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COMMENTARY

# Microbes modify soil nutrient availability and mediate plant responses to elevated $CO_2$

**Peter T. Pellitier · Robert B. Jackson**

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**Abstract** $CO_2$ fertilization of vegetation remains a critical offset to Anthropogenic emissions. Piñeiro et al, report the primary role of Phosphorus (P) in the growth responses of an understory plant community grown under experimentally elevated $CO_2$ ($eCO_2$). This study provides direct evidence that P constrains understory plant growth responses to $eCO_2$. By carefully tracing whole pot respiration, and patterns of carbon allocation, this study indirectly highlights the role of microorganisms in plant responses to $eCO_2$. In this commentary, we describe microbial processes that influence plant nutrition and growth in a $CO_2$ enriched world but remain challenging to integrate into process-based models. We summarize the current patchwork understanding of the role of microbes in plant growth responses to $eCO_2$, focusing primarily on plant-rhizosphere interactions, and mycorrhiza. Finally, we conclude by describing a series of research areas that stand to advance understanding of plant growth and nutrient acquisition under $eCO_2$.

**Keywords** Microbial physiology · Nitrogen · Phosphorus · CO2 · Assimilation

$CO_2$ fertilization of vegetation has increased the land carbon sink by approximately 12% (Piao et al. 2020). Large scale Earth system models, such as those in the Coupled Model Intercomparison Projects Phase 6 (CMIP6), project continued and increasing terrestrial carbon offsets concomitant with rising $CO_2$, throughout the remainder of the century, however there is overall weak confidence in the magnitude and duration of this response (Norby and Zak 2011; Walker et al. 2021). This is largely due to the fact that Earth System Models (ESM) are highly sensitive to the representation of the availability of growth-limiting soil nutrients, accurate representation of which has been the subject of study for several decades (Hungate 2003; Walker et al. 2021). Nitrogen (N) and Phosphorous (P) are widely understood to limit plant growth responses to $eCO_2$. Indeed, recent estimates suggest that $CO_2$ fertilization effects are driven primarily driven by N in ~ 65% and P in ~ 25% of global vegetation (Terrer et al. 2019). The availability of these resources can interact in complex ways to co-limit growth, for example, P limitation can limit biological N fixation (Niklaus and Körner 2004).

Soil P and N release are largely mediated by microbial activity, and plants rely on close microbial associations to acquire them (Terrer et al. 2019; Jiang et al. 2020a). Unsurprisingly then, microbial-explicit

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models of plant growth have long been suggested as means to improve predictions of soil nutrient availability, soil decay rates, and plant growth. However, aligning microbial community interactions or microbial traits into process-based models of plant growth responses to $eCO_2$ remains an ongoing challenge (Wan and Crowther 2022). Instead, most existing ESM latently or indirectly represent microbial controls on soil nutrient dynamics and plant-soil interactions.

In this commentary, we describe the results of a study by Piñeiro et al., who report the primary role of P in the growth responses of an understory plant community grown under experimentally elevated $CO_2$. The study focuses on the diverse plant community regenerating from a seedbank in a *Eucalyptus* woodland in Australia. Ongoing experimentation, such as this study, trace plant-soil interactions under $eCO_2$ conditions and offer insights into the cumulative role of microbial interactions in plant growth responses to global change. Piñeiro et al., however, do not directly study microbial communities or isolate microbe process-rate relationships, limiting the applicability of these findings into generalized models of plant growth. Here, we provide enhanced context for this study by discussing recent developments in our understanding of plant microbe interactions, as pertaining to nutrient acquisition and growth responses to $eCO_2$. We conclude by offering a series of outstanding research questions, answers to which would contribute to an improved mechanistic understanding of microbial interactions and their role in determining the duration and strength of ecosystem response to $eCO_2$.

## Plant community responses to $eCO_2$

Piñeiro and colleagues contribute to our understanding of whole plant community responses to $eCO_2$ using a factorial experiment that examines the interaction between plant growth, soil nutrients and water availability. The authors studied the growth of an understory *Eucalyptus* woodland plant community in response to $eCO_2$ under varying P amendments and water availability. The factorial pot-based experiment conserved both the native soil seedbank and soil microbial communities from the EucFACE experiments, grossly replicating soil structure. The plant community was allowed to develop for approximately 2.5 months under $eCO_2$ conditions prior to the commencement of flux measurements, and harvest occurred after 14 weeks of growth.

