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Amazon Forest Ecosystem Responses to Elevated Atmospheric CO_2 and Alterations in Nutrient Availability: Filling the Gaps with Model-Experiment Integration

Florian Hofhansl[1]*, *Kelly M. Andersen*[2], *Katrin Fleischer*[1,3], *Lucia Fuchslueger*[1], *Anja Rammig*[4,5], *Karst J. Schaap*[1], *Oscar J. Valverde-Barrantes*[1] and *David M. Lapola*[3]

[1] Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil, [2] Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK, [3] Laboratório de Ciência do Sistema Terrestre, Departamento de Ecologia, Universidade Estadual Paulista, Rio Claro, Brasil, [4] Land Surface-Atmosphere Interactions, Technical University Munich, Freising, Germany, [5] Earth System Analysis, Potsdam Institute for Climate Impact Research, Potsdam, Germany

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***Correspondence:**
Florian Hofhansl
florian.hofhansl@inpa.gov.br

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The impacts of elevated atmospheric CO_2 (eCO_2) and alterations in nutrient availability on the carbon (C) storage capacity and resilience of the Amazon forest remain highly uncertain. Carbon dynamics are controlled by multiple eco-physiological processes responding to environmental change, but we lack solid experimental evidence, hampering theory development and thus representation in ecosystem models. Here, we present two ecosystem-scale manipulation experiments, to be carried out in the Amazon, that examine tropical ecosystem responses to eCO_2 and alterations in nutrient availability and thus will elucidate the representation of crucial ecological processes by ecosystem models. We highlight current gaps in our understanding of tropical ecosystem responses to projected global changes in light of the eco-physiological assumptions considered by current ecosystem models. We conclude that a more detailed process-based representation of the spatial (e.g., soil type; plant functional type) and temporal (seasonal and inter-annual) variability of tropical forests is needed to enhance model predictions of ecosystem responses to projected global environmental change.

Keywords: Amazon, carbon allocation, elevated CO_2, free-air CO_2 enrichment (FACE), nutrient addition, tropical forest

INTRODUCTION

Tropical forests account for approximately one fourth of the total global forest carbon (C) stock (Phillips et al., 2009; Pan et al., 2011; Carvalhais et al., 2014). The Amazon basin represents the largest continuous region of tropical forests, storing about 150–200 Pg C (Feldpausch et al., 2012) and accounting for 14% of C fixed by photosynthesis in the terrestrial biosphere (Zhao and Running, 2010). A decrease or cessation of the Amazon forest C sink could create strong positive feedbacks on global climate change. It is therefore of paramount importance to enhance the mechanistic understanding of potential feedbacks between tropical C storage and projected global environmental change (Zhou et al., 2013; Zuidema et al., 2013).

Amazon forests appear vulnerable to increasing moisture stress, with the potential for large C losses to exert feedbacks on climate change (Phillips et al., 2009). Global circulation models project an increase of droughts affecting the Amazon region (Malhi et al., 2008) due to increasing frequency of climate anomalies associated to increasing sea surface temperatures (Lewis et al., 2011), which could lead to loss of Amazon forest further accelerating climate change (Rammig et al., 2010). Efforts to quantify the response of aboveground carbon storage derived from forest inventory plots concluded that such events have the potential to reverse a multi-decadal biomass C sink across Amazonia (Phillips et al., 2009). However, to date predicted responses of the Amazon forest to projected global climate changes (mainly precipitation and temperature) remain largely speculative due to a lack of direct experimental evidence (Malhi et al., 2009; Davidson et al., 2012; Cernusak et al., 2013). As a surrogate, ecosystem models that include the mechanistic representation of key ecosystem processes, such as photosynthesis, respiration, growth, and C allocation, have been used for projections of ecosystem responses to changes in climate, atmospheric CO_2 and nutrient availability (e.g., Goll et al., 2012; Huntingford et al., 2013; Joetzjer et al., 2014; Smith et al., 2014; Yang et al., 2014). However, due to differences in the representation of ecophysiological processes and their sensitivity to environmental stresses model simulations predict either dramatic Amazon forest dieback for the twenty first century due to changes in precipitation patterns (Cox et al., 2008) and rising temperatures (Cox et al., 2004), or simulate strong resilience of tropical forests due to a theoretically supposed CO_2 fertilization effect on primary productivity (Cox et al., 2013; Huntingford et al., 2013). As a consequence, climate-driven loss of tropical forest biomass could potentially be mitigated by CO_2 fertilization of forest productivity (Lapola et al., 2009; Rammig et al., 2010).

