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REVIEW

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Tropical root responses to global changes: A synthesis

Daniela Yaffar[1,2] | Laynara F. Lugli[3] | Michelle Y. Wong[4,5] | Richard J. Norby[6] | Shalom D. Addo-Danso[7] | Marie Arnaud[8,9] | Amanda L. Cordeiro[10] | Lee H. Dietterich[10,11] | Milton H. Diaz-Toribio[12] | Ming Y. Lee[13] | Om Prakash Ghimire[14] | Chris M. Smith-Martin[15] | Laura Toro[15,16] | Kelly Andersen[10,13] | Lindsay A. McCulloch[17,18] | Ina C. Meier[2] | Jennifer S. Powers[15] | Mareli Sanchez-Julia[4] | Fiona M. Soper[19] | Daniela F. Cusack[10,17]

Correspondence
Daniela Yaffar, Environmental Science Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA.
Email: danielayaffar@gmail.com

Abstract

Tropical ecosystems face escalating global change. These shifts can disrupt tropical forests' carbon (C) balance and impact root dynamics. Since roots perform essential functions such as resource acquisition and tissue protection, root responses can inform about the strategies and vulnerabilities of ecosystems facing present and future global changes. However, root trait dynamics are poorly understood, especially in tropical ecosystems. We analyzed existing research on tropical root responses to key global change drivers: warming, drought, flooding, cyclones, nitrogen (N) deposition, elevated (e) CO_2, and fires. Based on tree species- and community-level literature, we obtained 266 root trait observations from 93 studies across 24 tropical countries. We found differences in the proportion of root responsiveness to global change among different global change drivers but not among root categories. In particular, we observed that tropical root systems responded to warming and eCO_2 by increasing root biomass in species-scale studies. Drought increased the root: shoot ratio with no change in root biomass, indicating a decline in aboveground biomass. Despite N deposition being the most studied global change driver, it had some of the most variable effects on root characteristics, with few predictable responses. Episodic disturbances such as cyclones, fires, and flooding consistently resulted in a change in root trait expressions, with cyclones and fires increasing root production, potentially due to shifts in plant community and nutrient inputs, while flooding changed plant regulatory metabolisms due to low oxygen conditions. The data available to date clearly show that tropical forest root characteristics and dynamics are responding to global change, although in ways that are not always predictable. This synthesis indicates the need for

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Daniela Yaffar and Laynara F. Lugli should be considered joint first authors.

For affiliations refer to page 14.

replicated studies across root characteristics at species and community scales under different global change factors.

KEYWORDS
belowground, carbon allocation, disturbances, root traits, tropical forests

1 | INTRODUCTION

Tropical forests contain over half of the terrestrial global biodiversity and are one of the most productive ecosystems on Earth (Clark et al., 2013; Pan et al., 2011). However, the ability of tropical ecosystems to continue functioning as a carbon (C) sink under global change is challenging to predict due to their high biogeochemical heterogeneity and tree species diversity (Cusack et al., 2016). Although most tropical studies focus on measuring the aboveground component of the forests, our understanding of how global change will affect belowground functions, such as plant nutrient and water uptake, hinders our ability to predict the future of tropical forest responses. Because roots mediate critical belowground processes and significantly contribute to C stored in soils (Rasse et al., 2005), expanding and compiling the knowledge of how tropical tree roots are currently responding to different global changes, individually or in combination, is particularly important for predicting future scenarios of C cycling and informing conservation and restoration efforts.

