Tansley review

Plant phosphorus-use and -acquisition strategies in Amazonia

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Summary

In the tropical rainforest of Amazonia, phosphorus (P) is one of the main nutrients controlling forest dynamics, but its effects on the future of the forest biomass carbon (C) storage under elevated atmospheric CO_2 concentrations remain uncertain. Soils in vast areas of Amazonia are P-impoverished, and little is known about the variation or plasticity in plant P-use and -acquisition strategies across space and time, hampering the accuracy of projections in vegetation models. Here, we synthesize current knowledge of leaf P resorption, fine-root P foraging, arbuscular mycorrhizal symbioses, and root acid phosphatase and organic acid exudation and discuss how these strategies vary with soil P concentrations and in response to elevated atmospheric CO_2. We identify knowledge gaps and suggest ways forward to fill those gaps. Additionally, we propose a conceptual framework for the variations in plant P-use and -acquisition strategies along soil P gradients of Amazonia. We suggest that in soils with intermediate to high P concentrations, at the plant community level, investments are primarily directed to P foraging strategies via roots and arbuscular mycorrhizas, whereas in soils with intermediate to low P concentrations, investments shift to prioritize leaf P resorption and mining strategies via phosphatases and organic acids.

I. Introduction

The tropical rainforest of Amazonia provides significant global climate regulation services by sequestering carbon (C) in biomass, probably acting as a net C sink (Brienen *et al.*, 2015; Hubau *et al.*, 2020); this is possibly due to the CO_2 fertilization effect, which implies increased C uptake due to elevated atmospheric CO_2 concentrations (eCO_2) from anthropogenic activities (Walker *et al.*, 2021). However, the future of this biomass C sink remains unclear under eCO_2 and climate change, namely warming, changes in precipitation and increasing drought events (Phillips *et al.*, 2009; Zemp *et al.*, 2017; Sampaio *et al.*, 2019). Forest inventory data point to a potential saturation of the biomass C sink of Amazonia (Hubau *et al.*, 2020), while most dynamic vegetation models predict an increase in this C sink with eCO_2 (Fleischer *et al.*, 2019). Few of these vegetation models consider phosphorus (P) feedbacks,

though P is one of the crucial limiting nutrients for plant productivity (Vitousek *et al.*, 2010). The vegetation models that do consider P predict a significantly lower biomass C sink response to eCO_2 than those that do not (Fleischer *et al.*, 2019). In Amazonia, where very weathered and low-P soils characterize large areas, it is highly uncertain whether plants can meet the increased P demand for the projected biomass growth under eCO_2 conditions.

Plants only take up inorganic P (P_i) from the soil solution (available P_i) (Lambers, 2022). In young soils, P_i becomes available mainly through the weathering of parent material, and most of the total P (P_t) is lost or transformed to less available forms over geological timescales (Walker & Syers, 1976). Therefore, in highly weathered soils, only small amounts of P_i are available to plants, and most P is in organic forms (P_o) or bound to soil minerals or aluminum (Al) and iron (Fe) (hydr)oxides (Walker & Syers, 1976). In Amazonia, geological development has created soil P gradients (Quesada *et al.*, 2010, 2011). In the Andean Cordillera, in the western region, soils form mainly on younger geological substrates with soil P_t concentrations of up to 1000 mg kg^{-1} (Quesada *et al.*, 2010). By contrast, soils in central Amazonia vary in geological age but are highly weathered, with P_t concentrations ranging from 25 to 200 mg kg^{-1} (Quesada *et al.*, 2010). In the northern, southern and eastern regions, soils are formed predominantly on old, highly weathered parent material, with P_t concentrations rarely exceeding 200 mg kg^{-1} (Quesada *et al.*, 2010, 2011). Although large forest areas occur on soils with low P concentrations, the forests are highly productive (Quesada *et al.*, 2012).

Plants have adapted and evolved several strategies to cope with low P_i supply in soils (Lloyd *et al.*, 2001; Lambers *et al.*, 2008; Sánchez-Calderón *et al.*, 2010). They can increase their P-use efficiency by reducing their P requirement, optimizing P allocation and increasing the residence time of P, for instance by remobilizing P from senescing organs, including leaves, roots and the sapwood (Chapin III, 1980; Veneklaas *et al.*, 2012; Heineman *et al.*, 2016). They can enhance P_i acquisition by investing in absorptive roots and acclimating their root architecture and morphology to improve their P_i-foraging capacity and efficiency (Lynch & Brown, 2001; Lambers *et al.*, 2006). They can release phosphatase enzymes that mineralize P_o forms into available P_i (Nannipieri *et al.*, 2011) and release low-molecular-weight organic acids that can mobilize P_i and P_o from the soil matrix (Lambers *et al.*, 2006). Moreover, roots can interact with microorganisms such as fungi and bacteria in the rhizosphere, which might increase plant P_i availability and uptake (Box 1; Richardson & Simpson, 2011). Mycorrhizal fungi, in particular, can directly connect with plants by colonizing and acting as an extension of the roots, increasing soil surface area for P_i acquisition (Smith *et al.*, 2004).

The variation in plant P-use and -acquisition strategies among species and in communities depends on plant phylogenetic constraints, nutrient demand and supply, and environmental stimuli (Lambers *et al.*, 2008; Kramer-Walter *et al.*, 2016; Valverde-Barrantes *et al.*, 2016; Canarini *et al.*, 2019). Plant economic theory predicts that plants can adjust their internal resource allocation to acquire the most limiting resource (Bloom *et al.*, 1985). There is evidence that the energy costs of mechanisms and soil P concentrations can explain some of the variation in plant P-use and -acquisition strategies (Box 2; Lynch & Ho, 2005; Lambers *et al.*, 2008; Raven *et al.*, 2018). Plant communities shift and utilize different P-use and -acquisition strategies along soil P gradients, and in highly infertile soils, communities rely on a range of strategies (Zemunik *et al.*, 2015). Similarly, in the low-P soils of central Amazonia, plants have adopted multiple P_i-acquisition strategies to meet their P_i needs (Lugli *et al.*, 2020). However, there is no synthesized knowledge of how plant P-use and -acquisition strategies vary across soil P gradients in Amazonia.

Understanding the underlying mechanisms and variation in plant P-use and -acquisition strategies along soil P gradients is highly relevant to reliably project the resilience of Amazonia under climate change and eCO_2. Currently, projected P feedbacks to eCO_2 in Amazonia from process-based vegetation models diverge due to different representations of these plant strategies (Box 3; Fleischer *et al.*, 2019). Based on these model projections, the ability of plants to upregulate P-use and -acquisition strategies under eCO_2 is decisive for the future of Amazonia but remains unclear. Similarly, climatic changes have the potential to alter the structure

Box 1 Rhizosphere microorganisms and plant interactions.

Microorganisms (mycorrhizal and saprotrophic fungi, bacteria, archaea) constitute a significant pool of living biomass in soils. They may contain as much P as plant biomass (Turner *et al.*, 2013) and are the dominant metabolic machines driving organic matter decomposition and turnover, linking C and P cycling (Falkowski *et al.*, 2008). Specialized microorganisms can mobilize P_i through different pathways, such as exudation of phosphatase enzymes, organic acids and siderophores (Fe-chelating compounds; Khan *et al.*, 2014). By immobilizing P in their living biomass, the soil microbial community can act as a sink for P, and by remineralization after cell death, they can be a source of available P_i (Achat *et al.*, 2010). As microbial biomass P turns over rapidly, the dynamic exchange between the microbial biomass and the soil solution contributes significantly to replenishing P in the soil solution contributing to forest P nutrition (Achat *et al.*, 2010, 2012). Litter and soil organic matter availability, composition and stoichiometry can exert control over microbial activity (Mooshammer *et al.*, 2014). Under eCO_2, increased leaf P_i-resorption proficiency could decrease P returns for soil microbes and slow litter decomposition (Jin *et al.*, 2015). Increased plant investments in P acquisition under eCO_2, such as in longer and finer roots with faster turnover rates, increased root exudation of phosphatases, and labile C such as sugars and low-molecular-weight organic acids (LMWOAs), provide an easily available C source for microbial communities, stimulating their metabolic activity and biomass turnover (Spohn *et al.*, 2013; Jin *et al.*, 2014; but see Xu *et al.*, 2017). This stimulation of microbial activity has been related to increased P_o in the rhizosphere, which could contribute to enhancing plant P_i uptake under eCO_2 (Jin *et al.*, 2014). However, as microorganisms use plant-derived C sources, they may reduce the effectiveness of plant strategies to acquire P_i (Deubel & Merbach, 2005; Fujii *et al.*, 2012), which could be counteracted by increasing root surface area, for instance, increasing plant competitiveness for P_i in the solution. The methodological challenges associated with quantifying these interactions in the rhizosphere hinder our understanding and implementation of these dynamics in vegetation models (Deubel & Merbach, 2005).

Box 2 Costs of plant P_i use and acquisition.