Nonetheless, lack of experimental evidence, in particular for the tropics, hinders the validation of current ecosystem models in predicting responses to increasing atmospheric CO_2 concentrations and alterations in nutrient availability. In turn, one of the main limitations of state-of-the-art models for reliably projecting potential changes in the Amazon C pool is the uncertainty associated with critical underlying ecosystem processes such as the physiological response of tropical trees to eCO_2 and nutrient limitation (Medlyn et al., 2015; Norby et al., 2016; Reed et al., 2015). So far, manipulative ecosystem experiments have predominantly been conducted in temperate and boreal regions. These experiments have greatly enhanced our understanding of forest ecosystem responses to eCO_2 and increasing nutrient inputs from anthropogenic sources (e.g., Rastetter and Shaver, 1992; Reich et al., 2014; Norby et al., 2016). For instance, free-air CO_2 enrichment (FACE) experiments in temperate areas indicate an initial increase in forest productivity (Norby et al., 2005), which is ultimately limited by soil nutrient availability (Norby et al., 2010). However, temperate and boreal regions are predominantly limited by soil nitrogen (N) availability, whereas lowland tropical forests are relatively rich in N, but characterized by highly weathered soils with low soil phosphorus (P) availability (Walker and Syers, 1976; Vitousek and Sanford, 1986; Quesada et al., 2012). Because of differences between tropical forests and temperate forests in biological complexity, nutrient cycling, and climate regimes, we expect differential responses of tropical forest ecosystems to eCO_2 and alterations in nutrient availability.

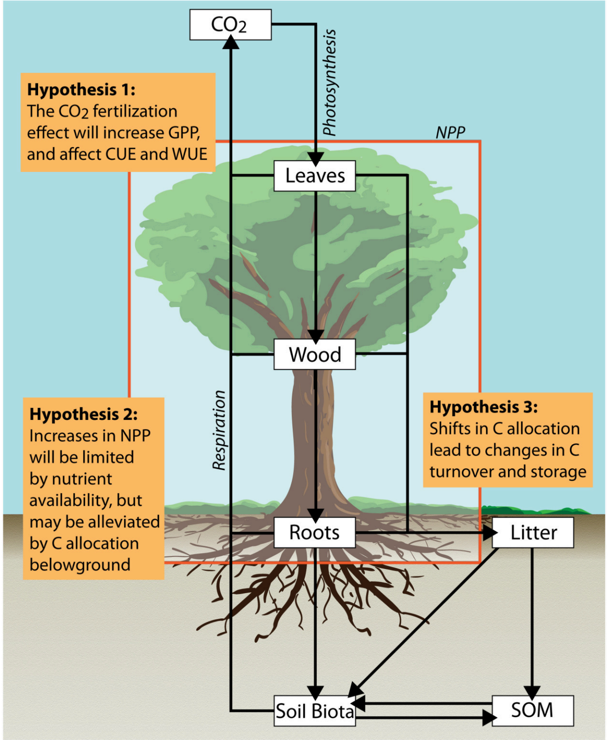
Ecosystem scale experiments subjecting mature forests to eCO_2 and nutrient addition in the tropics, and in particular the Amazon forest, are crucial for filling major gaps in our understanding of expected global change effects (Hickler et al., 2008; Cernusak et al., 2013; Norby et al., 2016). Two major endeavors are currently underway in Amazonia; the first free-air carbon enrichment experiment in a mature tropical old-growth forest (AmazonFACE; Lapola and Norby, 2014), as well as the first large-scale factorial nutrient addition experiment (AFEX; Amazon fertilization experiment). These experiments aim to assess the effects of eCO_2 and alterations in nutrient availability on biogeochemistry, ecology and resilience of the Amazon forest. Based on an assumption-centered integrated model-experiment approach (Medlyn et al., 2015), the goal of this paper is to discuss the plausibility and uncertainties of three hypotheses related to potential responses of tropical ecosystem processes to eCO_2 and alterations in nutrient availability: ***(1) Elevated CO_2 will increase C source activity (i.e., assimilation) and thus could stimulate C sink activity (i.e., growth) (2) Low nutrient (phosphorus) availability of tropical soils will limit C sink activity but may be alleviated by C allocation belowground; (3) Shifts in plant C allocation will increase C turnover and thus might decrease C storage in tropical forests.*** We explore each of these hypotheses in relation to current model assumptions and observational evidence (**Figure 1**).

