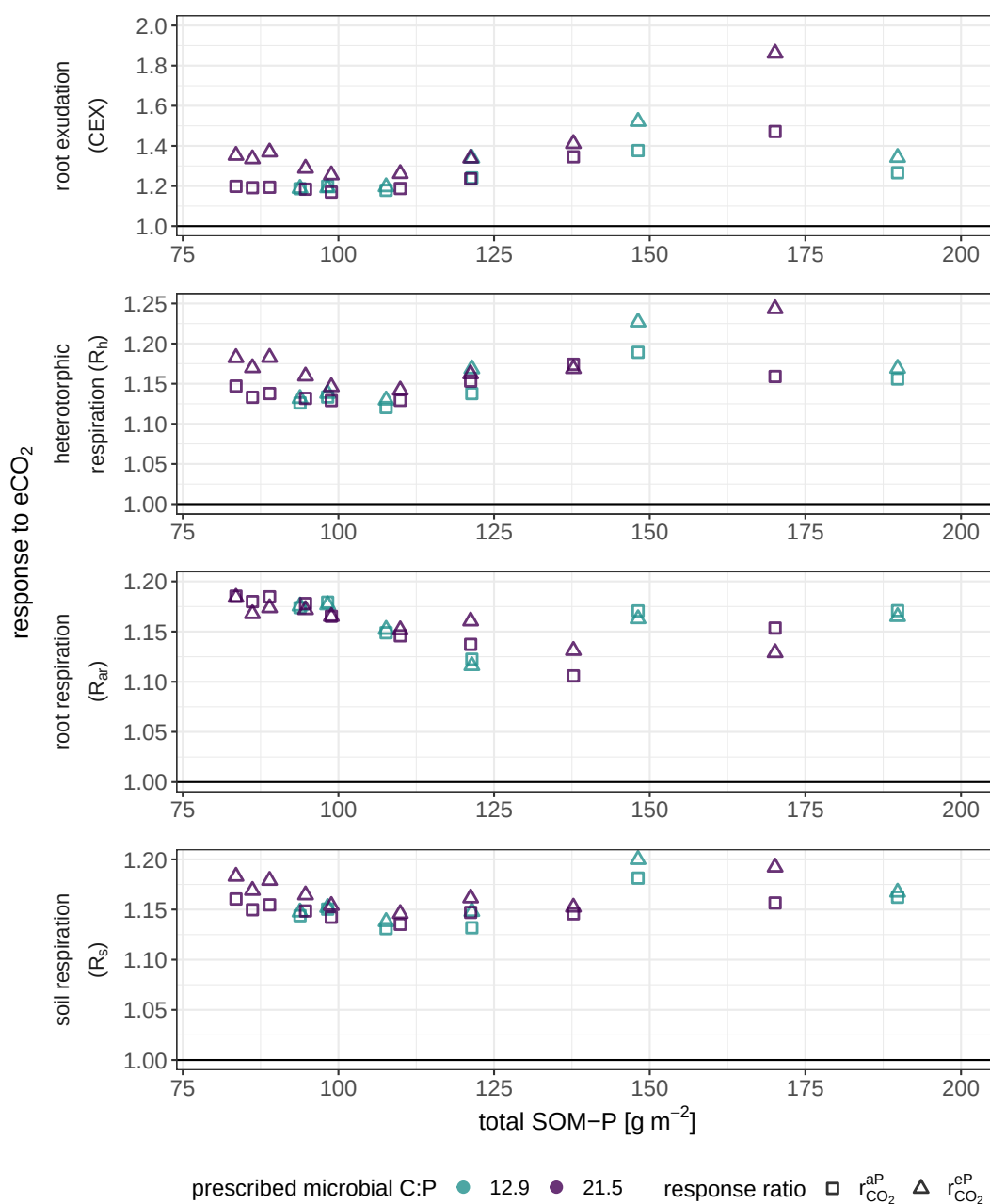


Figure 6. Simulated effect of eCO₂ under ambient P ($r_{\text{CO}_2}^{\text{aP}}$) and P addition treatment ($r_{\text{CO}_2}^{\text{eP}}$) for root exudation (CEX), heterotrophic respiration (R_h), fine root respiration (R_{ar}), and soil respiration (R_s) for two distinct fixed microbial C:P ratios ($C : P_{\text{Mic}}$) settings along an artificial gradient of increasing SOM-P (g m^{-2}). Values below one describe a decrease, while values above one describe an increase in the respective variable.



ratio of 12.9 and under ambient CO₂, 3 years of P addition (3 g m⁻² yr⁻¹) resulted in only a minimal increase in GPP, plant fluxes, and R_s response. However, continuation of P addition satisfied microbial demands after five years, allowing for additional plant PO₄ uptake. Therefore, GPP and litterfall increased substantially in the long-term by up to 193 g m⁻² yr⁻¹ and 75 g m⁻² yr⁻¹, respectively, compared to no P addition. Root respiration increased by up to 40 g m⁻² yr⁻¹ and root exudation decreased by up to 155 g m⁻² yr⁻¹. Consequently, R_h decreased by up to 30 g m⁻² yr⁻¹ through reduced root exudation and increased microbial CUE.

In simulations with lower microbial P demand for growth (C:P ratio of 21.5), P addition increased GPP, litterfall, and R_{ar} in three years of P addition, while the continuous P addition led to a continuation of the root exudation decline by up to 176 g m⁻² yr⁻¹. Heterotrophic respiration first decreased by up to 122 g m⁻² yr⁻¹ but slowly recovered with increased litterfall. Our results indicate that, with extended addition the effect on R_s shifts as increased litter input and root growth outweigh the initial decrease in root exudation rate.

With continuous P addition, labile PO₄ accumulated in soils. After ten years of P addition available PO₄ was 0.52 g m⁻² and 7.3 g m⁻² greater than under no-treatment conditions in simulations with microbial C:P ratio of 12.9 and 21.5, respectively. The accumulated PO₄ supported responses in plant and soil processes even after P addition ended.

Under eCO₂, responses to P addition had the same direction as under aCO₂ but were generally larger. For instance, the effect of P addition on GPP was up to 100 g m⁻² yr⁻¹ stronger than under aCO₂. At the same time, accumulation of PO₄ was smaller under eCO₂, leading to shorter continuation of effects after P addition ended (Fig. B7).