This study largely confirms previous work conducted in *Eucalyptus* dominated soils that P availability constrains above and belowground responses to $eCO_2$. Total plant biomass was stimulated in response to $eCO_2$when P was added to the soils, providing direct experimental evidence for this constraint. These results complement the authors previous studies documenting marginal increases in dominant grass species growth in response to $eCO_2$ despite increased phosphatase enzyme activity (Piñeiro et al. 2022). In the present study, they conclude that despite increased P foraging via roots and potentially stimulated soil microbial activity, plant growth may remain nutrient limited in the face of $eCO_2$. This conclusion is plausible, however the short duration of this study limits generalizability. In a recent quantitative meta-analysis by Jiang et al. (2020a), it was found that low P availability on average decreased plant aboveground, belowground, and total biomass responses to $eCO_2$, by 12–15%, approximately halving the $eCO_2$ responses observed under higher P availability.

This study complements existing work in *Eucalyptus* EucFACE experimental systems (Hasegawa et al. 2018; Jiang et al. 2020b). Existing studies in *Eucalyptus* dominated forests were conducted on long-lived overstory trees. Focusing instead on the growth response of understory plant communities is of interest because they provide high levels of ecosystem multifunctionality including supporting overstory tree growth (Landuyt et al. 2019). Scant studies have focused on understory plant growth responses to $eCO_2$. In one example, Edwards et al., (2006) documented that low P availability eliminated any $CO_2$-induced increase in biological nitrogen fixation in a clover. In an additional study (Hoosbeek 2016) found that P was lost from litter or mineral soils at elevated $CO_2$ in forest experiments, suggesting that plants (or microbes) may increase organic matter turnover or biogenic weathering.

## Microbial physiology and plant nutrient availability

The rise of molecular sequencing approaches have enabled detailed analyses of microbial communities (Bahram et al. 2018), and there is widespread recognition that plant responses to elevated $CO_2$ are