ELEVATED CO_2 WILL INCREASE C SOURCE ACTIVITY (I.E., ASSIMILATION) AND THUS COULD STIMULATE C SINK ACTIVITY (I.E., GROWTH)

Current model formulations assume that tropical forests have the potential to respond more strongly to eCO_2 compared to temperate and boreal forests, based on the eco-physiological understanding of photosynthesis that is represented by a scheme introduced by Farquhar et al. (1980). Therefore most ecosystem models incorporating the Farquhar scheme (Long, 1991; Drake et al., 1997; Hickler et al., 2008, 2015; Cernusak et al., 2013) suggest that eCO_2 increases rates of leaf-level photosynthesis (Lloyd and Farquhar, 1996) based on the following simplified relationship:

$$A = min \left\{ \begin{array}{c} JL = f\,(PAR) \\ Jc = f\,(ci,\,T,\,\sim H_2O) \\ Je = f\,(T) \end{array} \right\}$$

where the rate of gross photosynthetic CO_2 assimilation (A) is determined by the rate of carboxylation (J_c), and the potential rate of electron transport (J_e) at a particular irradiance (J_L). Several factors may limit the rate of carboxylation; i.e., the relative partial pressure of CO_2 and O_2 (c_i), the amount of activated



Hypothesis 1: The CO_2 fertilization effect will increase GPP, and affect CUE and WUE

Hypothesis 2: Increases in NPP will be limited by nutrient availability, but may be alleviated by C allocation belowground

Hypothesis 3: Shifts in C allocation lead to changes in C turnover and storage

FIGURE 1 | Simplified conceptual model depicting major pools and fluxes of carbon in tropical forests. Assumption-based hypotheses to be targeted by the proposed Amazonian long-term ecosystem experiments are discussed in the text.

Rubisco enzyme, and the rate of acceptor regeneration (Farquhar et al., 1980). Due to the influence of c_i and J_L on the temperature (T) dependence of A, and the fact that under eCO_2 carboxylation dominates over oxygenation and increases with T until limited by the maximum rate of J_e, we might expect a stronger positive response of net photosynthesis to eCO_2 in warmer environments, such as tropical forests (Lloyd and Farquhar, 2008).