The costs of plant P_i use and acquisition include resources allocated to the construction, function and maintenance of all the elements involved (Lynch & Ho, 2005). To improve tropical forest projections in vegetation models, a better understanding of these costs is essential, particularly the costs of C and N per P_i acquired and how they vary. Few studies have focused on this subject. For instance, Raven *et al*. (2018) estimated and compared the minimum C cost per P_i acquired via different strategies and discussed how they might vary. They proposed that the costs of acquiring P_i via foraging strategies increase with decreasing available soil P_i concentrations in the soil. At high soil P_i concentrations, the C cost per P_i acquired via roots and root hairs may be initially lower than via arbuscular mycorrhizal fungi (AMF) due to the high cost of P transport through hyphae. As P_i concentrations decline, the C costs of acquiring P_i via AMF become more competitive than those of roots, as hyphae can more efficiently explore large volumes of soils per unit of C invested (Raven *et al*., 2018). Similarly, with increasing concentrations of sorbed P in the soil, the C cost per P_i acquired via LMWOAs may decrease, as P_i return may increase, with roots probably being a more effective pathway than ectomycorrhizas (Raven *et al*., 2018). This relationship among soil P pools and the C costs of P_i acquisition can facilitate the implementation of these costs in vegetation models by making the C cost per P_i acquired a result of a function of soil P pools, for instance. A similar approach was taken by a nutrient uptake optimization model (FUN 3.0), which showed that C costs of acquiring P_i in dry tropical forests were about three times greater than those of temperate forests (Allen *et al*., 2020). However, the lack of data on C and P fluxes and pool dynamics related to different P-use and -acquisition strategies are still challenging the parameterization and validation of such modeling approaches.

Box 3 Plant P-use and -acquisition strategies in vegetation models.

Vegetation models differ in their representation of plant P-use and -acquisition strategies, while similarities can still be found. Leaf P_i resorption, for instance, is a fixed coefficient based on resorption efficiency, ranging from 50% to 75% (Fleischer *et al*., 2019). Resorption proficiency is a modeled outcome and can be benchmarked with field observations. So far, models neither consider nonlinear relationships of resorption efficiency with plant P stress nor energy costs. Fine root production based on fixed C allocation fractions is increasingly being replaced by dynamic modeling schemes considering resource availability and allometric relationships between roots and leaves (e.g. Thum *et al*., 2019). Currently, root P_i uptake from the soil solution is represented by functions of root biomass and parameters describing P_i-uptake efficiency or kinetics of uptake from the soil solution. Root exudation of phosphatases is represented implicitly as 'biochemical P mineralization', which can be upregulated under higher plant P demand and decouples P mineralization from organic matter decomposition (e.g. Goll *et al*., 2017). Similarly, root exudation of LMWOAs (or other exudates) is only implicitly represented in a few vegetation models, where P desorption is upregulated when plants experience P limitation (Fleischer *et al*., 2019). However, the benefits of P_i-mining strategies come at no cost for plants. Currently, there are emerging approaches to representing mycorrhizal P_i uptake explicitly. For instance, in the Coup-CNP model, plants allocate C to fungi as long as the P_i return is advantageous (He *et al*., 2021). The fungi can explore both the available P_i pool and P_o pool, but ultimately P_i uptake is limited by the fungal biomass (He *et al*., 2021). Moreover, vegetation models are designed for modeling large-scale vegetation dynamics; consequently, the challenge lies in finding generalities of microscale dynamics occurring at the root surface that allow upscaling along resource gradients and projecting impacts of global change at the ecosystem scale. Recently, more complex interactions between mineral surfaces, microorganisms and plants in their competition for P in the soil solution have been included (Zhu *et al*., 2016). However, such schemes require data for parameterization that may not be easily quantifiable in practice. Incomplete process understanding and a lack of data for parameterization contribute to uncertainties in P feedbacks to environmental change (Fleischer *et al*., 2019).

and functioning of Amazonia (Brando *et al*., 2008; Olivares *et al*., 2015); here, we focus on the effects of eCO_2 on plant P-use and -acquisition strategies that are currently considered in vegetation models, synthesize observational knowledge for model parameterization and benchmarking, and additionally inform future research.

We consider five strategies: leaf P_i resorption; root P_i foraging; arbuscular mycorrhizal fungal symbioses; and exudation of acid phosphatase enzymes; and low-molecular-weight organic acids (LMWOAs) (Fig. 1). Focusing on Amazonia, we discuss how plant P-use and -acquisition strategies vary with soil P concentrations and how eCO_2 may affect these strategies under low soil P availability in the short term (decades). We have categorized soil P_t concentrations and often refer to them as very high (> 800 mg P kg^{-1}), intermediate-high (800–501 mg kg^{-1}), intermediate-low (500–200 mg kg^{-1}) and very low (< 200 mg kg^{-1}). Although multiple P-use and -acquisition strategies can cooccur in individual plants and communities, we review them separately but discuss tradeoffs among root morphological traits and the strategies. Moreover, we suggest a conceptual framework for the relative distribution of plant P-use and -acquisition strategies along soil P gradients in Amazonia. Finally, we highlight critical knowledge gaps and measurements needed to deepen our understanding of variation in plant P-use and -acquisition strategies over space and time in Amazonia and improve their mechanistic representations in vegetation models.

II. Plant P-use and -acquisition strategies

Leaf nutrient resorption is an effective mechanism that increases plant nutrient-use efficiency, that is the biomass production per unit P taken up, by remobilizing nutrients from senescing leaves (Chapin III, 1980; Vitousek, 1982). Globally, it is estimated that leaf nutrient resorption supplies 31% of nitrogen (N) and 40% of plant P_i needs for new productivity; in tropical forests, resorbed P may supply up to 48% of P_i needs (Cleveland *et al*., 2013). Leaf nutrient resorption directly affects biogeochemical cycles, as nutrient concentrations in leaf litter affect decomposition rates (Box 1; Vitousek, 1984). Killingbeck (2004) suggested that the maximum nutrient resorption from leaves is probably a result of evolutionary processes and adaptations to biochemical limitations.

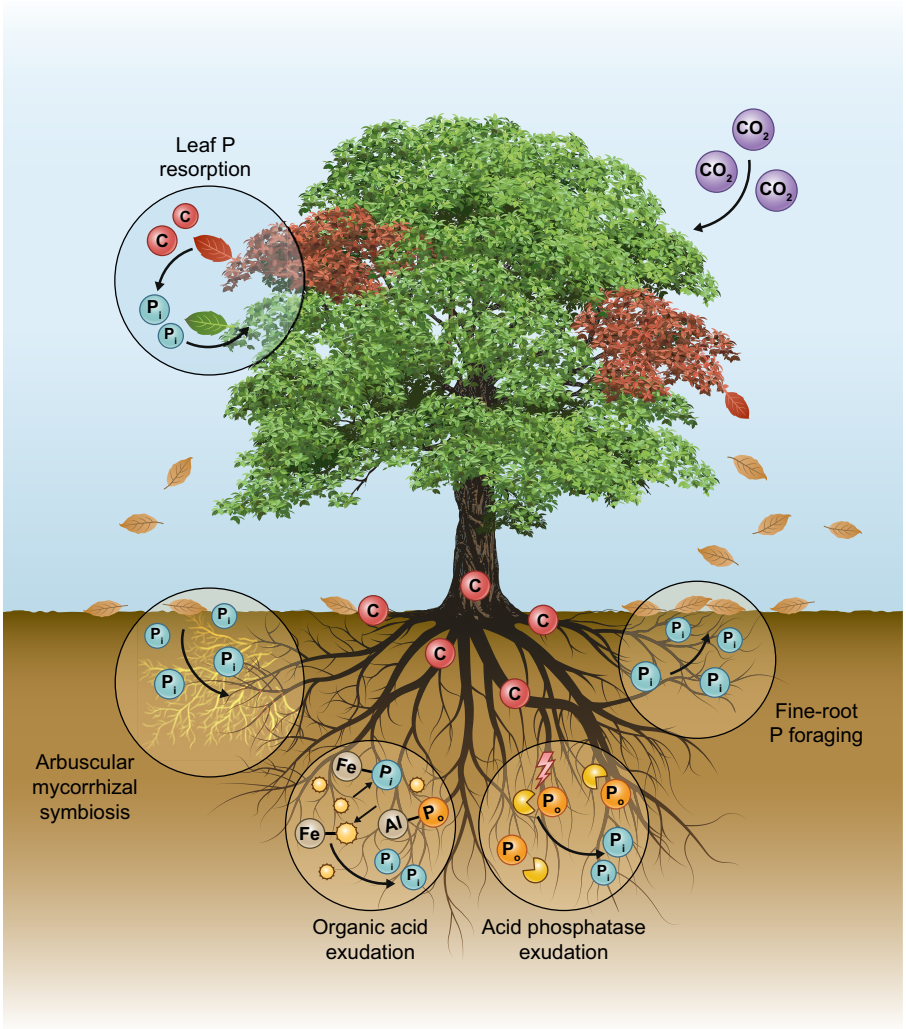

Fig. 1 Illustration of the plant P-use and -acquisition strategies reviewed in this study. Leaf P_i resorption is an indicator for plant P use; P is remobilized from senescing leaves before they fall and is reused in sink organs. Root P_i foraging can be characterized as the ability of the roots to find and explore soil P_i-rich patches. Arbuscular mycorrhizas act as an extension of absorptive roots and explore large volumes of soil in search of P_i in exchange for plant C. Acid phosphatases (yellow) are enzymes that mobilize P_i from organic compounds. Low-molecular-weight organic acids (yellow) exuded by roots can compete for and occupy sorption sites in the solid phase of the soil and form complexes with metals, increasing P_i and P_o dissolution, making P_i available for uptake, or P_o available for hydrolysis by phosphatases. Plants must allocate C to implement P-use and -acquisition strategies, which is commonly referred to as the 'C cost' or 'C investment'.