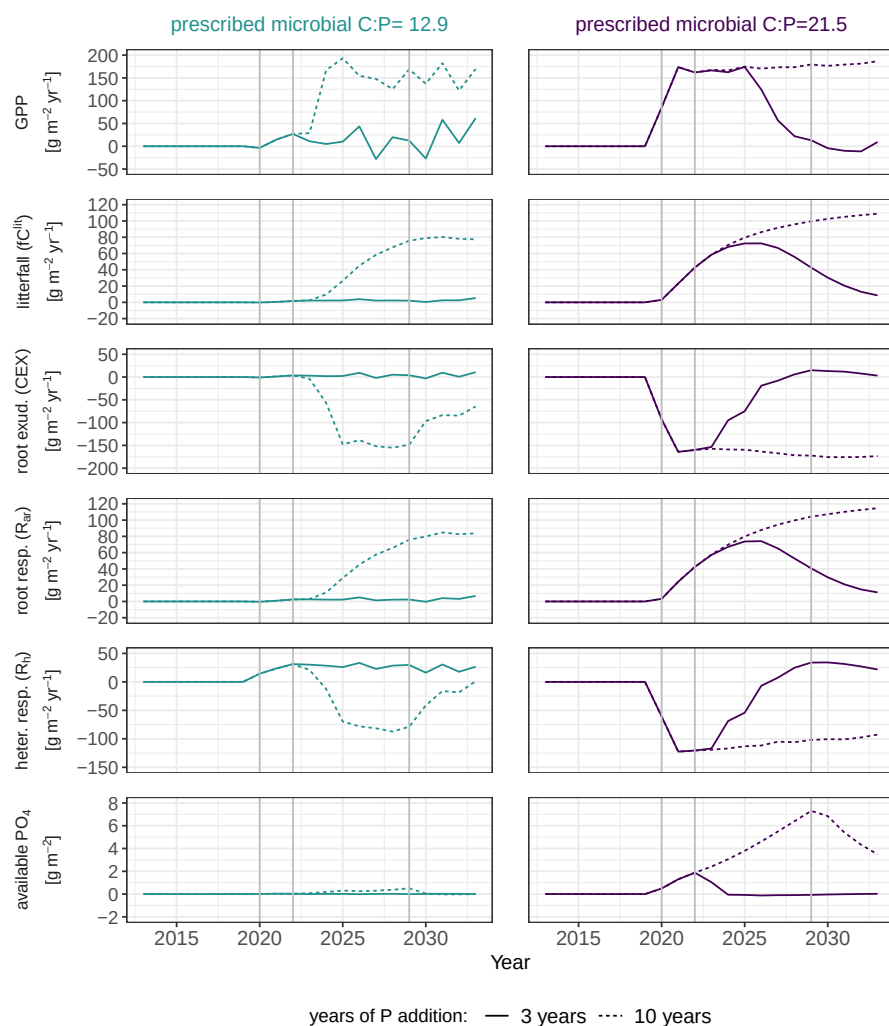


Figure 7. Simulated absolute effect of P addition under ambient CO_2 for 3 years and 10 years of P addition in available PO_4 [g m^{-2}], gross primary productivity (GPP [$\text{g m}^{-2} \text{yr}^{-1}$]), C litterfall (fC^{lit} [$\text{g m}^{-2} \text{yr}^{-1}$]), heterotrophic respiration (R_h [$\text{g m}^{-2} \text{yr}^{-1}$]) and fine root respiration (R_{ar} [$\text{g m}^{-2} \text{yr}^{-1}$]), for two different fixed microbial C:P ratios; grey vertical lines represent the start of P addition, the end of 3-year addition, and the end of 10-year addition.



4 Discussion

305 We tested whether the response of root exudation could explain the link between soil respiration and P availability in a mature Eucalyptus forest FACE experiment. While previous studies focused on the role of root exudation in carbon cycling and the R_s response under CO₂ fertilization (Schufft et al., accepted), this study investigated the effect of P addition and its interaction with CO₂ fertilization. We specifically focused on how plant-microbe competition, SOM-P availability, and treatment duration influenced the responses. The results provide key measurements needed to understand the underlying drivers and guide future
310 experimental work.

4.1 The influence of plant-soil interactions on soil respiration

The model reproduced the observed decline in R_s following P addition, but underestimated its effect size. QUINCY-JSM simulated a 3 % reduction in R_s , thereby underestimating the 19 % median reduction observed at EucFACE. These discrepancies can be partly explained by the parametrization of microbial C:P ratios and background SOM-P as the model simulated R_s
315 declines of up to 7 %, within the tested parameter space. This effect size is consistent with an 8 % decline observed at a P addition experiment in a *Eucalyptus pauciflora* forest (Keith et al., 1997a). The simulated decline in R_s contrasts with a recent model-intercomparison study using the same modeling protocol (Wang et al., 2026), as the model used here accounts for reduced root exudation and heterotrophic rhizosphere respiration as the main drivers for reduced R_s in response to P addition (Keith et al., 1997a).

320

In the model, increased plant P uptake following P addition reduced root exudation. The decrease in root exudation lowered microbial C substrate availability, which increased microbial CUE and reduced R_h , and consequently R_s (Yuan et al., 2026; Cui et al., 2024; Koyama et al., 2025). Observations indicate reduced root exudation under elevated N availability (Zeng et al., 2024; Meier et al., 2020; Ataka et al., 2020). Despite the role of root exudates in P acquisition (Reichert et al., 2022; Lambers,
325 2022), the sensitivity of root exudation to P addition remains poorly constrained (Han et al., 2026) and requires further experimental data (Table 3).

Additional discrepancies between simulations and observations may arise from mechanisms that are currently not represented in the model, such as altered root growth, decreased mycorrhizal colonization, or shifts in microbial communities. The
330 model assumes increased fine root growth following P addition. However, nutrient addition may also reduce plant C investments in roots and decrease fine root production (Yavitt et al., 2011; Xia et al., 2024; Wurzbürger and Wright, 2015). A decrease in root biomass would decrease autotrophic respiration, while also decreasing litter input, root exudation, and microbial substrate availability, exacerbating the reduction in R_s . Surprisingly, Lugli et al. (2024) observed increased fine root growth under P addition in a tropical forest. This indicates that we do not yet capture the full spectrum of plant P acquisition strategies and
335 their effect on microbes, plant nutrient availability and R_s (Reichert et al., 2022). Similarly, nutrient addition may reduce plant C allocation to mycorrhiza fungi (Treseder, 2004). While our model does not explicitly represent mycorrhiza, the effect would



mirror reduced root exudation, and decrease R_h through lowered microbial C substrate availability. Finally, R_s response to P addition is not solely driven by plant input but also by microbial communities (Zhang et al., 2021). Our model partially accounts for these shifts by flexibility in microbial CUE and enzyme allocation. However, we do not represent potential shifts in microbial turnover rates, substrate preferences, and stoichiometry, which may influence soil C and P cycling under P addition. Future research should evaluate these mechanisms in experimental work and model development to improve our understanding of plant-microbial drivers of R_s (Tab. 3).

4.2 Modulators in P addition effects on soil respiration

The sensitivity analysis demonstrated that, in the model, microbial P demand is a key modulator for the response of root exudation - and consequently R_s - to P addition. Assuming that C:P is an indicator of microbial P demand, the simulations indicate increased microbial competition for P under high microbial demand. The model predicts that under strong microbial competition for P, additional available PO_4 was primarily immobilized by microbes and transferred into SOM, even under plant P-limitation. As a consequence, vegetation remained P-limited, and the model did not reduce root exudation or R_s . Microbial competition remains a key factor in determining the fate of nutrients. Studies on N suggest that microbes can out-compete plants over short time scales, and that such mechanisms influence long-term soil nutrient availability (Kuzyakov and Xu, 2013; Jonasson et al., 1999). However, our understanding of plant-microbe competition for P remains limited. Isotopic tracer experiments or continuous observations of ecosystem pools after P addition may help to improve our understanding of plant-microbe competition for P (Tab. 3).

Our results identify microbial C:P ratio as a key parameter in biogeochemical models. Contrary to model assumptions, microbial stoichiometry is flexible to environmental changes. For example, microbial C:P can decrease under P addition (Rosinger et al., 2022; Griffiths et al., 2012; Yuan et al., 2026), due to adaptation in microbial communities and storage behavior (Butler et al., 2025; Butler and Warren, 2025). This may shift microbial demand and competition, and therefore responses in plant C allocation and R_s , during the experiment. We propose that measuring microbial stoichiometry and imbalances between microbial biomass and plant input stoichiometry can further help in understanding microbial P demand and improving biogeochemical models (Manzoni et al., 2012; Sistla et al., 2014) (Table 3).

Consistent with the findings of (Zheng et al., 2023), our simulations suggest that SOM-P modulates R_s responses to P addition. Phosphorus addition induced stronger responses in plant C fluxes under low SOM-P conditions, than at higher SOM-P levels, where plants were less P limited and therefore benefited less from additional P inputs (Fig. 4, Fig. 5). However, simulating P availability in plants and microbes remains challenging (Helfenstein et al., 2024; Wang et al., 2022). While SOM-P is often used as an indicator of ecosystem P status, it does not necessarily reflect the size of the inorganic, plant-available PO_4 pool. Furthermore, most biogeochemical models do not account for spatial heterogeneity of PO_4 availability within soils, and potentially overestimate P availability for plants by using bulk soil measurements. Nonetheless, it is necessary to measure solute inorganic, plant-available PO_4 , microbial P, SOM-P, and plant P pools before, during and after the experiment, to a) assess P availability for plants and microbes; b) understand the fate of added P and its cycling during addition and afterwards (Table 3).