However, because carbon gain and water loss are regulated by the rate of leaf stomatal closure, a downregulation of stomatal conductance due to high vapor pressure deficit has the potential to substantially reduce the eCO_2-induced increase in leaf-level photosynthesis (Beedlow et al., 2008; Körner, 2009; Holtum and Winter, 2010). Based on the observed coupling between photosynthesis and stomatal conductance such effects are included in most ecosystem model formulations and therefore under eCO_2, most models simulate an increase in water-use efficiency (WUE; De Kauwe et al., 2013) i.e., the rate of photosynthesis to transpiration. However, studies based on carbon isotope fractionation in tropical tree rings suggest that increasing WUE does not necessarily trigger increased tree growth (Nock et al., 2011) and thus found no stimulation of tree growth in response to CO_2 fertilization (van der Sleen et al., 2014). This dilemma might result from the fact that under sub-optimal conditions enhanced “source activity” (i.e., assimilation) of leaves in response to eCO_2 might not stimulate increased “sink activity” (i.e., growth) of tropical trees due to other factors limiting plant growth (Körner, 2003). Highlighting the interactive effects of instantaneous biogeochemical processes that have to be considered in global ecosystem models this illustrates why an eCO_2-induced stimulation of photosynthetic C assimilation might not necessarily result in enhanced C storage of tropical forests in response to eCO_2 (Körner, 2003).

Recent research indicates that during drought trees prioritize growth by reducing autotrophic respiration that is unrelated to growth instead of reducing total productivity (Doughty et al., 2015a). This indicates that projected global changes such as increasing drought frequency and mean annual temperatures influence the ratio of photosynthesis to respiration (R_a) and thus affect plant carbon use-efficiency (CUE) i.e., the rate of net primary production (NPP) to gross primary production (GPP; Gifford, 2003; DeLucia et al., 2007). Similarly, in process-based models the optimum temperature for maximum net primary production (where NPP = GPP$-R_a$) depends on the balance between temperature effects on photosynthesis and respiration. However, there are still large uncertainties to which extent these physiological processes can acclimate in response to projected global changes (Huntingford et al., 2013). Both photosynthesis and respiration are speculated to be capable of dynamic thermal acclimation as a long-term temperature response. For instance, when acclimation is not considered in ecosystem models this usually leads to widespread forest dieback compared to when photosynthetic temperature acclimation is accounted for (Sitch et al., 2008). However, acclimation is challenging to incorporate in models in a mechanistic way because different species appear to vary in their acclimation strategies (Medlyn et al., 2011). Thus, the overall effect of global changes on tropical forests represents the integration of simultaneous responses of ecophysiological processes, such as those discussed above but also on phenology, allocation, turnover, and decomposition. Ultimately, by integrating this mechanistic understanding based on empirical evidence from experimental studies in next generation ecosystem models we will be able to scale-up plot-level measurements to ecosystem-scale responses under sub-optimal conditions of resource availability.

LOW NUTRIENT (PHOSPHORUS) AVAILABILITY OF TROPICAL SOILS WILL LIMIT C-SINK ACTIVITY BUT MAY BE ALLEVIATED BY C ALLOCATION BELOWGROUND

Plants need a broad range of nutrients (N, P) and micronutrients in a certain stoichiometry to maintain NPP, growth and normal functioning (e.g., Liebig, 1840; Sterner and Elser, 2002; Körner, 2003). Hence, we expect that potential initial increases in NPP will be limited by low nutrient availability of tropical soils (**Figure 1**). In tropical forests N is mainly stored in biomass, and rapidly recycled from organic matter; and in addition to N deposition, symbiotic N_2-fixing plants appear at a high abundance (Houlton et al., 2008; Hedin et al., 2009). Phosphorus inputs in contrast are mainly rock-derived; P availability decreases with weathering, and with increasing soil age it becomes gradually transformed and bound in recalcitrant complexes (e.g., Walker and Syers, 1976; Vitousek et al., 2010). Hence, in old and highly weathered Amazonian soils P rather than N appears to limit plant growth. Moreover, P availability seems to exert an important control on N cycling (Quesada et al., 2010; Vitousek et al., 2010), but our understanding of the nature of P limitations and N:P interactions is still expanding (Vitousek et al., 2010; Lambers et al., 2015). Ecosystem C-N models integrating above- and belowground interactions, and including constraints of plant stoichiometry strongly improved the representation of eCO_2 responses of two temperate FACE experiments (Zaehle et al., 2014). There is growing recognition that P-dynamics and N:P interactions, particularly for the tropics, are poorly represented in ecosystem models (Wang et al., 2010; Yang et al., 2011; Goll et al., 2012; Powers et al., 2015; Reed et al., 2015) For example, when N and P availability are included in global ecosystem models NPP is reduced by up to 25%, potentially compensating eCO_2 effects and turning the terrestrial biosphere into a net C source by 2100 (Wieder et al., 2015).