By contrast, the actual resorption of nutrients from leaves varies within the lifetime of a plant and depends on factors such as resource availability (water, nutrients, light), available energy and disturbances. Leaf nutrient resorption is typically discussed in terms of efficiency, the proportion of nutrients resorbed, or in terms of proficiency, the final concentration of nutrients that remains in senesced leaves as they are shed (Killingbeck, 1996). We focus on leaf P_i resorption in terms of proficiency, which is less prone to methodological bias than efficiency (Supporting Information Notes S1).

Fine roots are commonly defined as below 2 mm in diameter (but see McCormack *et al.*, 2015). In highly weathered soils, where P input from parent material is negligible, P typically accumulates in the topsoil; therefore, root traits and adaptations that improve topsoil exploration are advantageous (Lynch & Brown, 2001, 2008). In Amazonia, fine roots in the upper 30 cm of soil can account for more than 50% of the total fine-root biomass in the soil profile (Nepstad *et al.*, 1994; Trumbore *et al.*, 2006; Cordeiro *et al.*, 2020). In some nutrient-impoverished soils of Amazonia, fine roots can be densely concentrated in the litter layer on top of the soil, forming superficial root mats up to 50 cm thick (Stark & Jordan, 1978; Jordan & Escalante, 1980; Medina *et al.*, 1980), which is a highly efficient strategy to intercept nutrients and prevent leaching (Stark & Jordan, 1978; Martins *et al.*, 2021).

Fine roots can acquire P_i through strategies that can be classified as foraging and mining. Here, we define fine-root P_i foraging as related to the capacity of the roots to find and explore soil P_i-rich patches, which has been associated mainly to root architectural traits, such as branching intensity and angles, and morphological traits, such as root hairs, length, diameter, specific root length, specific root area and root tissue density (Lynch & Brown, 2001, 2008; Hodge, 2004). By contrast, fine-root P_i mining is related to the capacity of the roots to acquire P_i from less available forms, for instance through the release of phosphatases or organic acids. Here, we focus on fine-root morphological traits and consider tradeoffs among traits fostering different P_i-acquisition strategies.

Mycorrhizal fungi provide various benefits to plants in exchange for C, including nutrients, water and pathogen defense (Tedersoo *et al.*, 2020). Arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi are commonly associated with trees (Brundrett & Tedersoo, 2018). In tropical forests, AMF are the most abundant, widespread and critical fungi for plant P_i uptake (Smith & Smith, 1990; Wang *et al.*, 2017). Although ectomycorrhizas can efficiently mine P (Plassard *et al.*, 2011), they are more often related to N-poor

Box 4 Soil organic P and mineralization.

Phosphomonoesters and phosphodiesters are the most common forms of P_o in soils (Turner, 2008). Inositol phosphates, primarily phytate, are a more complex form of phosphomonoester, yet are an important fraction of soil P_o. Simple phosphomonoesters are hydrolyzed by phosphomonoesterases, the dominant class of phosphatases expressed in roots (Jarosch *et al*., 2019), while phytate can be hydrolyzed only by phosphatases known as phytases. By contrast, phosphodiesters must first be hydrolyzed by phosphodiesterase and subsequently by phosphomonoesterases to make P_i available (Turner, 2008). We currently know little about the variation in the composition of P_o compounds in Amazonian soils. In general, phytate seems to accumulate in some soils as it is strongly adsorbed to the soil matrix (Gerke, 2015b); consequently, phytate must be mobilized before hydrolysis. In a range of tropical soils, P_o mineralized by phytases accounted for 51% of all hydrolyzable P (Darch *et al*., 2016). By contrast, more labile phosphomonoesters can be more rapidly utilized by phosphomonoesterases (Turner, 2008). Nevertheless, a study considering various soil types, including ferralsols, indicated that the hydrolysis of phytate and phosphodiesters in the soil might be limited by enzymes, while the hydrolysis of phosphomonoesters might be limited by substrate (Jarosch *et al*., 2019), although it is unclear if the same pattern applies to the rhizosphere. Root phytase activity is a research topic that has been little explored in tropical forests. In a low-P Bornean tropical rainforest, P_i fertilization reduced root phytase activity significantly, suggesting that P-limited trees might depend on phytate as a P_i source (Yokoyama *et al*., 2017). In another experiment with four tropical plant species with contrasting P_i-acquisition strategies, the nonmycorrhizal Proteaceae species showed significantly higher phytate usage (Steidinger *et al*., 2014). This could be related to the ability of Proteaceae species to exude large quantities of LMWOAs, thus mobilizing phytate in the rhizosphere. Previous studies suggest that phytate may be an important P_i source, particularly in low-P soils where plants may exude LMWOAs at rapid rates, probably representing the P_i-acquisition strategy with the highest C cost (Turner, 2008).

soils, supporting plant N uptake (Stuart & Plett, 2020), and their role in tropical forests has received less attention compared with AMF. In the neotropics, nearly 80% of the tree species may form symbioses with AMF, while it is estimated that only 6% of the species form symbioses with ectomycorrhizas, and 19% in the paleotropics (Corrales *et al*., 2018). In Amazonia, ectomycorrhizas are considered rare but may play a significant role in white-sand forests on arenosols (Roy *et al*., 2016). Since little is known about the role of ectomycorrhizas in Amazonia, and arenosols may cover less than 3% of the area of the Amazon basin (Quesada *et al*., 2011), we focus on AMF.

Plant P_i uptake through the AMF pathway relative to the direct root pathway is highly variable (Smith *et al*., 2004; Nagy *et al*., 2009; Stonor *et al*., 2014). The presence of AMF can suppress or deactivate the expression of P_i transporters involved in direct root P_i uptake (Smith *et al*., 2004; Courty *et al*., 2016), but the mechanisms controlling P_i uptake through the AMF vs the root pathway are not completely understood (see Kobae, 2019). Like roots, AMF hyphae rely on specialized P_i transporters and can only take up available P_i (Saito & Ezawa, 2016). The capacity of AMF to support plant P_i uptake has often been related to their P_i-foraging efficiency. AMF hyphae have a potential soil exploration efficiency estimated to be six times greater than that of fine roots alone (McCormack & Iversen, 2019), and the P_i uptake capacity of AMF is positively correlated with the extraradical hyphal network surface area (Jakobsen *et al*., 1992). Moreover, AMF may also mobilize P_i from various pools, for example organic and sorbed P, and possibly apatite (Bolan *et al*., 1987; Yao *et al*., 2001; Andrino *et al*., 2019, 2021). Studies in tropical forests suggest that the litter layer may be an essential source of nutrients to AMF (Posada *et al*., 2012; Sheldrake *et al*., 2018). Possible mechanisms include the release of phosphatases (Sato *et al*., 2015; Zeng *et al*., 2018) or the stimulation of P-mobilizing bacteria (Box 1; Zhang *et al*., 2016; Jiang *et al*., 2021).

Phosphatase enzymes hydrolyze a wide range of substrates (i.e. phosphorylated organic compounds) (Box 4). In Amazonia, P_i availability decreases with the intensification of geological weathering, so that P_o hydrolyzed by phosphatase enzymes becomes an increasingly important source of P_i for plants (Quesada *et al*., 2010). The expression and exudation of phosphatases by microorganisms and plant roots is regulated by P_i demand and availability (McGill & Cole, 1981; Allison *et al*., 2010), but in some soils, enzyme expression may be constrained by N availability (Notes S2). Phosphatase activities depend highly on the concentration of the enzymes and the substrate and factors such as pH and temperature (Tabatabai, 1994). Rates are typically measured in laboratory assays, most determining the potential but not the actual field activity rates (Nannipieri *et al*., 2018). We focus on the root surface potential activity of extracellular acid phosphomonoesterase enzymes (PMEs), the class of phosphatases most widely studied in tropical forests (but see Box 4).