Global change in tropical ecosystems encompasses a variety of changes in abiotic conditions and extreme events, which have become more frequent and intense in recent years. For instance: (1) *Warming* may cause tropical ecosystems to reach unprecedented temperatures in recent history—surpassing photosynthetic optimum temperatures (Cavaleri et al., 2015; Clark et al., 2013; Diffenbaugh & Scherer, 2011) and thereby decreasing productivity (Sullivan et al., 2020). (2) *Drought* events are anticipated to become more severe and last longer as the climate changes (Chadwick et al., 2016; Duffy et al., 2015), leading to a potential increase in tree mortality rates in tropical ecosystems (Brodribb et al., 2020). (3) *Flooding*, a result of extreme precipitation events, sea level rises, and human activities, is also increasing in the tropics (Groisman et al., 2005), leading to anoxic soil conditions, followed by the accumulation of potentially toxic compounds (Joly & Crawford, 1982; Wittmann, 2011) threatening plant survival. (4) *Cyclones*, a common disturbance for many tropical ecosystems (Everham & Brokaw, 1996; Lugo, 2008), are predicted to become highly variable in their frequency and intensity under a changing climate (Feng et al., 2013; Fu et al., 2013; Stocker et al., 2013) leading to abrupt changes in forest composition. (5) *Nitrogen* (N) deposition is increasing rapidly in tropical regions, which are already typically N-rich (Galloway & Cowling, 2021), potentially increasing the limitation of other plant nutrients. (6) *Atmospheric* CO_2 has been rapidly increasing globally, and although models indicate a positive photosynthetic response at the leaf level, tropical biomass responses may be limited in nutrient-poor soils (Fleischer et al., 2019; Yang et al., 2019). (7) *Fire* severity is predicted to increase with global warming (De Faria et al., 2017; Senande-Rivera et al., 2022), causing high tree mortality and threatening the remaining tropical forests worldwide (Juárez-Orozco et al., 2017). Considering the variability and interactions of these global changes and that roots perform multiple functions simultaneously (e.g., resource acquisition, tissue protection, and reuse and cycling of elements; Freschet et al., 2021), root responses to different global change drivers are difficult to predict.

Global change can modify the expression of root traits and their impacts on ecosystem processes from the individual plant to the Earth system scale (Bardgett et al., 2014). Roots account for an estimated 21% of total forest biomass in tropical ecosystems (Huaraca Huasco et al., 2021; Malhi et al., 2011), with fine roots representing the primary input of new C to subsurface soils through root turnover and root exudation (Cusack et al., 2018; Rasse et al., 2005). Thus, root responses to different global change drivers might affect the tropical forest ecosystem biomass dynamics and, therefore, the C cycle. Nonetheless, these responses have yet to be thoroughly quantified, presenting a significant knowledge gap in understanding the overall impacts of global change on tropical forest ecosystems belowground (Fleischer et al., 2019; Wieder et al., 2015).

Here, we assess the effects of the seven global change drivers mentioned above on tropical root characteristics. As plant roots are plastic organs, our overall expectation was that they respond to global changes by altering their trait expressions and/or function. However, we predicted that the magnitude and direction of these changes would vary among different global change drivers. To achieve this, we start this literature review by summarizing the number and distribution of root trait studies in the tropics, followed by the current empirical understanding of the effects of each global change on tropical roots, comparing them with expected responses based on our knowledge of tradeoffs mechanisms in the acquisition of different resources (Freschet et al., 2021). Finally, we interpret these trends and discuss their impacts on ecological processes, highlighting conceptual and empirical gaps for future studies.

2 | METHODS

We conducted a systematic literature review on Web of Science on the effect of the seven global change drivers on tropical root traits. We used standardized keywords (Table S1) in English, Spanish, and Portuguese and evaluated all relevant studies. Our keywords encompassed the most commonly measured root traits from different "root trait categories" following the definition adopted by a global root database FRED (Fine Root Ecology Database; https://roots.ornl.gov/data-inventory; McCormack et al., 2017; see Table 1 for description). We focused on root traits and characteristics linked to different plant functions, such as resource acquisition and cycling of elements (Freschet et al., 2021). Such traits span different root entities with no root order or diameter threshold. Our literature review considered all tropical experimental in situ and pot studies that reported data from forests or forest tree species in response to global changes. We also considered observational studies for abrupt disturbances, like cyclones and fire. The literature survey encompasses studies published from 1984 to April 2023. The full dataset with the metadata is available at the Next Generation Ecosystem Experiments, Tropics (NGEE-T) Archive (Yaffar et al., 2024).