4.3 CO₂ fertilization under P addition

Consistent with (Jiang et al., 2020b), eCO₂ increased R_s . However, in the model, this effect was only marginally increased by SOM-P or P addition (Fig. 6). Our results are consistent with observations from Zhao et al. (in review), who compared R_s measurements from before and after P addition, to show that P addition did not alter the eCO₂ effect on R_s . The model predicted a stronger response ratio to CO₂ fertilization for both root exudation and R_h under P addition. Phosphorus addition alleviated P limitation, thereby enabling CO₂ to have a stronger effect in increasing limitations again, causing an stronger effect in root exudation. While this may represent a plausible mechanisms, it contradicts with observations from Zhao et al. (in review), who concluded that under CO₂, P addition induces a shift in plant C allocation toward reduced root exudation and increased root growth. This highlights the need for improved representation of shifts in nutrient acquisition strategies in current models, which should be constrained by experimental data (Fleischer et al., 2019; Lugli et al., 2020) (Tab. 3). The model also showed low sensitivity in eCO₂ effects to P addition in GPP or BP (Fig. B5), contradicting meta-analysis that suggests that P addition will increase the CO₂ fertilization effect (Jiang et al., 2020a; Terrer et al., 2019) on photosynthesis and biomass production. While model results align with other models applied at EucFACE Wang et al. (2026), this may be a result of a missing representation of P-dependence in photosynthesis processes (Ellsworth et al., 2022). As plant-productivity will affect R_s (Fig. 1), it is necessary to further constrain this effect, especially for improving long-term model predictions.

4.4 Underlying drivers change with long-term addition

Simulated microbial demand and P availability, and therefore R_s response, changed with continuous P addition. (Feng and Zhu, 2019) showed that the duration of P addition is positively correlated with R_s response. The model suggests that the fast reduction in R_h through reduced allocation of C belowground is later overshadowed by increased root growth, litter input, and R_{ar} (Fig. 7). Additionally, continuous P addition will eventually satisfy microbial P demands, shifting the P-limitation state of the ecosystem and causing accumulation of plant-available P over time (Chen et al., 2026). The accumulated PO₄ can support microbial activity and plant growth even after P addition stops. These results highlight the need for long-lasting P addition experiments that focus on a) the effect on drivers like root exudation, root productivity and litterfall and b) the long-term dynamics of plant-microbes competition and soil pools (Table 3).

4.5 Observational and model constraints

The model provides a novel hypothesis for the role of plant-microbe interactions on ecosystem C cycling under P addition. However, our results are limited by observational data and model assumptions. We compared simulated responses over three years with response ratios calculated based on fortnightly observations taken over one year. Soil respiration varies heavily with season (Fig. A6) and therefore the observations used here can only be used as a proxy for an annual response on ecosystem level. Next to measurements of underlying drivers (Table 3), continuous R_s measurements by auto-chambers are needed to further interpolate annual fluxes and evaluate the hypotheses derived here.

Further, our simulations focus on plant C allocation and microbial processes. To reduce the impact of meteorological variability



and ensure comparability with (Wang et al., 2026) we constrained meteorological forcing at the site. However the site is dominated by strong variability in precipitation, and influence of soil moisture remains complex as soil moisture can increase or reduce R_s (Keith et al., 1997a; Feng and Zhu, 2019), elevate nutrient availability, alter root exudation patterns (Brunn et al., 2022), and interact with CO_2 fertilization on root growth (Piñeiro et al., 2020; Hursh et al., 2016). Finally, we modeled the EucFACE experiment by representing vegetation solely as trees. However, understory plant responses to eCO_2 or P addition may differ from those of trees due to distinct nutrient demands, faster turnover rates, different plant C allocation (Jiang et al., 2020b; Piñeiro et al., 2023). Future work should explicitly incorporate understory dynamics to improve model accuracy.

Table 3. Key processes and associated measurements required to improve understanding of nutrient availability effects on soil respiration under elevated CO_2

Processes	Measurements needed
altered plant belowground C allocation under P addition	root exudation under P addition
	fine root growth under P addition
	mycorrhizal colonization under P addition
plant-microbial competition and demand before and during P addition	stoichiometry and amount of plant input to estimate microbial demands
	shifts in microbial CUE under P addition and C limitation
	shifts in microbial community stoichiometry
	measure SOM-P, available P, and plant P before, during, and after the P addition to assess division of added P between pools
nutrient acquisition under combined CO_2 and P addition treatment	isotopic tracer experiments to assess plant-microbe competition for PO_4
	root exudation, fine-root growth, and mineralization rates under P and CO_2 fertilization
change in underlying drivers of R_s with long-term P addition	long-term experiments (5-10y) with continuous measurements of root exudation, litterfall, plant growth, microbial biomass and soil respiration



410 5 Conclusions

Our simulations suggest that changes in root exudation may be an important mechanism linking P availability to R_s , as an adaptation in root exudation flux controls substrate availability for microbial growth and therefore R_h . However, the response of R_s to P addition depends on the competition between plants and microbes for added P, as division of added P is strongly influenced by microbial P demand and background soil P availability. Our results offer a new perspective into how plant-
415 microbial interactions regulate R_s , though we currently lack the data to completely evaluate the proposed mechanisms. Our results identify key measurements for further experimental research and provide a basis for developing new hypotheses to advance our understanding of R_s responses to nutrient availability.



Code availability. The model is open source under the GNU GPL vs3 and MPI-M ICON software license agreement (depending on module). The code is available under <https://doi.org/10.17871/quincy-model-2019>. A copy of the scientific code can be found in this temporary
420 (15.3.2027) private link for review purposes: <https://nextcloud.bgc-jena.mpg.de/s/CWpHmBiTtrQFDJz> Forcing data to run the model for testbed simulations can be made available on request.

Data availability. Soil respiration data were taken together with the project described in Zhao et al. (in review) and can be made available by request.

Author contributions. KS, KF and SZ designed the study. KS wrote model implementation, ran the model and performed first analysis. KS,
425 SZ, BEM and KF interpreted the results. MZ collected and provided soil respiration data. KS prepared the manuscript with contributions from all co-authors

Competing interests. Some authors are members of the editorial board of journal Biogeosciences.