LMWOAs are C compounds containing one or more carboxyl groups (Ryan *et al*., 2001) and can originate from roots, microorganisms and organic matter in soils (Adeleke *et al*., 2017). In the soil, LMWOAs can occupy and compete for sorption sites and form complexes with Al and Fe (hydr)oxides at acidic pH or calcium at alkaline pH, preventing P sorption and accelerating desorption, making P_i available for uptake or P_o available for mineralization (Wang & Lambers, 2019). The rates of root LMWOA exudation are highly variable and depend mainly on the species (Jones, 1998), plant nutritional status (Lambers *et al*., 2006) and environmental stimuli (Canarini *et al*., 2019). The effectiveness of LMWOAs in mobilizing P in the soil increases with increasing LMWOA concentrations and differs among different LMWOAs (Jones, 1998; Adeleke *et al*., 2017). Dicarboxylates (malate, oxalate) and tricarboxylates (citrate) are often reported as most effective at mobilizing P, as they have a high affinity to sorption sites in the soil (Gerke, 2015; Darch *et al*., 2016), but in the soil solution, they may be rapidly biodegraded (Van Hees *et al*., 2002; Fujii *et al*., 2012), reducing their effectiveness (Box 1).

In extremely low-P soils, some species have developed specialized proteoid and dauciform roots, highly efficient in mobilizing P by accumulating and exuding large quantities of LMWOAs over a short period, resulting in very high LMWOA concentrations in the rhizosphere (Lambers *et al*., 2006). However, it remains unknown how frequently species forming such specialized roots occur and under what circumstances they are formed in Amazonia (Notes S3).

III. Soil P effects on plant P-use and -acquisition strategies

1. Leaf P_i resorption proficiency

Globally, at the plant community level, leaf P concentrations in senesced leaves consistently decline with declining soil P concentrations; that is, leaf P_i-resorption proficiency increases (Richardson *et al.*, 2005; Tang *et al.*, 2013; Hayes *et al.*, 2014). This phenomenon has been attributed to the plasticity of frequent species and species turnover along P gradients (Richardson *et al.*, 2005). The same pattern of leaf P_i-resorption proficiency has been observed along soil P gradients in the French Guianese and Colombian Amazonia (Lips & Duivenvoorden, 1996; Soong *et al.*, 2020), as well as other tropical forests (Fig. 2; Table S1; Vitousek, 1998; Hidaka & Kitayama, 2011; Tsujii *et al.*, 2017). For instance, along a soil P gradient in French Guiana (7–600 mg P_t kg^{-1}), P concentrations in senesced leaves varied approximately four-fold (Soong *et al.*, 2020). Moreover, several studies across Amazonia suggest a high variation in leaf P_i-resorption proficiency (Table S2). Measured P concentrations in senesced leaves can vary from 0.09 mg g^{-1} (Hättenschwiler *et al.*, 2008) to 0.75 mg g^{-1} (Dantas & Phillipson, 1989), while the average in tropical forests, as shown in a meta-analysis, is 0.4 mg g^{-1} (Yuan & Chen, 2009).

Soil P_i fertilization experiments additionally support the effect of soil P fertility on leaf P_i-resorption proficiency. A global meta-analysis showed that P_i fertilization increased P concentrations in senesced leaves by 82% (Yuan & Chen, 2015). Responses to P_i fertilization have not been reported in Amazonia; however, results from other tropical forests suggest that P_i-resorption proficiency may decrease in low-P soils with P_i additions, but not in high-P soils (Fig. 2; Table S3). In tropical forests with low-P soils in Hawaii, Indonesia and Ecuador, P_i fertilization significantly increased P concentrations in senesced leaves (Vitousek, 1998; Mirmanto *et al.*, 1999; Homeier *et al.*, 2012). In a tropical forest in Panama, with intermediate soil P_t concentrations, P_i fertilization slightly increased P concentrations in senesced leaves, but the differences were significant only for one out of four species (Mayor *et al.*, 2014). Moreover, in tropical forests with high-P soils in Hawaii and Costa Rica, P_i fertilization did not affect P concentrations in senesced leaves (Vitousek, 1998; Alvarez-Clare & Mack, 2015). Thus, plants may invest in leaf P_i resorption to conserve P only when soil P is scarce (Fig. 3). Studies suggest that the C and N costs of P resorption from leaves may increase with decreasing soil P concentrations, as plants in low-P soils achieve high proficiency by increasing P_i resorption from leaf fractions requiring hydrolysis, and thus investment in various enzymes (Hidaka & Kitayama, 2011; Veneklaas *et al.*, 2012; Tsujii *et al.*, 2017).

2. Root morphology and tradeoffs among P_i-acquisition strategies

Across Amazonia, root morphological traits vary significantly (Table S4), but their relationship with soil P concentrations remains mostly unclear. Root morphological traits such as length, specific root length, specific root area and root tissue density typically increase, while diameter decreases at the low end of a soil P gradient; thus, fine roots become thinner, longer and probably longer-lived (Lynch & Brown, 2001; Holdaway *et al.*, 2011; Kramer-Walter *et al.*, 2016). Nonetheless, high specific root length and specific root area were also observed in young soils (Holdaway *et al.*, 2011; Girardin *et al.*, 2013), which may be related to the acquisition of N (Freschet *et al.*, 2021). In different tropical forests, including forest sites in northeastern Amazonia, fine-root length, diameter, specific root length and specific root area followed the expected patterns (Table S1; Ostertag, 2001; Powers *et al.*, 2005; Metcalfe *et al.*, 2008; Zangaro *et al.*, 2008; Kochsiek *et al.*, 2013; Ushio *et al.*, 2015). Similarly, a meta-analysis of tropical forests worldwide showed that specific root length tended to be higher in sites with very low soil P_i availability (Addo-Danso *et al.*, 2020). By contrast, root tissue density did not change along a soil P gradient in Borneo (Ushio *et al.*, 2015), whereas in central Amazonia, it was positively correlated with available P_i, although the range of soil P variation was small (Lugli *et al.*, 2020). Despite the low data availability, changes in root morphological traits along soil P gradients suggest increased fine-root nutrient uptake capacity and increased soil exploration efficiency (C per length unit) with declining P_i availability (Fig. 2).

In tropical forests, soil P_i fertilization rarely affected root morphological traits (Fig. 2; Table S3). It neither affected fine root length along a soil chronosequence in Hawaii (Ostertag, 2001) nor various fine root morphological traits in central Amazonia and Panama (Yavitt *et al.*, 2011; Wurzburger & Wright, 2015), apart from increasing root diameter in central Amazonia, comparably the most P-impoverished forest (Lugli *et al.*, 2021). By contrast, in a subtropical forest in China, P_i fertilization significantly decreased root length (Liu *et al.*, 2015). This suggests that multiple nutrients may control fine root morphological traits (Wurzburger & Wright, 2015) or that these traits and their plasticity may be highly constrained by plant phylogeny (Holdaway *et al.*, 2011; Kramer-Walter & Laughlin, 2017; Valverde-Barrantes *et al.*, 2017). For instance, in a pot experiment with seedlings of 17 Amazonian species growing at different P levels, only a few species showed plastic responses in specific root length (Quintero-Vallejo *et al.*, 2015).

The distinction among plants that meet their P_i needs through fine root foraging, from those that outsource P_i uptake to mycorrhizal fungi, and those that actively mine P_i, is challenging based on root morphological traits alone. This distinction should be based on additional P_i-acquisition indicators, such as root elongation rate and hair density (Freschet *et al.*, 2021), and the tradeoffs among traits fostering different P_i-acquisition strategies. For instance, absorptive roots in low-P soils of central Amazonia have high specific root length and area and small diameter (Lugli *et al.*, 2020). Roots hosting AMF are often characterized by low specific root length and large diameter, as a large root cortical area might better accommodate fungal structures (McCormack & Iversen, 2019; Bergmann *et al.*, 2020); this suggests that most plants in low-P_i Amazonian soils might depend less on this strategy. However, it is unlikely that roots, such as those in central Amazonia, are primarily foraging for P_i; such a strategy would be costly and yield low P_i returns. Moreover, root phosphatase activity