The lack of replicated data across global change drivers and root characteristics made a formal meta-analysis not possible, so we conducted nonparametric contingency analyses (significance level for Pearson chi-squared $p < .05$) to address two overarching questions: (1) Are tropical forest root characteristics responsive to different global change drivers? (2) Is responsiveness to global change different among root characteristics? Statistical analyses were carried out in Rstudio using R version 4.3.2 (R Core Team, 2023; Posit Team, 2024) and JMP 17.0 (SAS, 2023). For these analyses, we assigned a rating to each root characteristic (excluding NA's) for responsiveness among (1) global change drivers and (2) root trait categories for each study, as: "1" = positive or negative response, or "0" = no response based on our overall synthesis of the literature. This resulted in one score per available study per global change driver (Table S2; $n = 95$) and root trait category (Table S3; $n = 146$). If there were mixed responses in the literature, we scored this as "1" as evidence that responsiveness is possible. We then performed a contingency analysis comparing responsiveness among the global change drivers and root characteristics using the chisq.test() function from the Stats R package (Royston, 1995).

3 | RESULTS

3.1 | Root trait studies in the tropics

We found 266 observations of root traits from 93 studies in 24 tropical countries investigating root responses to global changes (Figure 1; Tables S4–S10). Around 70% of the observations were from Panama, Brazil, Hawaii, China, and Puerto Rico, while most African

TABLE 1 Definition of "root trait categories" used to group root functional traits in this study. For each of the eight categories, we list their corresponding traits in our literature survey. These root trait categories encompass different root entities, and their specific level (e.g., whole-plant; within cores; and among root orders) for each study are specified along the result section and used throughout Tables S4–S10.

Root system	Root biomass, C allocation to roots, rooting depth, root mass fraction (root mass:total plant mass), root:shoot ratio, leaf area:root mass, root necromass
Root anatomy	Root stele/root cortex ratio, root cortical porosity, thickness of cortex
Root architecture	Branching ratio, root branching intensity
Root chemistry	Concentration of carbon (C), nitrogen (N), phosphorus (P), potassium (K), N:P ratio, non-structural carbohydrates (NSC), ^{14}C, water content
Root dynamics	Root productivity, root area and length growth, root lifespan/longevity, turnover, root mortality rate, root decomposition
Root-microbial association	AMF (arbuscular mycorrhizal fungi) and ECM (ectomycorrhizal fungi) colonization per root length, AMF richness in soils and roots, N-fixers, root nodules biomass/number
Root morphology	Root diameter, root length per plant mass, root surface area, specific root length (SRL), specific root area (SRA), root tissue density (RTD)
Root physiology	Root respiration, NH_4^+, NO_3^- or PO_4^{-3} uptake rate, alcohol fermentation, alcohol dehydrogenase activity (ADH), hydraulic conductance, root metabolome, root phosphatase, and phosphodiesterase activity

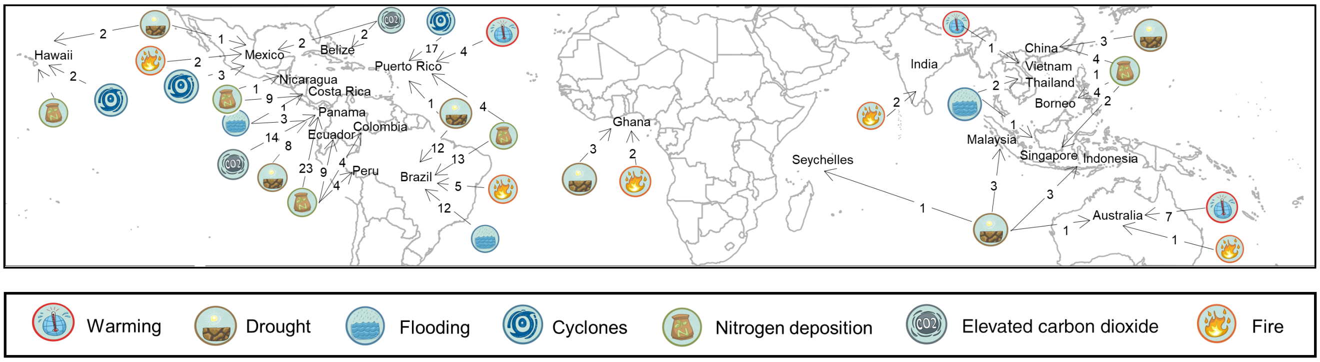


FIGURE 1 Map showing the number of root trait observations for all the studies included in this literature review in response to global changes in different tropical countries (light green band). Different symbols in circles depict each of the seven different global change drivers reviewed in this study. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