Appendix A

A1 model details

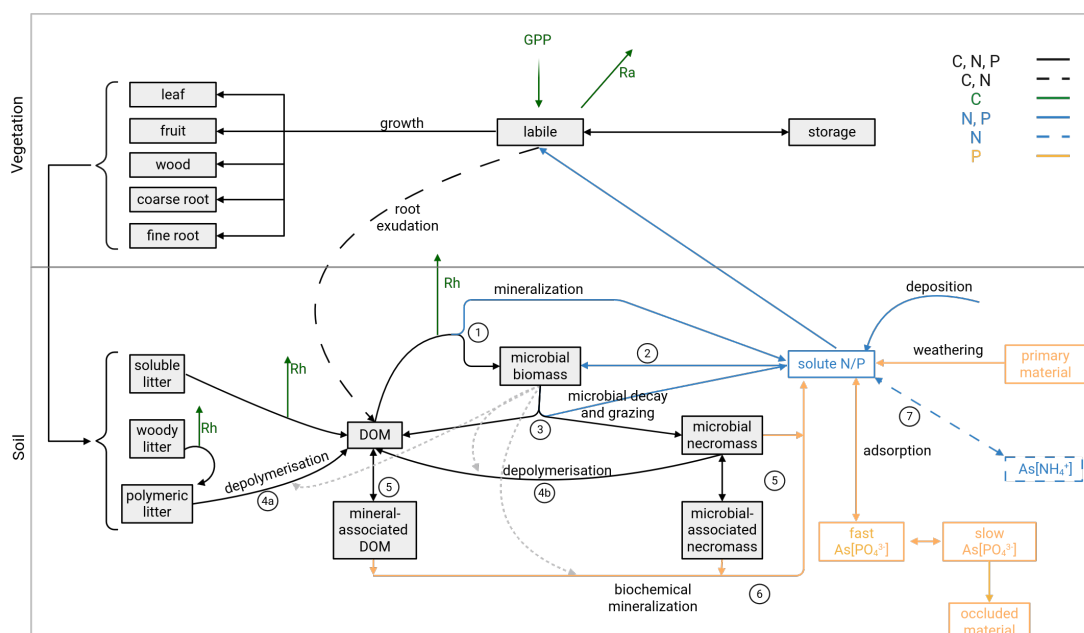


Figure A1. Schematic overview for QUINCY-JSM from Schufft et al. (accepted). Pools and Fluxes for different elements are coded by color and linetype: Black solid line for C, N, P; black dashed line for C, N only; green solid line for C only; blue solid line for N, P only; blue dashed line for N only; yellow solid line for P only. Grey dashed lines represent processes that are mediated by microbial enzyme allocation. Nutrients are mineralized on microbial uptake of organic substrate (1) and immobilized (2) by microbes. Upon turnover microbial biomass is partitioned into DOM and necromass (3). Microbial necromass and polymeric litter are depolymerized by enzymatic processes (4 a,b). DOM and microbial necromass are in sorption equilibrium with mineral soil surface (5). In addition to depolymerisation microbes can mineralize organic P via biochemical mineralization (6). Inorganic nutrients are partially sorped to mineral surface (As) (7). Created in BioRender. Schufft, K. (2026) <https://BioRender.com/7hbj3d>

430 A2 Simulation evaluation

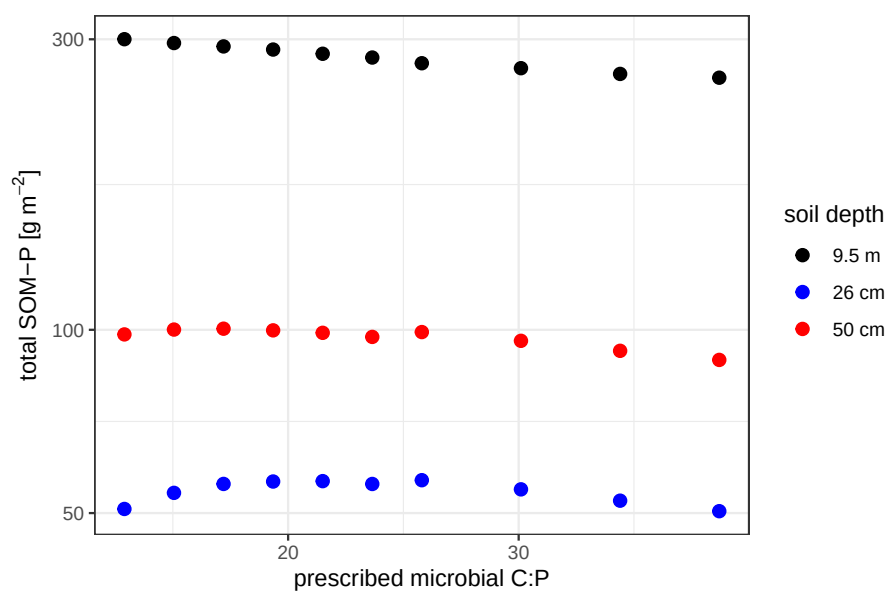


Figure A2. Simulated pre-treatment (annual mean 10y before CO₂ treatment) total SOM-P for different soil column depths for simulations with different prescribed microbial C:P ratios

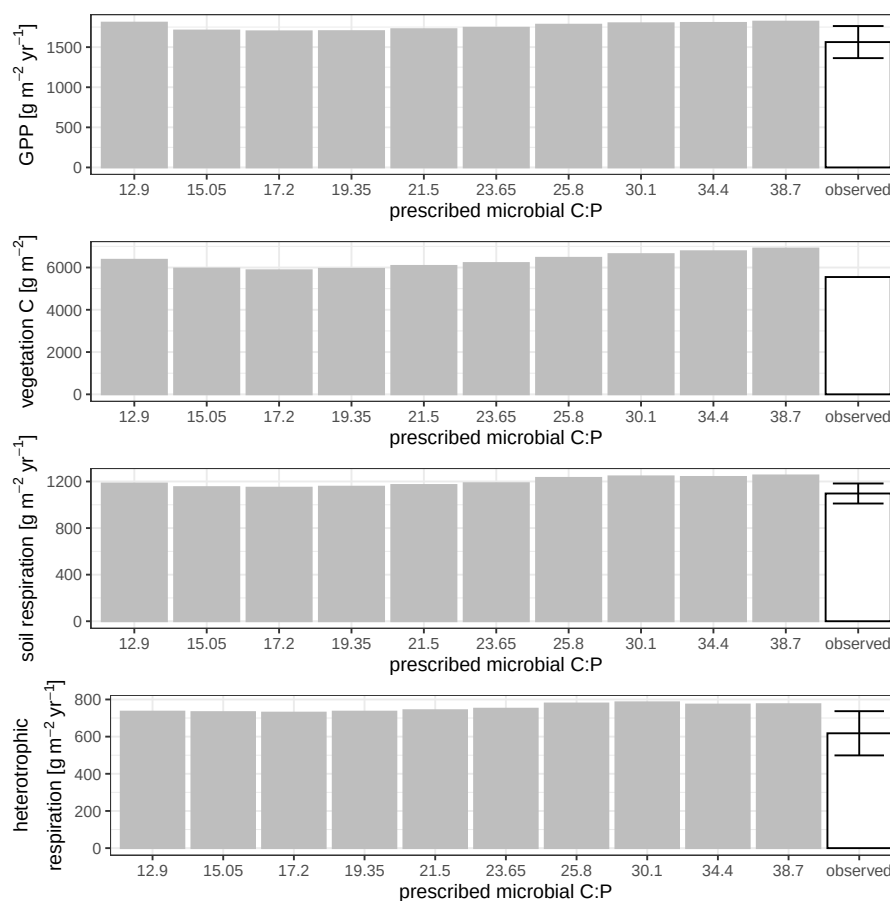


Figure A3. Simulated pre-treatment (annual mean 10y before CO₂ treatment, 2001–2011) ecosystem C fluxes/pools, gross primary productivity (GPP), total vegetation C, soil respiration and heterotrophic respiration along a gradient of prescribed microbial C:P ratio, observed values based on ambient measurements from 2013–2016 from Jiang et al. (2020b)