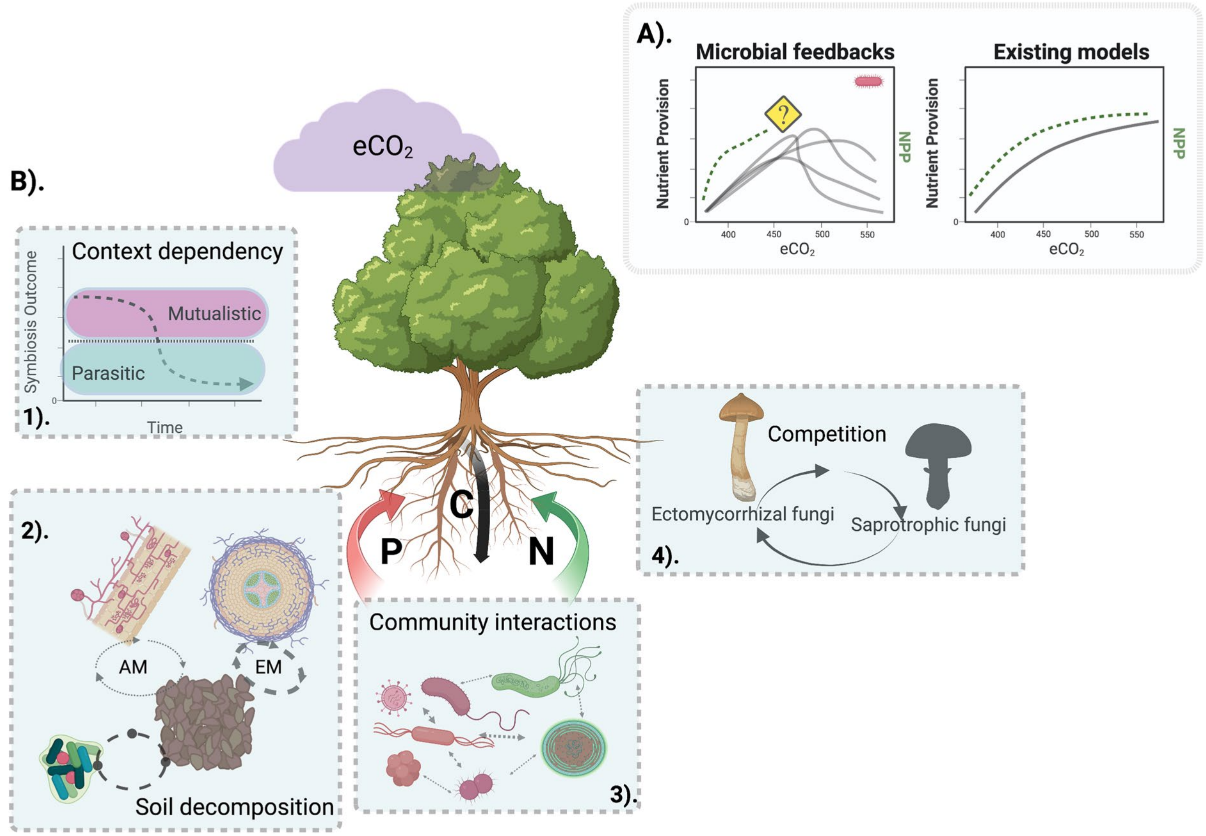

**Fig. 1** Microbially mediated processes that influence plant growth under elevated $CO_2$ **A**). Microbial interactions with nutrient availability (black lines) complicate representation of Net Primary Productivity (NPP; green dashes) with increasing atmospheric $CO_2$ (x-axis). The graph on the right depicts a cartoon representation of nutrient availability stimulating increasing NPP, as depicted in certain CMIP6 models. **B**). A subset of the multitude of microbial interactions that influence plant acquisition of Phosphorus (P) and Nitrogen (N) under elevated $CO_2$. Pathway 1). depicts potential shifts in the functioning of nutritional symbioses under new climatic contexts. This shift can apply to mycorrhiza, rhizosphere-associated bacteria or other endophyte assemblages 2). Rates of soil organic matter decomposition and nutrient release can be influenced by altered physiology of arbuscular (AM), ectomycorrhizal (EM) fungi, and other members of the soil microbiome 3). Microbial community interactions, such as altered growth rates, facultative and antagonistic interactions can alter enzyme release and nutrient release 4). Competitive dynamics between dominant fungal members of the soil microbiome such as EM and saprotrophic fungi, i.e. the 'Gadgil effect', can reduce nutrient availability and slow soil organic matter cycling

contingent on the activity and coordinated functioning of root and soil microbial communities (Fig. 1). However generalized responses across systems remain elusory. For example, contrasting impacts of $eCO_2$ are reported for soil microbial biomass (Castañeda-Gómez et al. 2021), microbial growth rates (Blagodatskaya et al. 2010), enzymatic activity (Thakur et al. 2019), functional genes (Yu et al. 2019) and microbial community composition (Chung et al. 2007). Altogether, these responses complicate the attempts to understand microbial mechanisms driving plant biomass and soil C responses under $eCO_2$.

A slew of recent work has interrogated some of the key microbial mechanisms governing plant growth responses to $eCO_2$, which when considered together provide essential context for the responses observed by Piñeiro et al. An influential meta-analysis by Terrer and colleagues, integrating evidence across more than 80 field studies, identified the primary role of mycorrhizal fungi in generating heterogeneous plant growth responses to $eCO_2$ (Terrer et al. 2016). Indeed, the modest plant biomass responses reported by Piñeiro et al., are consistent with this meta-analysis. Terrer et al., report that arbuscular mycorrhizal (AM) associated plants display neutral biomass responses to $eCO_2$, particularly under nutrient poor conditions. The understory plant communities studied by Piñeiro and colleagues are primarily associated with AM fungi and they are likely to strongly impact the findings of this study. AM fungi can acquire both mineral and organic forms of P with varying degrees of efficiency (Andrino et al. 2021) and AM acquisition of organic P, can be enhanced by co-occurring bacterial taxa (Jiang et al. 2020b), suggesting that plant P uptake is contingent on complex microbial interactions. Plant roots may directly mobilize organic and inorganic forms of P (Richardson et al. 2009) however the contribution of organic and inorganic P, as well as the relative reliance on AM for P acquisition is critically unknown. Under $eCO_2$ conditions, the plants communities studied in this *Eucalyptus* understory woodland, may be unable to acquire sufficient P to overcome P limitation, or alternatively, N to meet stochiometric demand.