countries were underrepresented. Most studies reported fine root system traits and measured root biomass and depth distribution, and very few reported root anatomy, morphology, stoichiometry, or architecture (Figure 2a,b). From all the global changes investigated in the tropics, 53% of observations were based on N fertilization studies, 14% on drought, 8% on cyclones, 7% on elevated (e) CO_2, 7% on flooding, 5% on fire, and 4% on warming. Most results (74%) across all global change drivers come from in situ rather than pot experiments (26%), especially for N fertilization and drought studies (Figure 2a). Finally, about 65% of all studies report results at the community versus 35% at the species level (Figure 2b).

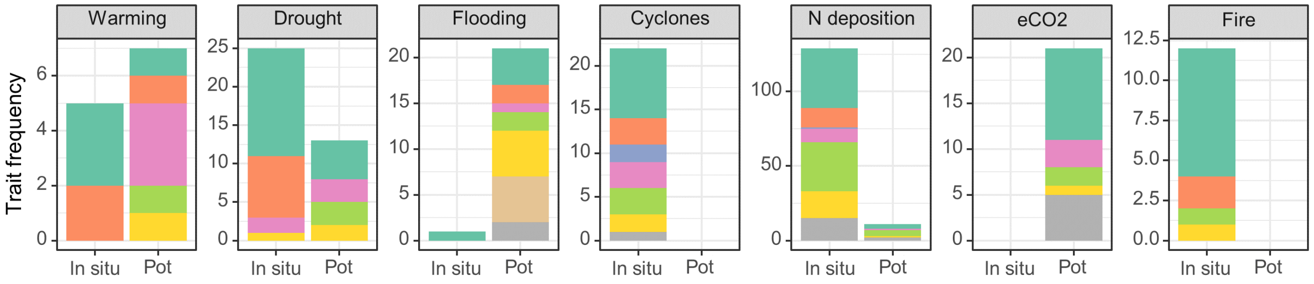
From the contingency analysis, we found significant differences in the proportion of root responsiveness to global change among different global change drivers ($\chi^2 = 25.14$, $p < .01$; Figure 3a; that is, root response rankings to different global change drivers are not all from a single distribution) but not among the different root trait categories ($\chi^2 = 11.85$, $p = .11$; Figure 3b; root response rankings in each root trait category are all from a single distribution). Specifically, warming, drought, fire, and N deposition had mixed change and no-change responses across root characteristics, whereas CO_2 fertilization, cyclones, and flooding resulted in more uniform changes in root characteristics. The width of the bars in the mosaic plots indicates that more data were available for N fertilization studies versus other global change drivers (Figure 3a), and more data were available for root system and dynamics traits, such as biomass, root: shoot ratios, and root production versus other root characteristics (Figure 3b). Below, we explore variations in the specific responses of different root characteristics to the various global change factors across tropical forest studies and suggest mechanisms that account for these patterns.

3.2 | Root responses to global changes

3.2.1 | Warming

Air and soil warming directly influence plant growth and development by affecting enzymatic reactions, photosynthesis, respiration, water loss, and other metabolic functions (Mau et al., 2018; Tunison et al., 2024). Additionally, warming indirectly impacts plants by reducing soil water content and increasing soil N availability (Bai et al., 2013; Feng et al., 2017; Jiang et al., 2022; Xiong et al., 2018; Xu et al., 2013), which can also affect root traits. Overall, we expect that warming will increase plant biomass production, including roots, due to increased nutrient availability and photosynthesis (Figure 4; Wu et al., 2019). This would lead to greater fine root biomass, with minimum to some changes in root mortality, potentially increasing root turnover (Arnaud et al., 2020; Jiang et al., 2022; Liu et al., 2019; Figure 4). We anticipate no changes in root: shoot ratios if warming does not alter nutrient and water availability (Figure 4). However, if

(a) Number of traits measured in global change studies in situ versus in pots



(b) Number of traits measured in global change studies in species versus community level