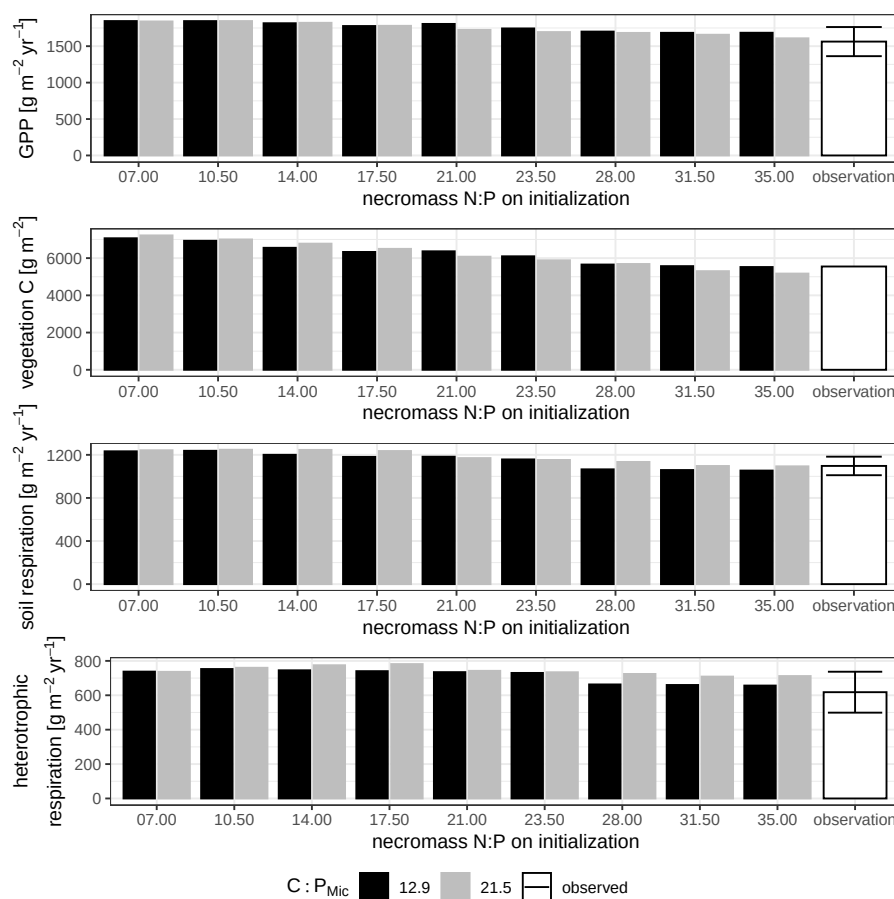


Figure A4. Simulated pre-treatment (annual mean 10y before CO₂ treatment, 2001-2011) ecosystem C fluxes/pools: gross primary productivity (GPP), total vegetation C, soil respiration and heterotrophic respiration for simulations with two prescribed microbial C:P ratio and different necromass initialization N:P ratios, observed values based on ambient measurements from 2013-2016 from Jiang et al. (2020b).

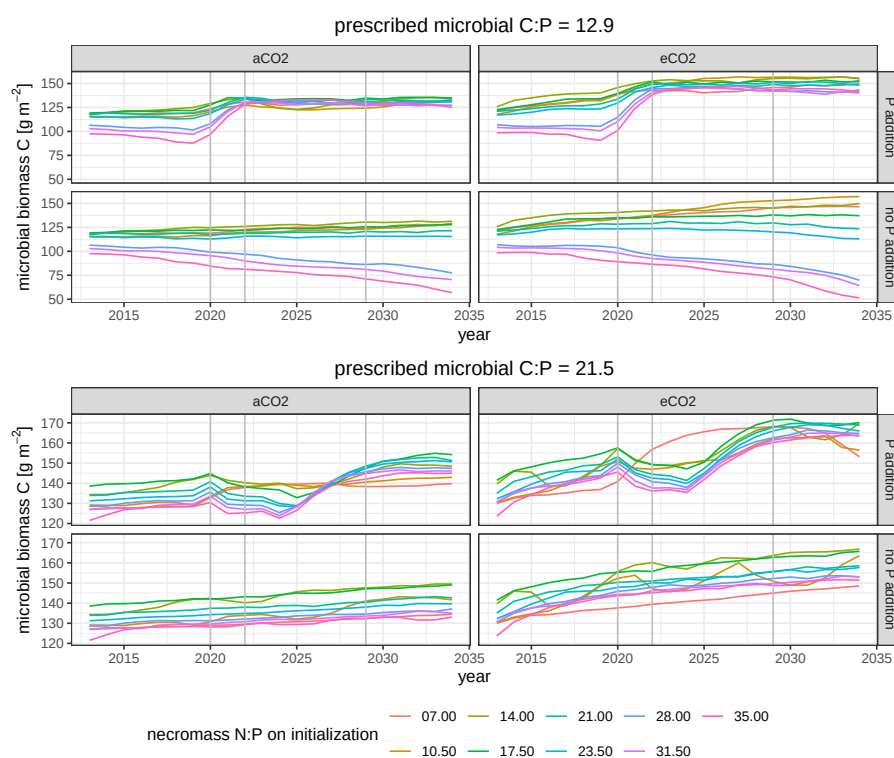


Figure A5. Simulated microbial C for top 26 cm under ambient and elevated CO₂ with and without P addition, for two different fixed microbial C:P ratios and different necromass initialization N:P ratios; grey vertical lines represent start of P addition, end of 3-year addition and end of 10-year addition.



A3 soil respiration data

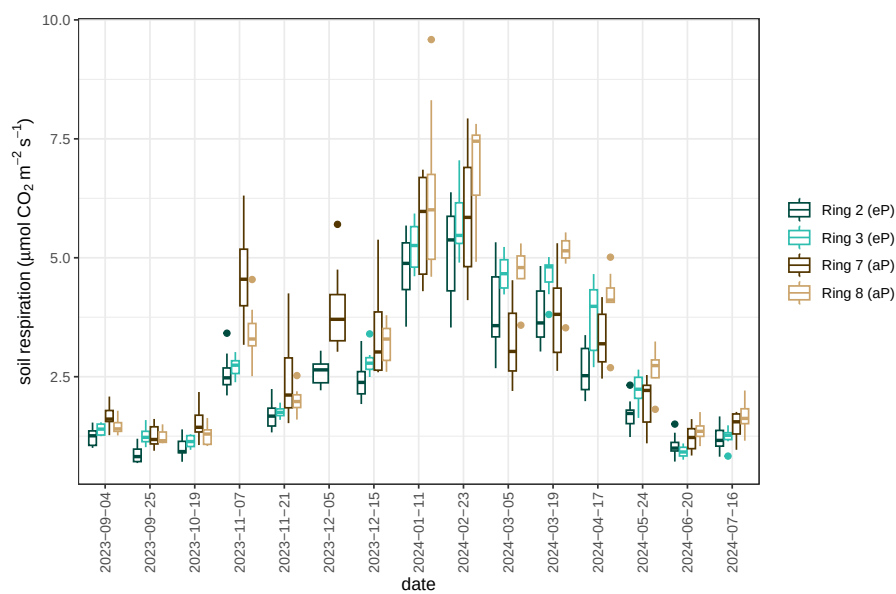


Figure A6. Soil respiration measurements taken bi-weekly in rings 1 and 2 (ambient CO_2 and elevated P (eP)) and rings 7 and 8 (ambient CO_2 and ambient P (aP)).