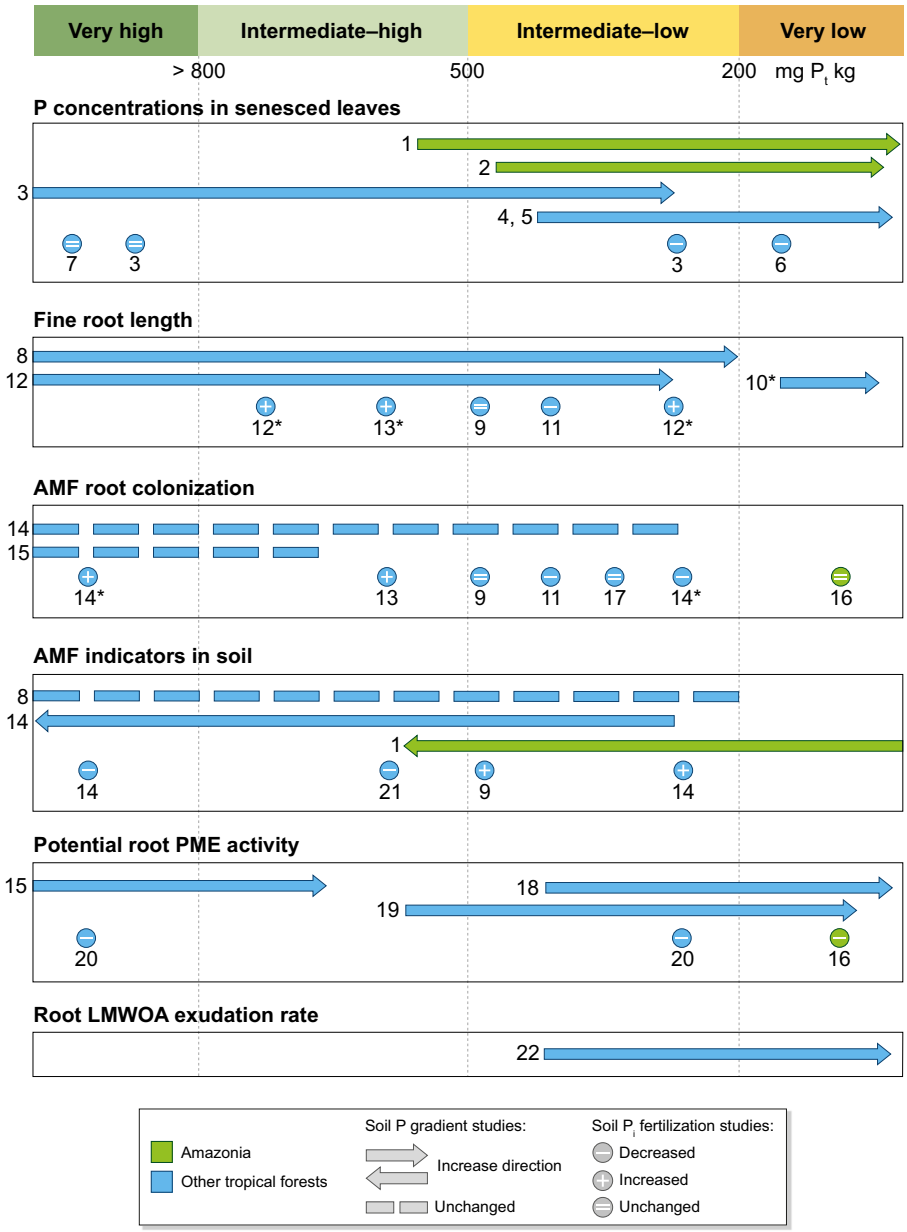

Fig. 2 A summary of some of the main soil P effects on different indicators of plant P-use and -acquisition strategies. AMF, arbuscular mycorrhizal fungi; PME, acid phosphomonoesterases; LMWOA, low-molecular-weight organic acids. AMF indicators in soil include measures of hyphal length, biomass or abundance. Arrows represent studies along soil P gradients, and the length of the arrow shows the extent of the gradient covered by the study, while the direction of the arrows determines whether a strategy increased or decreased with soil P. Symbols in the circles represent results from P_i fertilization experiments, and their placement indicates soil P_t concentrations in control plots. Note that the effects of soil P_i fertilization on different indicators could be influenced by the initial P_t concentrations and composition in soils, soil properties and the quantity and form of P added, which may vary among studies. We classified soil P_t concentrations as high (> 800 mg kg^{-1}), intermediate-high (800–501 mg kg^{-1}), intermediate-low (500–200 mg kg^{-1}) and very low (< 200 mg kg^{-1}). Numbers point to references that are summarized in Supporting Information Tables S1 and S3. References marked with an asterisk refer to results that showed tendencies, but differences were not statistically significant. [1]Soong *et al*. (2020); [2]Lips & Duivenvoorden (1996); [3]Vitousek (1998); [4]Hidaka & Kitayama (2011); [5]Tsujii *et al*. (2017); [6]Mirmanto *et al*. (1999); [7]Alvarez-Clare & Mack (2015); [8]Powers *et al*. (2005); [9]Camenzind *et al*. (2016); [10]Kochsiek *et al*. (2013); [11]Liu *et al*. (2015); [12]Ostertag (2001); [13]Wurzburger & Wright (2015); [14]Treseder & Allen (2002); [15]Nasto *et al*. (2014); [16]Lugli *et al*. (2021); [17]Camenzind *et al*. (2014); [18]Ushio *et al*. (2015); [19]Cabugao *et al*. (2017); Cabugao *et al*. (2021); [20]Treseder & Vitousek (2001); [21]Sheldrake *et al*. (2018); [22]Aoki *et al*. (2012).

was positively correlated with specific root length and area in central Amazonia and other tropical forests (Ushio *et al.*, 2015; Lugli *et al.*, 2020; Cabugao *et al.*, 2021). Similarly, root organic acid exudation rates were positively correlated with specific root area in tropical forests in Borneo (Aoki *et al.*, 2012; Fujii *et al.*, 2021). These results suggest that long and fine roots in low-P Amazonian soils are primarily mining P_i to meet their needs. We speculate that along soil P gradients in Amazonia, independent fine-root P_i foraging would be a viable primary strategy for plants in soils with high P_i availability (Fig. 3). In such soils, fine-root P_i foraging is probably

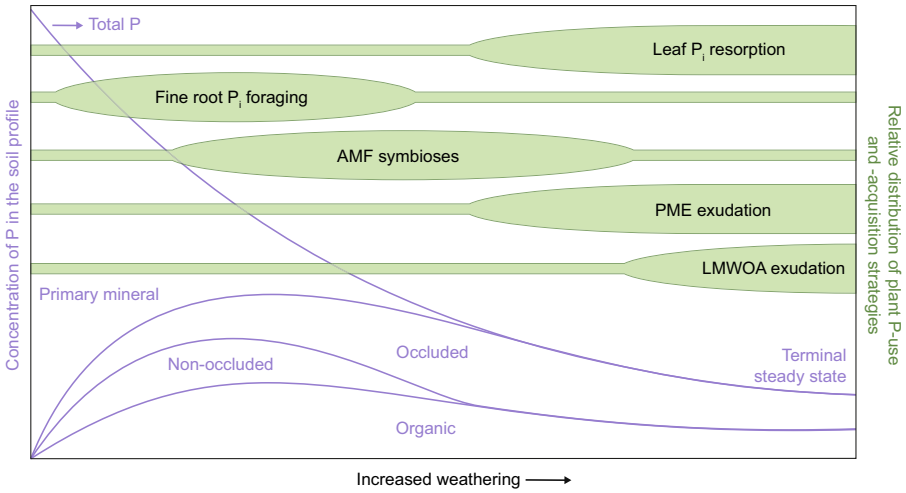

Fig. 3 Conceptual representation of the predicted distribution in plant phosphorus (P)-use and -acquisition strategies at the plant community level along soil P gradients in Amazonia. The elongated green bubbles represent where, along a soil P gradient, the respective strategies receive the most resource investments from plant communities and where they contribute the most to meet plant P_i needs, as they offer advantages under those soil conditions. The conceptual framework was built upon our synthesis and extending previous work on how plant P_i acquisition may vary along soil nutrient gradients (see Lambers *et al*., 2008). We predict that P_i foraging by independent fine roots or in symbioses with arbuscular mycorrhizal fungi (AMF) are primarily used in soils with intermediate to high soil P concentrations. By contrast, mining strategies, namely exudation of phosphomonoesterase enzymes (PMEs) and low-molecular-weight organic acids (LMWOAs), along with finer and longer roots, are prioritized in soils with low to intermediate P concentrations. Similarly, leaf P_i resorption is increasingly relevant at the low end of the soil P gradient. The image was modified from Turner & Condron (2013) based on the Walker & Syers (1976) model of soil P changes with long-term soil development and supported by soil P data throughout Amazonia (Quesada *et al*., 2010).

achieved by constructing short-lived roots that may cost more C per unit of soil explored, compared with low-P soils, but yield high P_i returns, as they can quickly move further from the root P-depletion zone (see Aragao *et al*., 2009; Lugli *et al*., 2021).

3. Arbuscular mycorrhizal fungi

The abundance of AMF in roots (intraradical colonization) is commonly indicated by the percentage root length colonized by fungal structures. Although this measure is often considered an indicator for plant benefits, it requires careful interpretation, as differences can arise from the level of AMF abundance and/or standing root length (Allen, 2001; Treseder, 2013). Moreover, fungal structures along the root length may not contribute equally to resource exchange, depending on the age of the structures (Tisserant *et al*., 1996). Nonetheless, a meta-analysis showed percentage root length colonized by AMF explained 23.5% of the changes in plant P content (Treseder, 2013). In contrast to the expectation that AMF root colonization increases with decreasing soil P concentrations, we found no consistent patterns in tropical forests (Fig. 2; Table S1). Along soil P gradients in Hawaii and Costa Rica, AMF root colonization was unchanged (Treseder & Allen, 2002; Nasto *et al*., 2014). On the other hand, in southwest Brazil, root AMF colonization increased with decreasing P_i availability, although forest sites had different succession stages, and root AMF colonization also increased with decreasing succession stage (Zangaro *et al*., 2008).