Nutrient limitations might restrain plant productivity, and reduce the proposed C sink strength of Amazonian forests, as has been shown for other tropical forests (Kaspari et al., 2008; Wright et al., 2011; Lambers et al., 2015; Powers et al., 2015). To date, three stand-scale nutrient addition experiments conducted in high diversity lowland tropical forests, indicate co-limitations of several nutrients regulating key plant physiological and ecosystem processes (Mirmanto et al., 1999; Kaspari et al., 2008; Wright et al., 2011; Pasquini and Santiago, 2012; Alvarez-Clare et al., 2013). However, even in relatively P-rich soils in Central America (Cleveland et al., 2011) P additions tend to have the strongest impacts, increasing decomposition rates (Kaspari et al., 2008) and stimulating growth of trees in smaller size classes (Wright et al., 2011; Alvarez-Clare et al., 2013). We therefore expect soil P to be the key nutrient restraining responses to eCO_2, buffering the proposed C sink strength (Aragão et al., 2009; Cleveland et al., 2011; Baribault et al., 2012; Quesada et al., 2012).

FACE-experiments conducted in temperate forest ecosystems showed that under eCO_2 an initial increase in NPP by enhanced photosynthesis was allocated to fine root production and root exudation to overcome increasing N limitation (Körner et al., 2005; Iversen et al., 2008; Norby et al., 2010). The low P-availability in the Amazon, however, rather hints toward a gradual P-limitation, but similarly as in temperate forests, this may be alleviated by increasing C allocated belowground into root production, exudates, and to mycorrhizal or N-fixing symbionts (Finzi et al., 2007; Houlton et al., 2008; Iversen, 2010). While increased root biomass might promote C sequestration, higher labile C inputs into the rhizosphere will provide energy for microbes and change microbial community composition and turnover (Deng et al., 2016). Increased root exudation could stimulate enzyme (phosphatase) production (Nottingham et al., 2012; Spohn et al., 2013; Stone et al., 2013) and induce changes of soil pH in the close vicinity of fine roots (Lloyd et al., 2001; Jones et al., 2009; Lambers et al., 2015), and enhance decomposition of leaf or root litter or of older soil organic matter ("priming-effect"; Fontaine et al., 2003; Kuzyakov, 2010). This could enhance P availability for microbial and plant uptake, but could lead to CO_2 losses as autotrophic respiration (R_a), and enhance heterotrophic soil CO_2 efflux (R_{het}) due to higher microbial growth and activity (Fontaine et al., 2004; Blagodatskaya et al., 2010; Kelley et al., 2011). If this is the case, we predict that increases in soil respiration will decrease a likely C fertilization effect in tropical forests. Alternatively, eCO_2 could increase leaf longevity and alter litter quality (e.g., increase C:P and lignin content), which could reduce decomposition and buffer CO_2 losses by R_{het}. Hence, conducting a FACE, as well as a factorial nutrient addition experiment will increase our mechanistic understanding of N and P limitation in mature, old growth tropical forests (Cleveland et al., 2011), and allow improving model-assumptions to enhance predictions of tropical ecosystem responses to eCO_2 and alterations in nutrient availability.