Appendix B

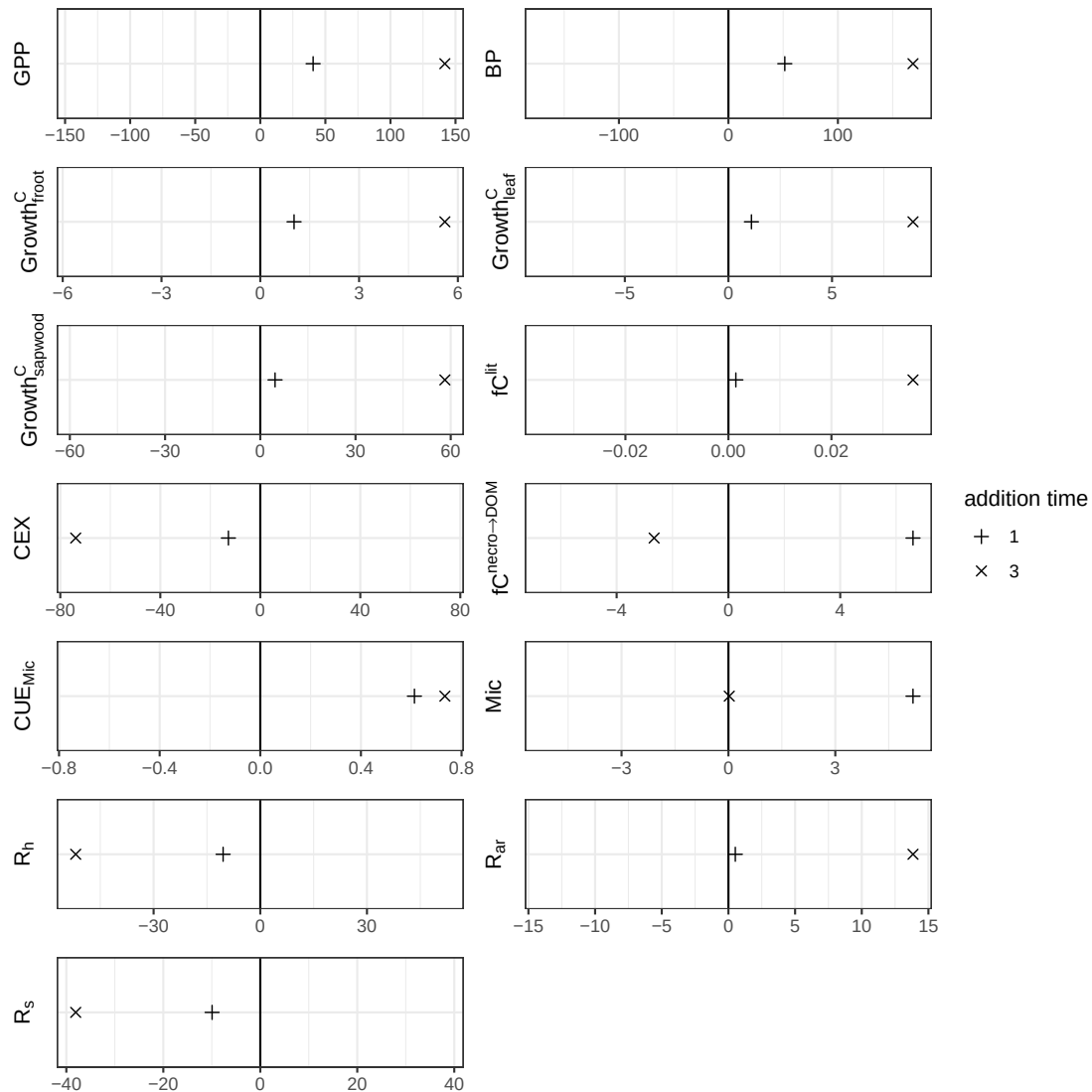


Figure B1. Simulated absolute response for 3y of P addition under ambient CO_2 in gross primary productivity (GPP), biomass production (BP), production of fine roots ($Growth^C_{\text{root}}$), leaves ($Growth^C_{\text{leaf}}$) and sapwood ($Growth^C_{\text{sapwood}}$), total litterfall (fC^{lit}), root respiration (R_{ar}), root exudation (CEX), microbial biomass (Mic), microbial carbon-use efficiency in first soil layer ($CUE_{Mic,L1}$), necromass depolymerisation flux ($fC^{\text{necro} \rightarrow \text{DOM}}$), heterotrophic respiration (R_h), and soil respiration ($R_s = R_{ar} + R_h$).

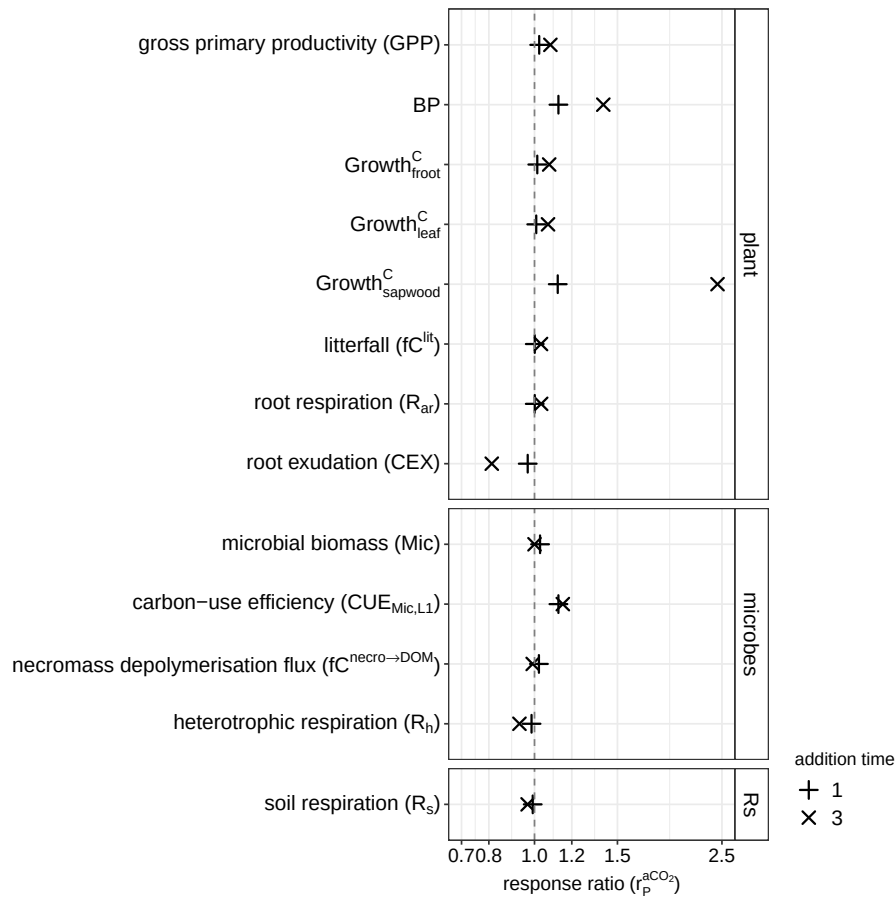


Figure B2. Response ratio ($r_p^{aCO_2}$) of plant and microbial processes, and R_s to P addition. Simulated response after 1 year ('+') and 3 years ('x') of P addition under ambient CO_2 using model default parameters for EucFACE configuration (Schufft et al., accepted) in gross primary productivity (GPP), biomass production (BP), production of fine roots ($Growth_{froot}^C$), leaves ($Growth_{leaf}^C$) and sapwood ($Growth_{sapwood}^C$), total litterfall (fC^{lit}), root respiration (R_{ar}), root exudation (CEX), microbial biomass (Mic), microbial carbon-use efficiency in first soil layer ($CUE_{Mic,L1}$), necromass depolymerisation flux ($fC^{necro→DOM}$), heterotrophic respiration (R_h), and soil respiration ($R_s = R_{ar} + R_h$). Values smaller than one describe a decrease, while values above one describe an increase in the respective variable.