AMF measures of soil colonization (i.e. extraradical hyphal length, biomass or abundance) could be an excellent complementary indicator of AMF P_i-uptake capacity (see Jakobsen *et al*., 1992; Sheldrake *et al*., 2018). Along soil chronosequences in Hawaii and Australia, AMF extraradical hyphal length and biomass decreased with decreasing soil P concentrations (Table S1; Treseder & Allen, 2002; Balser *et al*., 2005; Teste *et al*., 2016). A similar pattern emerged along a soil P gradient in French Guiana, where AMF abundance in soil declined with declining soil P_t concentrations (Soong *et al*., 2020). These previous studies support the soil P control on AMF abundance and functioning and suggest that AMF may play a smaller role in soils with very low P concentrations (Treseder & Allen, 2002). By contrast, in a study including forest sites in Peru, Panama and Costa Rica, mostly in high-P soils, AMF extraradical hyphal length was not affected by soil P (Powers *et al*., 2005). Hyphal length in soils was much lower than in other tropical forests and ecosystems, and various sites did not contain hyphae in the soil, particularly in Panama, suggesting that plants may meet their nutrient needs exclusively through roots (Powers *et al*., 2005). However, that is contradictory to later studies conducted in the same area in Panama, suggesting AMF are abundant both in roots and in soil (Wurzburger & Wright, 2015; Sheldrake *et al*., 2018).

Responses of AMF to soil P_i fertilization varied in tropical forests (Fig. 2; Table S3). In soils with intermediate to very low P_t concentrations, the percentage root length colonized by AMF was unchanged or decreased in response to P_i fertilization. In central Amazonia and Ecuador, P_i fertilization did not change root colonization by AMF (Camenzind *et al*., 2014, 2016; Lugli *et al*., 2021), while it decreased in Hawaii and subtropical China (Treseder & Allen, 2002; Liu *et al*., 2015). By contrast, in soils with intermediate to very high P_t concentrations in Hawaii and Panama, AMF root colonization increased (Treseder & Allen, 2002; Wurzburger & Wright, 2015). Moreover, in soils with

intermediate to very high P_t concentrations in Hawaii and Panama, P_i fertilization decreased AMF extraradical hyphal length and biomass, suggesting that plants shifted strategies to rely more on their roots to acquire P_i, probably through foraging (Fig. 2; Treseder & Allen, 2002; Sheldrake *et al.*, 2018). By contrast, AMF extraradical indicators increased in soils with low P_t concentrations in Hawaii and Ecuador (Fig. 2; Treseder & Allen, 2002; Camenzind *et al.*, 2016), suggesting plants increased investments in AMF symbioses when P_i availability increased.

Overall these studies corroborate that at the plant community level, AMF symbioses may be a more beneficial P_i acquisition strategy for plants in soils with intermediate P_i concentrations (Fig. 3), as suggested in previous studies (Treseder & Allen, 2002; Lambers *et al.*, 2008). This may be due to AMF and plants being limited by P in low-P soils, and, by contrast, AMF being limited by C in high-P soils due to decreased C investments by plants (Treseder & Allen, 2002). The decrease in C investments in high-P soils could be caused by interactions with low N, for example in young soils, as N can limit C uptake, increasing C trade costs for P (Johnson, 2010). This has been supported by evidence in a dune chronosequence in Australia and in rupestrian grasslands in Brazil, where the number of plants associated with AMF declines significantly with decreasing soil P concentrations (Oliveira *et al.*, 2015; Zemunik *et al.*, 2015, 2018).

4. Root acid phosphatase exudation and activity

Root PME exudation and activity, although variable among species (Ushio *et al.*, 2015; Png *et al.*, 2017), are highly responsive to changes in plant P demand and soil P_i availability. These direct plant responses are well established; increasing soil P_i availability often represses PME expression and activity (Tian & Liao, 2018; Wang & Liu, 2018). Accordingly, root PME activity was negatively correlated with soil P_i availability in tropical forests in Costa Rica, Borneo, Puerto Rico and Panama (Nasto *et al.*, 2014; Ushio *et al.*, 2015; Cabugao *et al.*, 2017, 2021; Guilbeault-Mayers *et al.*, 2020). However, for Amazonia, there are currently no published studies on how root PME activity varies across soil P gradients. In central Amazonia, root PME activity varied between 15 and 65 μmol 4-methylumbelliferyl-P g^{-1} fine-root h^{-1} (Lugli *et al.*, 2020), which is similar to what was observed in tropical forests in Puerto Rico and Borneo with a similar range of soil P_t concentrations (Kitayama, 2013; Cabugao *et al.*, 2017), but higher than in more fertile soils in Costa Rica and Puerto Rico (Table S5; Nasto *et al.*, 2014; Cabugao *et al.*, 2017).

In P_i fertilization experiments, root PME activity consistently decreased, following the expected inverse relationship with increasing P_i availability (Marklein & Houlton, 2012). In central Amazonia, P_i fertilization significantly decreased root PME activity by 23% (Lugli *et al.*, 2021). The same trend was observed in other tropical forests; root PME activity in response to P_i fertilization decreased by *c.* 37% and 46% in Hawaii and Borneo, respectively (Treseder & Vitousek, 2001; Yokoyama *et al.*, 2017). Consistent with observations along soil P gradients, the results from P_i fertilization experiments additionally support the control of soil P on root PME activity.

Variation in root PME activity is also expected to be partially controlled by substrate concentrations. Along a soil P gradient in a Bornean tropical forest, root PME activity showed a strong negative relationship to the most labile form of P_o, but not total P_o in the soil (Kitayama, 2013). Similarly, there was no relationship between total soil P_o and root PME activity along a soil P gradient in Puerto Rico (Cabugao *et al.*, 2021). The lack of relationship between total soil P_o and root PME activity might be explained by the composition of the soil P_o pool. For instance, phytate is strongly adsorbed to the soil matrix and can only be mineralized by phytases (Box 4; Gerke, 2015a). It is therefore plausible that root PME activity was only correlated with the most labile form of P_o in the soil since simple forms of P monoesters hydrolyzed by PMEs are more labile than phytate, which is not hydrolyzable by PMEs (Gerke, 2015b). Moreover, substrate availability probably affects the plant C and N costs per P_i acquired through PMEs; root PME activity increases with substrate availability, probably increasing the cost–benefit ratio of this strategy. Overall, we expect higher rates of PME activity in soils with low P_i availability and a high proportion of substrate, as PME expression is driven by P_i demand and supply, and the rate of activity may be determined by substrate concentrations (Fig. 3).

5. Root low-molecular-weight organic acid exudation

Rates of root LMWOA exudation in various plant species have mostly been measured in controlled environments and are commonly greater under low soil P_i supply; these findings have been extensively reviewed in the literature (Jones, 1998; Gerke, 2015a; Adeleke *et al.*, 2017; Wang & Lambers, 2019). Similarly, an increase in the abundance of species that appear to rely on LMWOA exudation for P_i acquisition has been observed with declining soil P concentrations in different ecosystems (Oliveira *et al.*, 2015; Zemunik *et al.*, 2015, 2018). However, studies investigating rates of root exudation of LMWOAs in natural ecosystems remain rare due to the inherent challenges in collecting exudates in the field (Oburger & Jones, 2018). To date, only one study has investigated root LMWOA exudation rates along a soil P gradient in a tropical forest (Fig. 2; Aoki *et al.*, 2012; see also Fujii *et al.*, 2021). Total LMWOA exudation varied with species but increased with decreasing soil P_t concentrations, with rates of citrate exudation alone up to 1648 nmol C g^{-1} root h^{-1} from a Myrtaceae species in the poorest forest (Aoki *et al.*, 2012), which may be similar to rates of citrate exudation in proteoid roots of *Lupinus albus* reported in different studies (Roelofs *et al.*, 2001 and references therein).

Concentrations of LMWOAs are thought to be high in soils dominated by organic and adsorbed P, such as highly weathered tropical soils (Aoki *et al.*, 2012; Darch *et al.*, 2016). In tropical soils, the efficacy of LMWOAs seems to be site-dependent; low concentrations of citric acid (10 μmol g^{-1} soil) were able to mobilize up to 8.06 mg P_t kg^{-1} (Darch *et al.*, 2016). In low-P soils in subtropical China, citric, malic and oxalic acids significantly mobilized P_i and P_o, although P_o more effectively (Hou *et al.*, 2018). In another study, low concentrations of citric acid significantly mobilized P_o but not P_i (Wei *et al.*, 2010). Hence, the exudation of LMWOAs in tropical

soils might be an efficient strategy even without cluster-root formation, and may be particularly important to mobilize P_o (Andrade *et al.*, 2003; Gerke, 2015a; Darch *et al.*, 2016). Although no study has investigated the role of LMWOAs in Amazonia, given observations from other ecosystems and under controlled conditions, we expect faster rates of LMWOA exudation in highly weathered Amazonian soils, where a greater proportion of P_t is adsorbed to the soil matrix (Fig. 3).