SHIFTS IN PLANT C ALLOCATION WILL INCREASE C TURNOVER AND THUS MIGHT DECREASE C STORAGE IN TROPICAL FORESTS

Due to potentially increased NPP in response to eCO_2, and a subsequent relative investment into belowground compartments we expect a general shift in plant C allocation (**Figure 1**). Nonetheless, the allocation of NPP between plant compartments, as well as to carbohydrate reserves and export to symbionts is usually not accounted for in ecosystem models (Fatichi et al., 2014) or often represented by constant fractions:

$$\frac{dCi}{dt} = \alpha NPP - \frac{Ci}{\tau}$$

where *Ci* represents a given plant C pool (e.g., leaves, wood, fine roots), α is a parameter in percentage and τ the turnover rate of *Ci*. Such constant allocation schemes perform poorly when reproducing eCO_2 effects (De Kauwe et al., 2014). This is partly due to the fact that key processes such as carbon allocation to leaf, root and wood, plant mortality and soil carbon decomposition fluctuate over time and space (Rowland et al., 2014) and thus this variability should be represented in ecosystem models. Therefore, allocation schemes based on functional relationships among biomass fractions that vary with resource availability perform best in capturing field-based observations (De Kauwe et al., 2014).

Recent observations indicate that photosynthesis and plant carbon usage are temporally decoupled allowing C to be allocated when it is ecological beneficial, rather than when C is environmentally most available (Doughty et al., 2015b). Hence, seasonal reductions in wood NPP were found associated with carbon preferentially allocated to either root or canopy NPP during the dry season (Doughty et al., 2015b). Due to significant differences in turnover times of plant tissues (i.e., leaves, wood, fine roots) this suggests that projected increases in temperature and dry season length could strongly affect tropical C storage by shifting C allocation away from wood NPP (Hofhansl et al., 2015) and toward canopy and root NPP to alleviate drought-induced resource limitation (Doughty et al., 2014). As a result, tropical C storage will differ considerably depending on if C is stored in long-lived wood or allocated to plant tissue with reduced lifespan (Körner et al., 2005). In accordance, global vegetation models diverge considerably between estimates based on the representation of C allocation and pool turnover patterns. Nonetheless, despite the fact that residence time of C was found to dominate the uncertainty in the response of terrestrial vegetation to eCO_2 (Friend et al., 2014), most models predict increasing C sequestration in both biomass and soils in response to eCO_2 (De Kauwe et al., 2014).

Over the last decades the Amazon C sink has been substantial (Pan et al., 2011), however, recent observations suggest that the sink strength is declining due to increasing tree turnover and mortality rates (Brienen et al., 2015). Therefore, a realistic scenario in line with long-term inventory data (Phillips et al., 1998, 2008) seems that global alterations in atmospheric CO_2-concentration and nutrient availability could have generated a more dynamic tropical forests (Körner, 2004). As a result, accelerated life cycles of tropical trees (Bugmann and Bigler, 2011) and associated increases in turnover times and decomposition rates have the potential to adversely affect the Amazonian C sink strength in the long-term (Brienen et al., 2015).

THE WAY FORWARD: MODEL-EXPERIMENT INTEGRATION

It is becoming increasingly evident that high diversity tropical forests, and in particular the Amazon, pose great challenges for global ecosystem models. Hence, the common use of 1 or 2 plant function types (PFT) with fixed parameterization and thus a common response to environmental change does not apply to highly diverse flora. Recent studies indicate that tropical C storage may be strongly determined by the hyperdominance (Fauset et al., 2015) and functional composition of tropical tree communities in association with different life-history strategies of tropical trees (Fauset et al., 2012). A CO_2 induced shift to shorter average tree life span could favor fast-growing tree species that invest in low-cost tissue, which could increase the turnover of C and thus decrease the C storage at the landscape scale (Phillips et al., 2009; Fauset et al., 2012; Cernusak et al., 2013). In accordance, simulations of nonrandom species loss for fast-growing species with low wood density increased C storage by 10%, whereas the loss of high statured slow-growing species decreased C stocks by over 30% (Bunker, 2005). This further highlights that impacts of climate change and eCO_2 on the Amazon forest could be more subtle than projected by a catastrophic dieback scenario, and already ongoing.