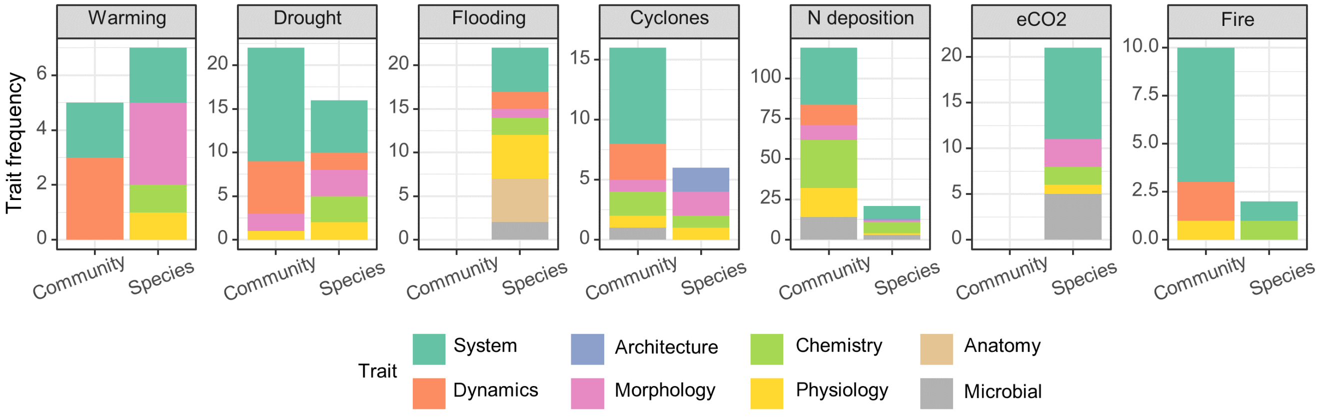


FIGURE 2 Number of trait observations per root trait category (represented by different colors; see Table 1 for definition) is shown on the y-axis, with groups of global change driver shown for (a) experiments conducted in situ or in pots and (b) at the species or community level. Note differences in the y-axis.