In contrast plants associating with ectomycorrhizal (EM) fungi, a polyphyletic group of soil fungi that associate with the majority of tree stems worldwide (Steidinger et al. 2019), are found to exhibit positive biomass responses to $eCO_2$ (Terrer et al. 2016, 2021). There are multiple plausible mechanisms governing divergent responses between AM and EM associated plants. Unlike AM fungi, EM fungi can obtain organic forms of soil nitrogen from soil organic matter, thereby short-circuiting slow mineralization of inorganic N. Critically however, EM fungal lineages differ in their relative physiological capacity to obtain organic forms of N, potentially providing a microbe-centric explanation for the wide range of $eCO_2$ responses observed among trees associating with EM fungi (Lindahl and Tunlid 2015; Pellitier and Zak 2018). Pellitier et al., provide additional support for this mechanism as a primary axis responsible for alleviating reliance on inorganic N and fueling positive $eCO_2$ responses (Pellitier et al. 2021). In a temperate forest system, they demonstrated that EM communities with elevated genomic potential to degrade soil organic matter and access the organic N therein, fueled enhanced tree growth responses to increasing historic atmospheric $CO_2$. Studies of EM associated plants on P limited soils provide an important test of the primacy of organic N in these responses (Jiang et al. 2020b) but thus far remain limited in their capacity to infer the importance of EM organic N acquisition on plant growth.

Plants are well documented to increase root exudates in response to $eCO_2$, thereby stimulating rhizosphere activity. Rhizosphere stimulation could potentially manifest in increased or decreased nutrient uptake, however this cannot be effectively deduced in the present study. Piñeiro et al. record relatively minor shifts in rhizosphere enzyme activity. Similarly, this observation provides relatively minimal insight into underlying microbial community dynamics. Enzyme assays remain a coarse tool to probe shifts in microbial function, and large changes in microbial community composition and physiology could underpin even subtle enzymatic shifts. Although, Piñeiro and colleagues did detect substantial shifts in the activity of enzymes related to nutrient cycling, their hypothesis, that $eCO_2$ would alter or even increase enzyme activity is well founded (Phillips et al. 2011; Walker et al. 2021).

Mycorrhizal foraging and biomass may be augmented by increased photosynthate allocation under $eCO_2$ conditions (Treseder 2004). Increased hyphal biomass and enzyme activity are well documented, with possible increases to the efficiency of nutrient exchange per unit C (Field et al. 2012; Andrino et al. 2021). Elevated mycorrhizal colonization is plausible in the study however, interpreting the consequences of this on plant nutrition are complicated by the possibility that P amendments could also drive a reduction in colonization rates. Alterations to mycorrhizal foraging could have implications on whole microbial community interactions (Bahram et al. 2020). Microbial biomass may be stimulated with concomitant shifts in enzyme activity, and hormone and metabolite production (Drigo et al. 2008). Additionally, stimulated EM fungal growth could alter interaction dynamics between ectomycorrhizal fungi and free-living soil saprotrophic fungi, generating the so-called Gadgil effect. Competition for N and carbon substrate between these guilds could additionally impact nutrient cycling (Fernandez and Kennedy 2016) potentially leading to reduced N availability to plant hosts, generating a negative feedback and enhanced soil organic matter (SOM) sequestration. To our knowledge, this response has not been studied under $eCO_2$ conditions, but available evidence suggests that it is contingent on the taxonomic identity of ectomycorrhiza involved and on soil nutrient conditions (Fernandez et al. 2020). Finally, cryptic mycorrhizal like root-symbionts such as Mucoromycotina also colonize a wide array of plant roots, potentially including those studied here, and their activity and biomass can be bolstered under $eCO_2$ (Field et al. 2016).