Recent studies evaluating the sensitivity of wood NPP to seasonal and interannual variations in climate showed that the growth response of tropical trees is associated to site-specific differences in drought sensitivity (Hofhansl et al., 2014), such that consistent with a hypothesized tradeoff between maximum potential growth rate and hydraulic safety the strength of the growth seasonality response among trees is significantly correlated to functional traits (Rowland et al., 2013). This suggests that changes in future climate seasonality could differentially affect the C sink strength of tropical forests due to local resource availability and tree species composition (Hofhansl et al., 2014). The recently developed set of ecosystem models based on plant-traits (van Bodegom et al., 2012; Pavlick et al., 2013; Fyllas et al., 2014; Sakschewski et al., 2015) has the potential to capture these changes, since differences in vegetation communities are depicted as a continuum, rather than discretely. Implementation of ecosystem models capable of incorporating more flexible C allocation schemes as well as trait-based parameterization could strongly improve model predictions (Franklin et al., 2012) to simulate the response of tropical forest ecosystems to climate anomalies and other short-term disturbances.

Overall, these observations indicate strong feedbacks of species specific and edaphic factors on ecosystem C storage (see Körner, 2009) and strongly suggest that the interaction between biodiversity and forest dynamics should be considered when making projections about the role of tropical forests in the global C cycle in a CO_2-rich future (see Körner, 2004). This highlights the importance of manipulative *in-situ* experiments that simulate projected future conditions in high diversity tropical forest ecosystems and can be used to improve model-based predictions. Although given the time horizon of the two experiments neither AmazonFACE nor AFEX might capture the change in forest species composition, undoubtedly both experiments provide unique opportunities to investigate which life-history strategies and functional traits will be favored or disfavored under eCO_2 and increased nutrient availability. Furthermore, AmazonFACE and AFEX, will provide crucial information on tropical C allocation schemes and the response to global changes by investigating allocation of C to structural and non-structural compounds such as the relative investment belowground to fine roots, associated mycorrhizae, and the rhizosphere as well as monitoring potential feedbacks on autotrophic and heterotrophic CO_2 efflux. To that end, these manipulative and long-term ecosystem scale experiments aim to assess how predicted increases in atmospheric CO_2 concentrations and alterations in resource availability will affect the growth response and thus the C sink strength of the Amazon forest ecosystem under projected global changes.

SYNTHESIS

Following an integrated model-experiment approach guiding the design of *in-situ* investigations of tropical forest ecosystem responses to eCO_2 and nutrient manipulation in the proposed ecosystem-scale manipulation experiments will enable us to test whether eCO_2 has the expected fertilization effect at organ-, plant,- and ecosystem-level. We attempt to enhance the mechanistic understanding of potential responses of highly productive Amazonian forests thriving on highly weathered soils, and investigate whether nutrient (P) limitation affects the proposed CO_2 fertilization effect. Specifically, we will investigate *in-situ* if nutrient limitation triggers belowground C allocation to root biomass, mycorrhizal symbionts, and into the rhizosphere in exchange for nutrients, or stimulates microbial decomposition enhancing P recycling. By conducting the proposed long-term *in-situ* ecosystem manipulation experiments we aim to resolve whether projected increases in atmospheric CO_2 concentration and alterations in nutrient availability will induce shifts in plant C allocation which could in turn increase C turnover, and decrease the long-term C storage capacity of the Amazon forest ecosystem. Generating this novel process-based understanding will further improve model-based predictions that can be used to upscale mechanistic principles to larger spatial scales.

AUTHOR CONTRIBUTIONS

All authors listed have made substantial contributions to the manuscript. FH, KA, KF, LF and OV wrote the paper; KS designed the conceptual scheme; AR and DL conceived the analysis and contributed valuable comments on earlier manuscript versions.

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