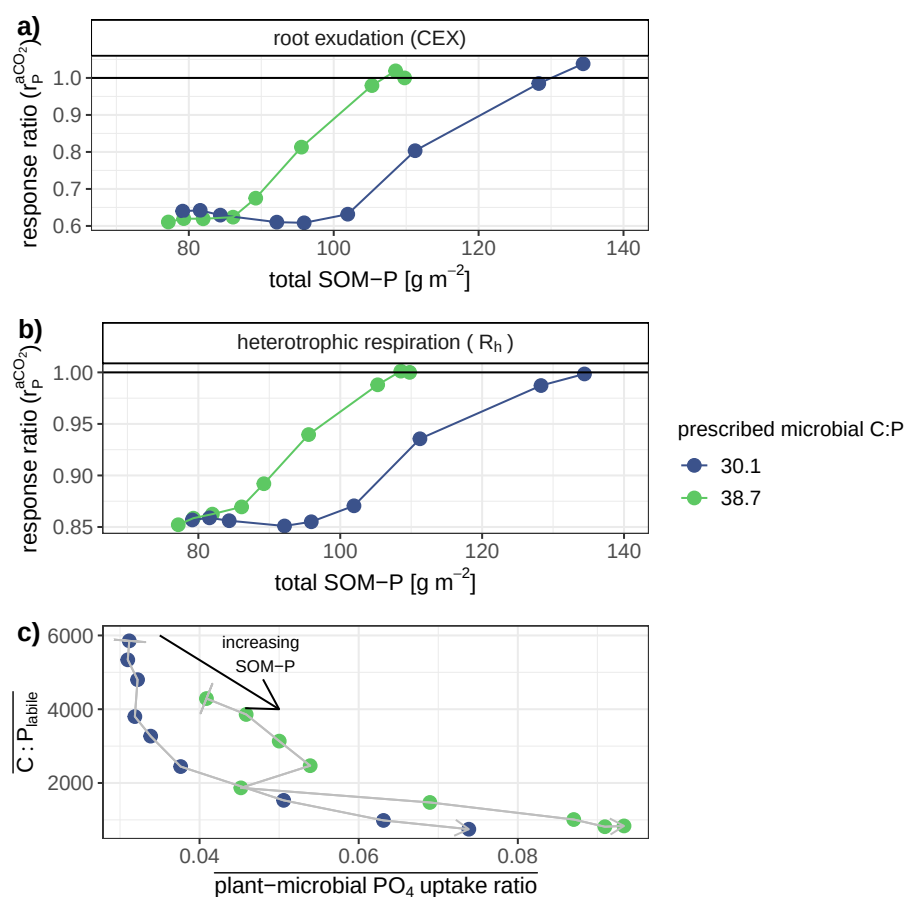


Figure B3. Simulated response ratios to 3 years of P addition under ambient CO_2 in C litterfall ($Litterfall_C$), fine root respiration (R_{ar}), first soil layer microbial CUE ($CUE_{Mic,L1}$) and soil respiration (R_s) for 2 different fixed microbial C:P ratios ($C:P_{Mic}$) along an artificial gradient of increasing SOM-P.

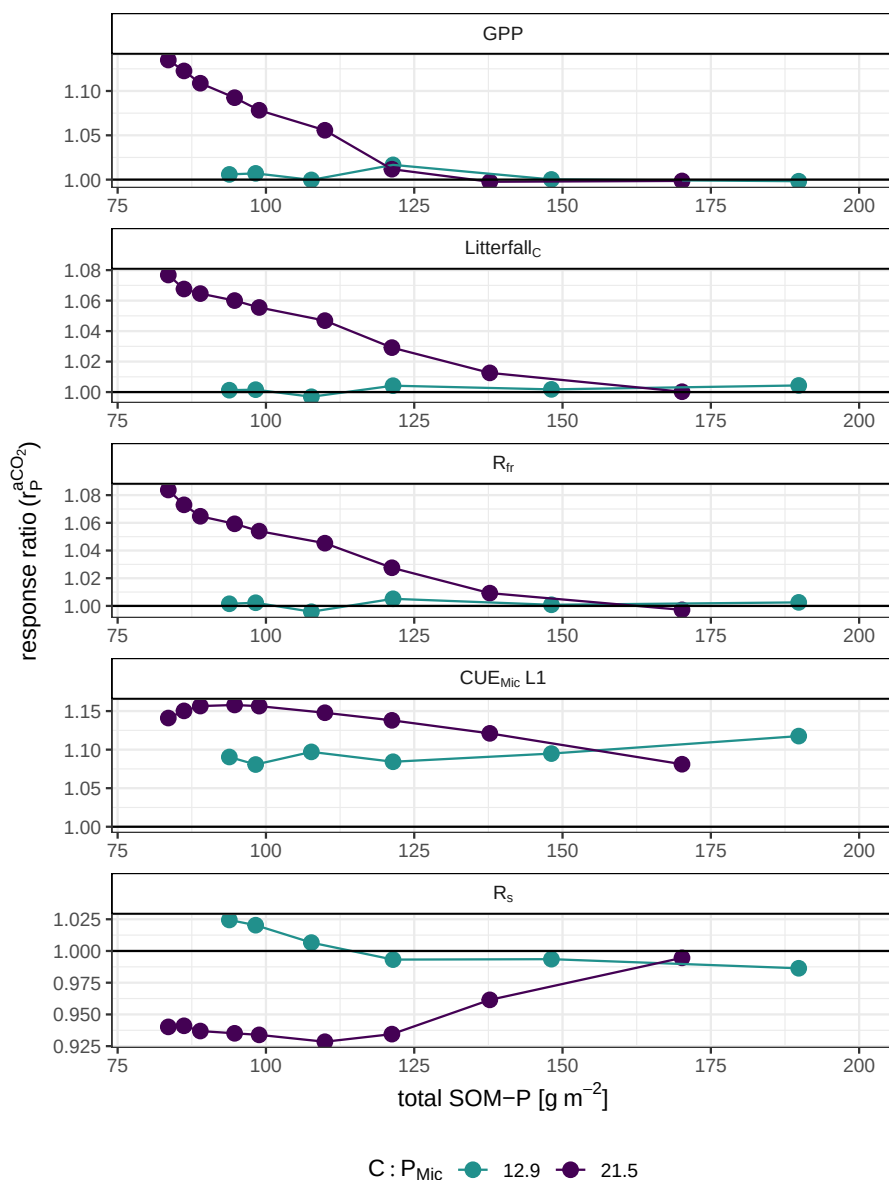


Figure B4. Influence of background SOM-P on the response to P addition for distinct assumed microbial C:P ratios, achieved by different assumptions about the initial organic soil P at the beginning of the simulation. Simulated response ratios to 3 years of P addition under ambient CO₂ in a) root exudation (*CEX*) and b) heterotrophic respiration (*R_h*) for two distinct fixed microbial C:P ratio (*C : P_{Mic}*) settings along an artificial gradient of increasing background SOM-P (g m⁻²). Values below one describe a decrease, while values above one describe an increase in the respective variable. c) Characterization of the long-term P-Ecosystem-state, defined by plant labile C:P ratio, as an indicator for plant P limitation and plant-microbial PO₄ uptake ratio ($\frac{\text{plant } PO_4 \text{ uptake}}{\text{microbe } PO_4 \text{ uptake}}$), as an indicator for microbial competitiveness. Values calculated for two fixed microbial C:P ratios based on simulated 10-year annual mean before the start of treatment. Arrow direction indicates increasing SOM-P.

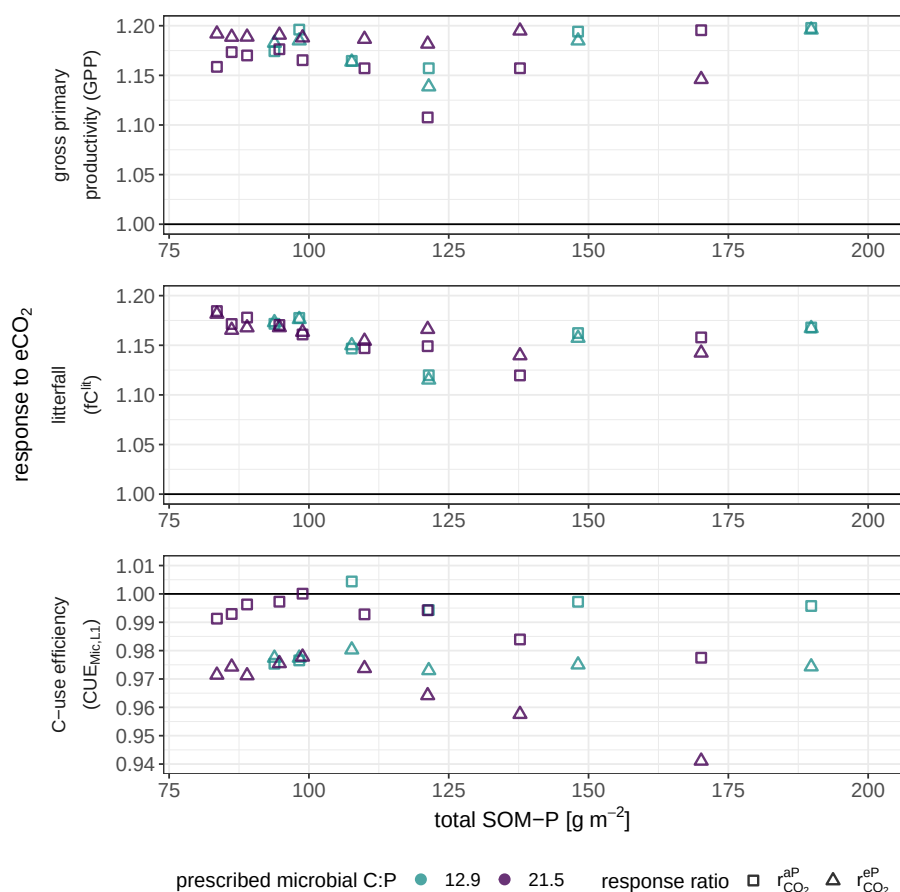


Figure B5. Simulated effect of eCO₂ under ambient P ($r_{CO_2}^{aP}$) and P addition treatment ($r_{CO_2}^{eP}$) for gross primary productivity (GPP), litterfall (fC^{lit}), and microbial carbon-use efficiency in first soil layer ($CUE_{Mic,L1}$) for two distinct fixed microbial C:P ratios ($C : P_{Mic}$) settings along an artificial gradient of increasing SOM-P (g m⁻²). Values below one describe a decrease, while values above one describe an increase in the respective variable.