Understanding key microbial interactions represents an important frontier in depicting soil N and P cycling under $eCO_2$. Immobilization of nutrients, particularly N, within fungal biomass has been reported in certain mycorrhizal systems, with the potential to exacerbate host nutrient limitation (Henriksson et al. 2021). The generality of this phenomena, as well as its relative importance on plant nutrition is uncertain, but rests on the assumption that fungal competition for inorganic nutrients will exhaust availability for plants (Alberton et al. 2007). This mechanism however, is challenged in light of the finding that EM fungi may be able to directly obtain organic forms of nitrogen from SOM (Lindahl and Tunlid 2015). Understanding the balance between microbial nutrient immobilization and provisioning over the long-term remains a central challenge (Cavicchioli et al. 2019). Altogether, available studies remain inconclusive on whether enhanced C allocation belowground may bolster N and P provisioning to the plant host.

## Belowground carbon dynamics under $eCO_2$

A particular strength of Piñeiro et al., is their joint focus on above and belowground biomass responses to $eCO_2$. The authors report both root and shoot responses, finding reduced belowground investment under $eCO_2$ across all treatment, especially under P amendment. The relative rapidity and strength of this response is notable given that it is a mixed understory plant community, which could have buffered this response, but may reflect the preponderance of fast-growing grasses present in the study. Moreover, this response may indirectly manifest from root-microbe interactions, in which a stimulated rhizosphere and mycorrhizal community reduce investment in root biomass. The consequences of increased exudates for fungal and bacterial members of the soil and root microbiome have been studied in a variety of systems, but the consequences for plant P and N acquisition remain poorly generalized (Jin et al. 2015). Depressed belowground investment under elevated $CO_2$ may be common, but studies that do not measure root turnover such as this one, may not adequately capture net C dynamics, because root-turnover can be elevated under $eCO_2$ conditions (Norby and Zak 2011).

In an effort to understand SOM dynamics and microbial activity, this study additionally reports whole-pot respiration responses at several time points across the course of the experiment. Using $CO_2$ flux measurements for the whole pot ‘ecosystem’, the authors suggest that gross primary productivity (GPP) was relatively unaffected by $eCO_2$, whereas net ecosystem sequestration was greatest under $eCO_2$ and P addition. This result could be due to reduced autotrophic respiration. It is important to note that root and microbial respiration cannot be disentangled using this approach. Some reports have shown that soil decomposition rates can be enhanced under $eCO_2$ due to microbial priming effects (van Groenigen et al. 2014). Recent efforts have clarified apparent context dependency in the response of soil C stocks to $eCO_2$. Terrer and colleagues (2021), used a meta-analytic framework to determine that soils dominated by AM associated plants exhibited relatively neutral C stock responses to $eCO_2$. In contrast SOM stocks may be reduced in soils dominated by EM associated plants. These contrasting responses to $eCO_2$ are thought to occur as a result of the unique capacity of EM fungi to produce extracellular enzymes that decay SOM. Certain studies are beginning to emerge that probe this possibility, however conflicting reports limit current generalizability (Lindahl et al. 2021; Argiroff et al. 2022).

## Going beyond, open questions and study areas for the field

### How are microbial physiology and community dynamics impacted by $eCO_2$, and what are the consequences for plant nutrient assimilation?

**Study approaches** The key microbial taxa responding to, and important in plant growth responses to increased $eCO_2$ can be identified using molecular network analysis. Identification of both fungi and bacterial taxa can be conducted using standardized metabarcoding approaches. Paired with statistical network analysis, community complexity, connectivity, modularity can be compared under different experimental treatments, such as water and nutrient availability. This approach was recently deployed in a long-term field based warming experiment carried out in a tallgrass prairie. In response to warming, community reorganization was observed with suggestions that the community was more robust, and certain ‘keystone’ taxa were identified (Yuan et al. 2021). These network analyses are correlational, and therefore cannot strictly identify microbial interactions per se (Yuan et al. 2021). Ultimately, understanding plant nutrient assimilation will be most powerful when network analyses are paired with measurements that link microbial function, nutrient mobilization and plant assimilation. Transcriptomic analyses that identify microbial activity in responses to plant stress (Malik et al. 2020) paired with enzyme assays and measurements of plant nutrient uptake could be suitable for this approach. Similarly quantitative Stable Isotope Probing (qSIP), represents one of many exciting opportunities to inform network properties, and identify key taxa that remain most active under $eCO_2$ (Hatzenpichler et al. 2020).