IV. Elevated CO_2 effects on plant P-use and -acquisition strategies

1. Leaf P_i resorption proficiency

Only a few experiments have investigated leaf P_i resorption under eCO_2. Of these, most experiments have been performed in temperate regions, where P concentrations in fully senesced leaves have not changed or have declined only slightly and not significantly (Finzi *et al.*, 2001; Frost & Tuchman, 2005; Zheng *et al.*, 2010; Dray *et al.*, 2014). The lack of response to eCO_2 in temperate regions may have occurred because the plants were not limited by P. However, in free-air CO_2 concentration enrichment (FACE) studies in a eucalypt forest in Australia (EucFACE, Crous *et al.*, 2019) and in shrubs in the Mojave Desert (Housman *et al.*, 2012), both ecosystems considered to be P-limited, no significant changes in leaf P resorption were observed under eCO_2. In the EucFACE, very low P concentrations were found in senesced leaves (0.32 ± 0.04 mg g^{-1}); this very high proficiency could mean that the trees had already reached maximum leaf P_i resorption levels (Crous *et al.*, 2019). Similarly, plants in the most P-poor soils of Amazonia may be unable to upregulate leaf P_i resorption further in response to eCO_2, as the reported proficiency may be near their maximum (Table S2). Therefore, the potential to upregulate leaf P_i resorption in response to eCO_2 might be limited to relatively more fertile regions of Amazonia, where plants have not yet reached their maximum resorption proficiency.

2. Root morphology

Most root morphological traits have received very little attention in eCO_2 studies, with fine root length being the most commonly measured root trait. Overall, fine root diameter and length responded positively to eCO_2 across various plant types and ecosystems and increased by 8% and 26%, respectively (Nie *et al.*, 2013). Similarly, a meta-analysis including mostly crop species grown under eCO_2 indicated that soil P did not affect root length responses to eCO_2, and, overall, root length increased (Jiang *et al.*, 2020a). It is worth noting that soil P concentrations classified as low in the previous analyses may vary (Jiang *et al.*, 2020a). Consistent with the previous studies, in glasshouse experiments with tropical species in fertilized and unfertilized low-P soils (soil P concentrations not provided), community-level root length increased by *c.* 50% under eCO_2 independent of the soil P level (Körner & Arnone, 1992; Arnone III, 1997). However, at low P, root proliferation towards artificially created nutrient-enriched soil patches was unchanged, and it was suggested that root foraging efficiency did not increase under eCO_2 (Arnone III, 1997). The interactive effects of soil P concentrations and eCO_2 on root morphological traits in tropical species remain uncertain; however, species-specific responses are expected. Overall, root length shows potential for upregulation by plants under eCO_2 in Amazonia. However, in very low-P Amazonian soils, roots may already be highly efficient at exploring the soil, and root productivity is limited by P (Lugli *et al.*, 2021); hence, responses at the community level might be less pronounced than in relatively more fertile soils.

3. Arbuscular mycorrhizal fungi

Globally, mycorrhizas have the potential to moderate the CO_2 fertilization effect on plant growth through their role in nutrient acquisition (Terrer *et al.*, 2019). Although less representative of tropical ecosystems, several meta-analyses showed eCO_2 promoted positive responses of various measures in host plants and AMF abundance in roots and soil (Table S6; Treseder, 2004; Alberton *et al.*, 2005; Terrer *et al.*, 2016; Dong *et al.*, 2018). Nonetheless, responses were highly variable, depending on the combination of plant and mycorrhizal species and P_i supply (Dong *et al.*, 2018). Under eCO_2, low P_i availability constrained the extraradical hyphal length, while no significant differences were observed in soil fungal biomass or root colonization (Dong *et al.*, 2018). Similarly, in a P-limited eucalypt forest (EucFACE), eCO_2 appeared to have prompted only a slight increase in plant C investments in mycorrhizas, which resulted in a small nonsignificant increase in the mycorrhizal C pool (Jiang *et al.*, 2020b).

Our understanding of the eCO_2 effects on AMF in tropical species is restricted to small-scale experiments with immature plants. In a seedling experiment with four tropical species, root length colonized by AMF increased in response to eCO_2 in intermediate- and high-fertility treatments but not in low-fertility treatments (Nasto *et al.*, 2019). Additionally, responses were species-specific, and mostly driven by one of the species, considered a low-P specialist in Panama (Nasto *et al.*, 2019). Moreover, in an artificial glasshouse tropical system with seven species, no hyphal growth or root colonization was observed in response to eCO_2, although these plants were regularly fertilized (Insam *et al.*, 1999). Overall, AMF responses to eCO_2 seem to be species-specific and may be constrained in soils with very low P concentrations. Therefore, at the community level, the positive effects of eCO_2 on AMF are expected to be more pronounced in Amazonian soils with intermediate to high P concentrations. This is in line with the observations that AMF functioning may already be constrained by low P or other nutrients in low-P soils at current CO_2 levels (Treseder & Allen, 2002; Wurzburger & Wright, 2015; Lugli *et al.*, 2021).

4. Root acid phosphatase exudation and activity

Only a few studies have investigated root PME activity under eCO_2, and responses were weak. In the P-limited EucFACE, no changes were detected in root PME activity under eCO_2 (Ochoa-Hueso *et al.*, 2017). Similarly, in *Pinus densiflora* seedlings, root PME activity was unaffected by eCO_2 independent of P supply

treatment (Norisada *et al.*, 2006), and in seedlings of *Pinus ponderosa*, root PME activity decreased (DeLucia *et al.*, 1997). Moreover, among seedlings of four tropical species, eCO_2 induced an overall increase in root PME activity, which was mainly driven by two N_2-fixing species, suggesting the strength of the eCO_2 effect on this strategy in tropical forests might depend on community species composition (Nasto *et al.*, 2019). However, root PME activity responses to eCO_2 will additionally depend on changes in the quantity and quality of organic matter inputs. While increased plant C availability may increase root PME expression, the actual efficacy of these enzymes will depend on the substrate available. For instance, at EucFACE, leaf litter input and quality did not change significantly under eCO_2 (Crous *et al.*, 2019; Jiang *et al.*, 2020b). An increase in root PME activity in Amazonia in response to increased P demand under eCO_2 is more likely to occur in soils where organic matter is the most dominant P source for plants. Upregulating PME expression may increase plant competitiveness for P_o, while higher litter inputs may favor PME activity, but lower litter quality may constrain this response.

5. Root low-molecular-weight organic acid exudation

A recent meta-analysis including various model plants, crops and *Pinus* species showed that exudation of LMWOAs significantly increased in response to eCO_2 (Dong *et al.*, 2021). However, few studies have focused on the interactive effects of eCO_2 and soil P concentrations on LMWOA exudation. For instance, citrate exudation in *Lupinus albus*, a species that forms proteoid roots, tended to increase under eCO_2 in plants with a low P_i supply compared with that in plants with a high P_i supply, but differences were not significant (Campbell & Sage, 2002; Wasaki *et al.*, 2005). There is currently a small amount of data to speculate on how eCO_2 may change root LMWOA exudation in Amazonia. However, considering the overall positive responses (Dong *et al.*, 2021) and assuming plant C uptake will increase due to increased photosynthetic rates, increases in root LMWOA exudation are expected under eCO_2, particularly in the most weathered Amazonian soils, where this strategy might offer more advantages. Since a high proportion of P_t in low-P Amazonian soils is in less available forms, root exudation of LMWOAs may be one of the most critical strategies for plants under eCO_2. Moreover, a possible increase in root length density and overlap under eCO_2 might cause an increase in LMWOA concentration in the rhizosphere, further enhancing the positive effects of increased exudation by individual roots (Dong *et al.*, 2021).

V. Discussion and conclusions

Based on our synthesis, we provide a conceptual framework on the relative importance of five plant P-use and -acquisition strategies that work in concert at the plant community level to supply the plants' P_i needs along soil P gradients in Amazonia (Fig. 3). Our conceptual framework builds upon previous work on how P_i-acquisition strategies may vary with soil age (see Lambers *et al.*, 2008) and extends it to include other P_i-use and -acquisition strategies, but focuses mainly on tropical forests across Amazonia. We further speculate on the response of these strategies to eCO_2. In summary, we found that:

(**1**) Leaf P_i-resorption proficiency consistently increases with decreasing soil P concentrations. P_i fertilization causes a rapid negative response in leaf P_i resorption in low-P soils, suggesting this strategy may be energy costly and increasingly relevant in low-P soils. Under eCO_2, leaf P_i resorption was unaffected in low- and high-P soils, possibly because in low-P soils, maximum resorption rates were reached. By contrast, in high-P soils, increasing resorption may be more energy costly than acquiring P_i from the soil. We expect the same pattern in Amazonian soils, so that in soils with intermediate P concentrations, changes in leaf P_i resorption may be more notable under eCO_2.