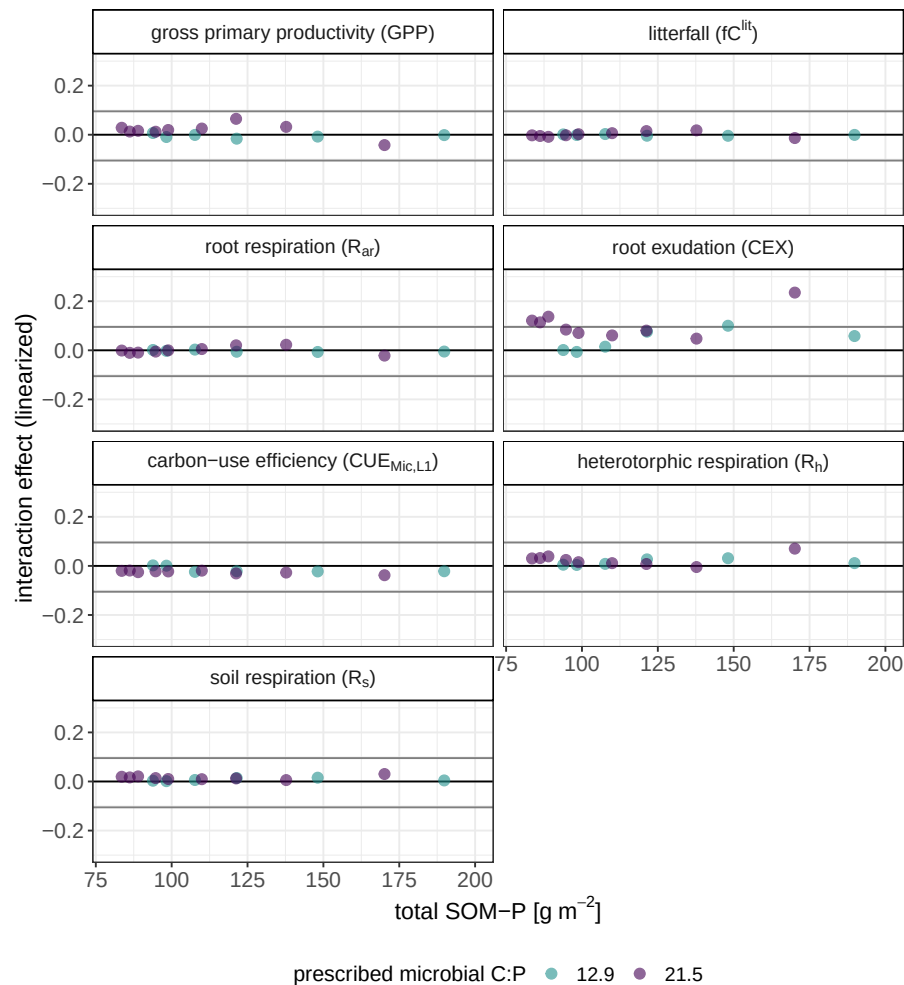


Figure B6. Simulated interaction effects of P addition and CO_2 fertilization for gross primary productivity (GPP), C Litterfall (fC^{lit}), root exudation (CEX), first soil layer microbial CUE ($CUE_{mic,L1}$), heterotrophic respiration (R_h), fine root respiration (R_{ar}) and soil respiration (R_s). Values below zero describe a decrease, while values above zero describe an increase in the respective variable. Grey lines at $\ln 0.9$ and $\ln 1.1$ indicate that the effect of P addition on the respective variable was 10 % weaker or stronger under aCO_2 than under eCO_2 .

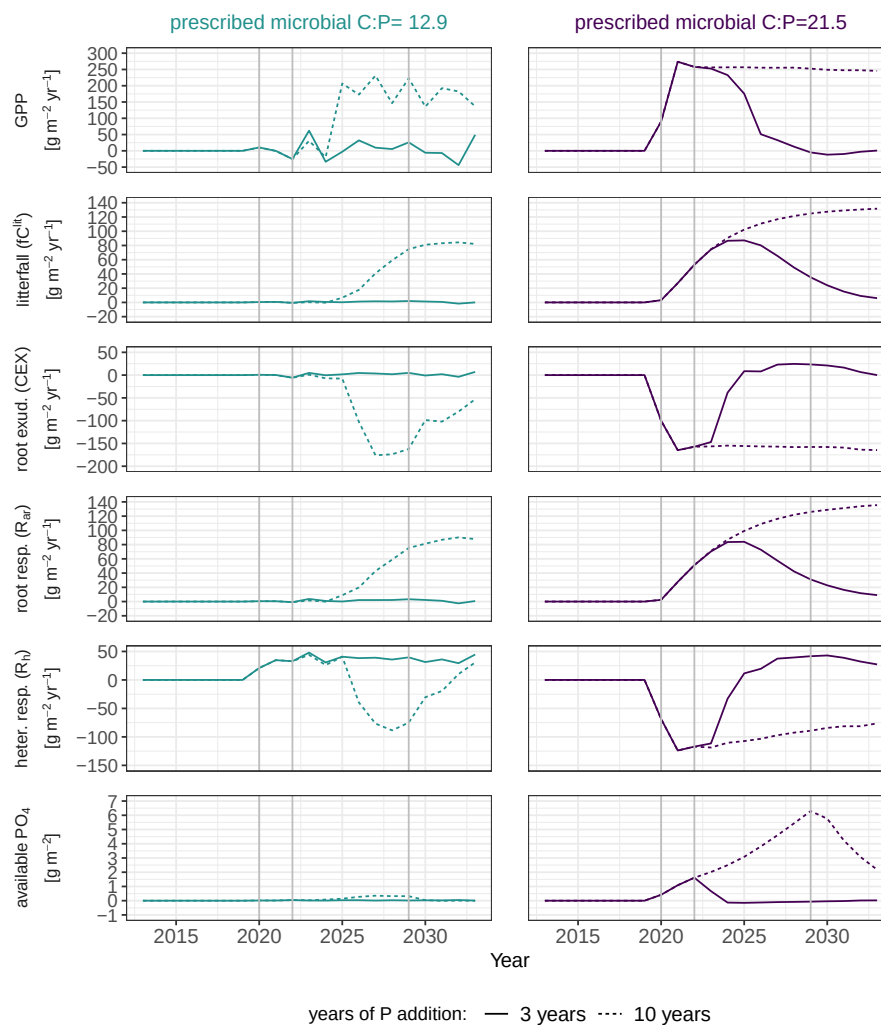


Figure B7. Simulated absolute effect of P addition under elevated CO₂ for three years and ten years of P addition in available PO₄, gross primary productivity (*GPP*), C litterfall (*Litterfall*^C), heterotrophic respiration (*R_h*) and fine root respiration (*R_{ar}*), for two different fixed microbial C:P ratios; grey vertical lines represent start of P addition, end of 3-year P addition and end of 10-year P addition.



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