### How will mycorrhizal resource exchange dynamics shift in response to elevated $CO_2$?

**Study approaches** Mycorrhizal fungi exert a primary control on plant nutrient uptake, jointly impacting plant growth and soil C dynamics under $eCO_2$. This insight is primarily drawn from short-term manipulative field experiments; however, it is critically uncertain how mycorrhizal nutrient foraging and provisioning will shift over time. Nutrient-for-carbon exchange rates are liable to shift with climatic stressors via a variety of complementary pathways such as altered enzymatic expression, shifts in community composition, or altered competition dynamics with saprotrophic fungi. Non-linear feedbacks in plant-mycorrhizal exchange are likely, with the possibility that mycorrhiza, in particular EM fungi could exacerbate plant host nutrient limitation via immobilization of N in mycelial networks (Almario et al. 2022). Studying nutrient exchange in the mycorrhizal symbiosis is challenging, particularly under field conditions. To address this, manipulative greenhouse experiments could enable tracing P and N from both inorganic and organic soil compartments into fungal and plant biomass.

### Unearthing cryptic microbial interactions that influence $eCO_2$ responses

**Study context** Mycorrhizal fungi remain the overwhelming focus of studies on microbial-plant interactions in the face of $eCO_2$. However, a multitude of other microbes, such as free-living nitrogen fixing bacteria and foliar and root endophytes can also modify plant nutrition. For example dark-septate endophytes (DSE) can stimulate plant responses to $eCO_2$ (Alberton et al. 2010); similar to EM fungi, this response may also depend on increased organic N acquisition via extracellular enzymes that degrade recalcitrant organic matter (Hill et al. 2019). Similarly, in a soybean system exposed to $eCO_2$, (Christian et al. 2021) demonstrate a reduction in the colonization of a keystone bacterial foliar endophyte, reporting knock-on effects on inter-kingdom microbiome interactions between bacteria and fungi (2021). Studying cryptic microbial members and their role in plant nutrient assimilation represents a critical frontier.

### How can we align microbial processes into mechanistic models?

**Study approach** Identifying and quantifying molecular microbial traits involved in plant growth as well as the controls on the distribution of these traits, provides a tractable opportunity to incorporate microbial activity into ESM. Experimental studies such as the one discussed in this *Commentary* linked with microbe process-based measurements, such as enzyme activity, microbial community composition and function, using transcriptomic or metagenomic profiling, could build toward improving microbial representation in ESM. Field based studies that focus on multiple spatial grains of microbial functioning are essential as they can inform scaling functions needed for integration into ESM (Wan and Crowther 2022). Certain elements of the study by Piñeiro are particularly useful in that they focus on the understory plant community, which necessarily integrates across heterogeneous plant taxon responses, and can complement previous studies conducted at larger spatial scales (Jiang et al. 2020b).

## Concluding remarks

Overall, Piñeiro et al., detail the role of P availability in modulating plant growth responses to $eCO_2$ in a *Eucalyptus* woodland. This study confirms that the availability of soil nutrients constrains plant growth in a $CO_2$ enriched world. In this *Commentary* we highlight a range of microbial mechanisms that are liable to influence soil nutrient and soil C cycling, with plausible knock-on effects for plant growth under $eCO_2$ conditions. We describe a set of research areas where understanding of microbial dynamics can improve representation of plant growth responses to $eCO_2$. The central role of microbial communities in the persistence of the terrestrial carbon sink is clear; accurately constraining how soil C fluxes will respond to both warming, $eCO_2$ and other climatic disturbances represents a grand challenge for microbial and ecosystem ecology.

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