(**2**) Most studies suggest root nutrient uptake capacity and exploration efficiency (i.e. root length and specific root length) increase as soil P concentrations decline across soil P gradients. However, most root morphological traits did not significantly respond to P_i fertilization, suggesting they may be limited by multiple nutrients or phylogeny. Trade-offs among morphological traits fostering other P_i-acquisition strategies suggest fine-root P_i foraging may be more relevant at higher P_i availability, where roots can rapidly move past the P-depletion zone. Under eCO_2, root length showed high potential for upregulation, including under soil P conditions reported as low. Therefore, we expect that eCO_2 may increase root length in vast areas of Amazonia if roots have not yet reached their maximum length.

(**3**) Root length colonized by AMF does not show consistent patterns in response to soil P changes, while AMF abundance in soil mostly increased with increasing soil P concentrations. Results from P_i fertilization studies suggest AMF symbioses may be an essential strategy for plants in soils with intermediate P concentrations. Under eCO_2, responses of extraradical hyphae in soil were constrained by low soil P concentrations; thus, we expect notable plant investments in this strategy in Amazonian soils with intermediate and towards high P concentrations, but not in soils with very low P concentrations.

(**4**) We found a consistent pattern that potential root PME activity increased with decreasing soil P concentrations, but actual activities and PME efficacy at field conditions remain unknown. We speculate that this strategy is highly relevant for plants growing in soils with low P_i availability and high substrate availability. Root PME activity in most studies did not respond strongly to eCO_2, although some species showed increased potential for upregulation. Hence, we expect an increase in PME expression for some species in Amazonia under eCO_2, but PME efficacy might depend on substrate availability.

(**5**) Root LMWOA exudation rates increased with decreasing soil P concentrations in a tropical forest, following a trend observed in various species and other ecosystems. Therefore, we predict that LMWOA exudation is essential in highly weathered Amazonian soils, where most soil P is in less available forms, giving plants a competitive advantage. Under eCO_2, root LMWOA exudation often increased, but interactions between eCO_2 and soil P remain mostly uncertain. In Amazonia, this strategy may have the greatest potential to mobilize significant P amounts under eCO_2, especially on the low side of the soil P gradient. However, the efficacy of this

strategy may depend on the interplay of roots and rhizosphere microorganisms.

Overall, our review provides evidence that community-level patterns in the investment and the relative importance in plant P-use and -acquisition strategies may exist across soil P gradients in Amazonia and possibly other tropical forests (Figs 2, 3). These patterns may result from species composition and functional trait turnover along soil gradients, as some species have adapted to different nutrient conditions (Condit *et al.*, 2013; Umaña *et al.*, 2021). Although highly variable among species, we also show that most plants have some degree of plasticity to upregulate P-use and -acquisition strategies under eCO_2. However, in Amazonia, upregulation under eCO_2 may be constrained under a very low P_i supply, as plants are already highly efficient at using and acquiring P_i. In the short term, as P demand for biomass increases due to the CO_2 fertilization effect, plants may also shift C investments to other P_i-use and -acquisition strategies that may have a better cost-to-benefit ratio (e.g. DeLucia *et al.*, 1997). In the long term, eCO_2 may induce gradual changes in species composition by favoring species that are better adapted in terms of P-use and -acquisition efficiency (see Turner, 2008; Turner *et al.*, 2018; Esquivel-Muelbert *et al.*, 2019).

The overall response of the forest to increased P demand for biomass under eCO_2 will also depend on other factors, such as the interplay with soil microorganisms (Box 1) and possible climatic changes, namely warming, increasing drought events and changes in precipitation patterns, which may affect how plants invest their resources and may affect the P-use and -acquisition strategies themselves (Ho *et al.*, 2005). Moreover, increased resource investments by plants in the different strategies in response to eCO_2 are expected to have differential effects on C cycling. For instance, increased leaf P_i-resorption proficiency inevitably leads to lower quality leaf litter and may decrease decomposition rates (Jin *et al.*, 2015; Sayer *et al.*, 2020). Investments in belowground P_i acquisition will increase C fluxes to the soil, although the fate and long-term stability of newly input C are uncertain under eCO_2 and the accompanying climate changes (Cleveland *et al.*, 2010; Terrer *et al.*, 2021).

VI. Ways forward

As a way forward, we suggest further utilizing and extending the large network of Amazonian forest inventory sites (Malhi *et al.*, 2002; Quesada *et al.*, 2011; Brienen *et al.*, 2015) by selecting a subset of sites along a representative soil P gradient that minimizes the confounding effects of climate, biogeographic regions or topography. Although measurements at the species level are highly desirable, they are notoriously challenging for belowground traits in diverse tropical forests. We argue that identifying patterns in traits and indicators of plant P-use and -acquisition strategies at the community level, along with the use of permanent measurement sites and standardized methodologies, may allow estimates of community investment in different strategies and evaluate and adapt our conceptual framework (Fig. 3). Repeated measurements over the year are additionally encouraged to identify temporal patterns in plant P-use and -acquisition strategies. Following our conceptual framework (Fig. 3), we propose the measurement of different traits and indicators to experimentally test the predicted patterns in plant P-use and -acquisition strategies, which we considered feasible under coordinated efforts among the scientific community over time:

(**1**) Leaf P_i resorption is relatively more important for plants in low-P soils – we recommend measuring P resorption from different chemical fractions in senesced leaves to identify the underlying mechanisms allowing high P resorption proficiency in Amazonia and the role of leaf P_i resorption efficiency (e.g. Hidaka & Kitayama, 2011; Tsujii *et al.*, 2017). This may allow an estimation of where plants may invest proportionally more resources in this strategy. Additionally, the measurement of P_i resorption from other organs would significantly improve our understanding of plant P use.

(**2**) Fine-root P_i foraging is relatively more important in soils with high P_i availability – classifying roots according to their functions (McCormack *et al.*, 2015) and measuring root morphological and architectural traits and dynamics (e.g. root elongation rate and turnover), as well as accounting for the effects of other edaphic factors, can significantly improve our understanding of fine-root P_i uptake and functioning (Freschet *et al.*, 2021). These measurements, in addition to the measurements suggested for the other strategies, may allow us to identify possible areas in Amazonia where roots primarily forage for P_i.

(**3**) AMF symbioses are relatively more important in soils with intermediate soil P_i availability – measurements of intraradical colonization are often preferred in most studies, but the extent of the AMF hyphal network in the soil may be an essential complementary measure of P_i acquisition capacity and plant C investments. We recommend measuring AMF intraradical and extraradical indicators (hyphal length and biomass) while also analyzing root traits promoting AMF colonization, as well as their dynamics in space and time (i.e. production and turnover rates).

(**4**) Root phosphatase exudation is relatively more important in soils with low P_i availability and high substrate availability – we recommend measuring and extending our knowledge on potential activity rates of root-associated PMEs and phytases complementary to root traits fostering these strategies, as well as a better understanding of enzyme production and turnover rates and their efficacy *in situ* is needed for model development and benchmarking (see Wallenstein & Weintraub, 2008; Razavi *et al.*, 2019).

(**5**) Fast rates of root LMWOA exudation are relatively more important where most P is in less available forms – we recommend quantifying root exudation rates while also analyzing associated root traits (e.g. Phillips *et al.*, 2008; Aoki *et al.*, 2012). We additionally recommend testing the use of leaf manganese (Mn) concentrations to serve as a proxy for LMWOA exudation in Amazonia, as they are easier to measure and have the potential to uncover large patterns in plant investment in this strategy (see Lambers *et al.*, 2015; 2021). Additionally, investigating LMWOA effectiveness in mobilizing P and residence time in Amazonian soils would significantly improve our understanding of their role in the rhizosphere.

By measuring the same traits and indicators previously suggested, nutrient manipulation and eCO_2 experiments (FACE or open-top chambers) provide the opportunity to advance our

understanding by revealing species plasticity to adjust P_i-use and -acquisition strategies. Likewise, process-based model efforts may find value in testing and challenging our current understanding of the role of the strategies discussed (Box 3). The variation in plant investments in different strategies and their relative importance in supplying plant P_i needs can be investigated using different modeling approaches, for instance by incorporating different mechanistic possibilities into a modular framework and constraining the consequences of uncertain mechanisms on plant function and C storage. Moreover, the current challenge lies in overcoming the low agreement between actually measurable entities and model parameters. Coordinated efforts among field studies, experiments and modeling need to be used to address the challenge of mechanistically representing P and eCO_2 interactions (Reed *et al.*, 2015; Hofhansl *et al.*, 2016). Likewise, the impacts of climatic changes and plant–microbial interactions (not focused on here) need to be assessed to reliably project the response of Amazonia to global change so that suitable management actions can be taken.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Leaf P_i-resorption efficiency.

Notes S2 Effects of N on acid phosphatase exudation and activity.

Notes S3 Cluster roots in Amazonia.

Table S1 Summary of soil P gradient studies.

Table S2 Phosphorus concentrations in senesced leaves in different regions of Amazonia.

Table S3 Summary of P_i fertilization studies.

Table S4 Root morphological traits in Amazonia, other tropical forests and meta-analyses.

Table S5 Potential root acid phosphatase activity in Amazonia and other tropical forests.

Table S6 Plant and mycorrhizal responses to eCO_2 in meta-analyses.

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