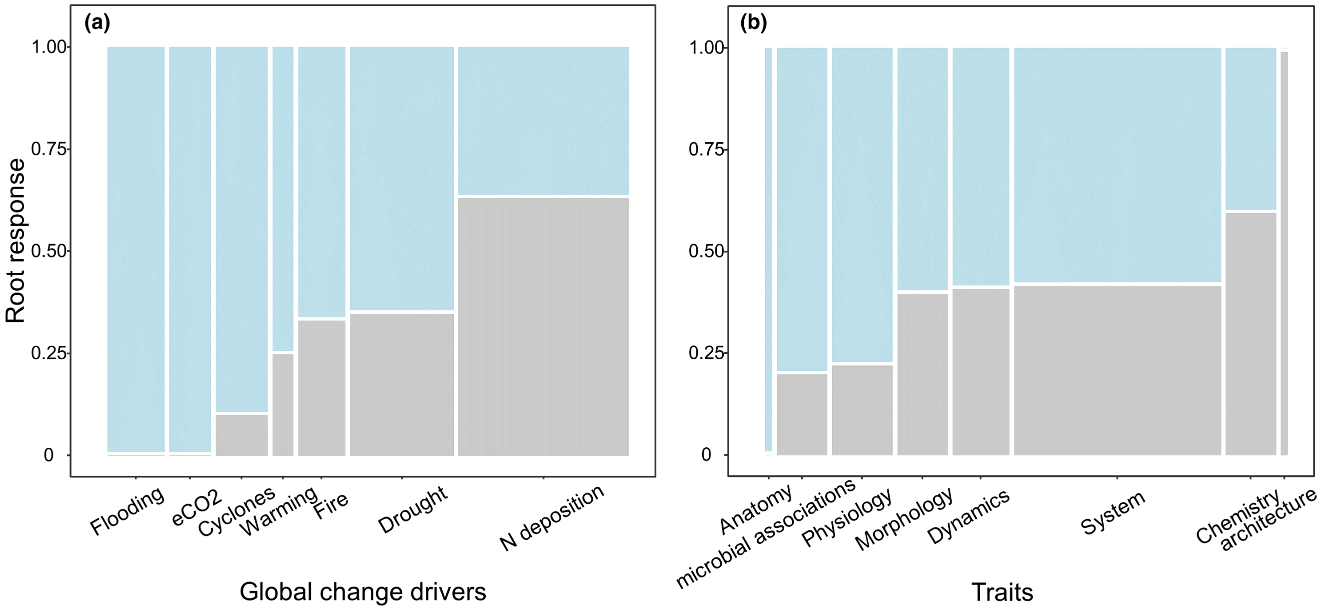


FIGURE 3 Mosaic plots give results from nonparametric contingency analyses, showing the proportion of root traits that had "change" in light blue or "no change" in gray among: (a) different global change drivers ($n=95$ scores) and (b) different root trait categories ($n=146$ scores). The thickness of the bars represents the number of scores per available data. Results from the contingency analyses showed a significant effect of global change driver on root responsiveness levels (a) but no effect of root trait category (b) on root responsiveness. Root responses are for pot and in situ studies as well as species and community-level studies combined.

water availability becomes limited, more biomass may be allocated to roots and mycorrhizal colonization to enhance resource acquisition for plant growth. We also expect that warming will not significantly alter morphological and architectural traits, such as specific root length (SRL) and root diameter, as these traits are highly conserved within species (Kong et al., 2014).

Few studies measured root responses to experimental warming in tropical ecosystems (Figure 2a; Table S4). Here, we report on in situ experiments that have used infrared heaters to warm understory vegetation and soil (Yaffar, Wood, et al., 2021), as well as incubations, laboratory- and glasshouse-based studies with controlled conditions (Apgaua et al., 2019; Arnaud et al., 2020; Noh et al., 2020). In accordance with our expectations, we found that root biomass increased at the species level during 5 months of experimental warming in Australia (Noh et al., 2020; Figure 4). Yet, we also found a decrease in root biomass at the community level after 7 months in an experiment in Puerto Rico (Yaffar, Wood, et al., 2021). These contradictory results are likely attributed to the differences in vegetation, environmental conditions (e.g., soil type and the forest strata occupied by the tree), and experimental design (Table S4). For example, the study in Australia was conducted in a greenhouse with seedlings of known species and a controlled environment (same soil fertilization treatment and soil water availability). In contrast, the study in Puerto Rico was an in situ field experiment including roots from a mix of species from different ages and no control of the environmental conditions except for the warming treatment. With warming, upper canopy trees from some tropical sites could already exceed their leaf photosynthetic temperature optima (Doughty et al., 2023), and in this case, further warming could lead to less C stored in plant tissues overall and lower allocation to the roots (Yaffar, Wood, et al., 2021). Nonetheless, fine root mortality did not vary with warming in a community-level experiment (Yaffar, Wood, et al., 2021), nor did C allocation to roots compared with shoots in a short-term species-level experiment (Apgaua et al., 2019). We did not find any studies reporting the effect of warming on mycorrhizal colonization (Figure 2a,b).

We found changes in root morphological traits in contrast to our expectations. Root tissue density (RTD) and SRL increased with 5 months of warming in a greenhouse experiment in a species-specific study in Australia (Noh et al., 2020), yet root diameter did not change (Figure 4). Similar to root diameter, rooting depth was not altered by warming at the community level (Yaffar, Wood, et al., 2021). Greater SRL and specific root area (SRA) might be a strategy to alleviate water resource limitations caused by warming, allowing a greater volume of soil to be explored. Moreover, despite the expectation of warming increasing N mineralization in soils, warming did not change root N concentration in an experiment in Australia (Noh et al., 2020). Yet, root decomposition was faster under warming for mangrove fine roots (*Rhizophora apiculata*, South Vietnam; Arnaud et al., 2020). Elevated temperature did not change root autotrophic respiration in seven species, except *Cryptocarya mackinnoniana*, for which root respiration decreased in response to warming (Noh et al., 2020). From the few studies on root responses synthesized here, the mixed and sometimes unexpected patterns suggest the importance of the inclusion of a greater diversity of root traits, such as architecture, mycorrhizal colonization, and anatomical traits and methodological approaches to reduce or account for the drying effects caused by soil warming.

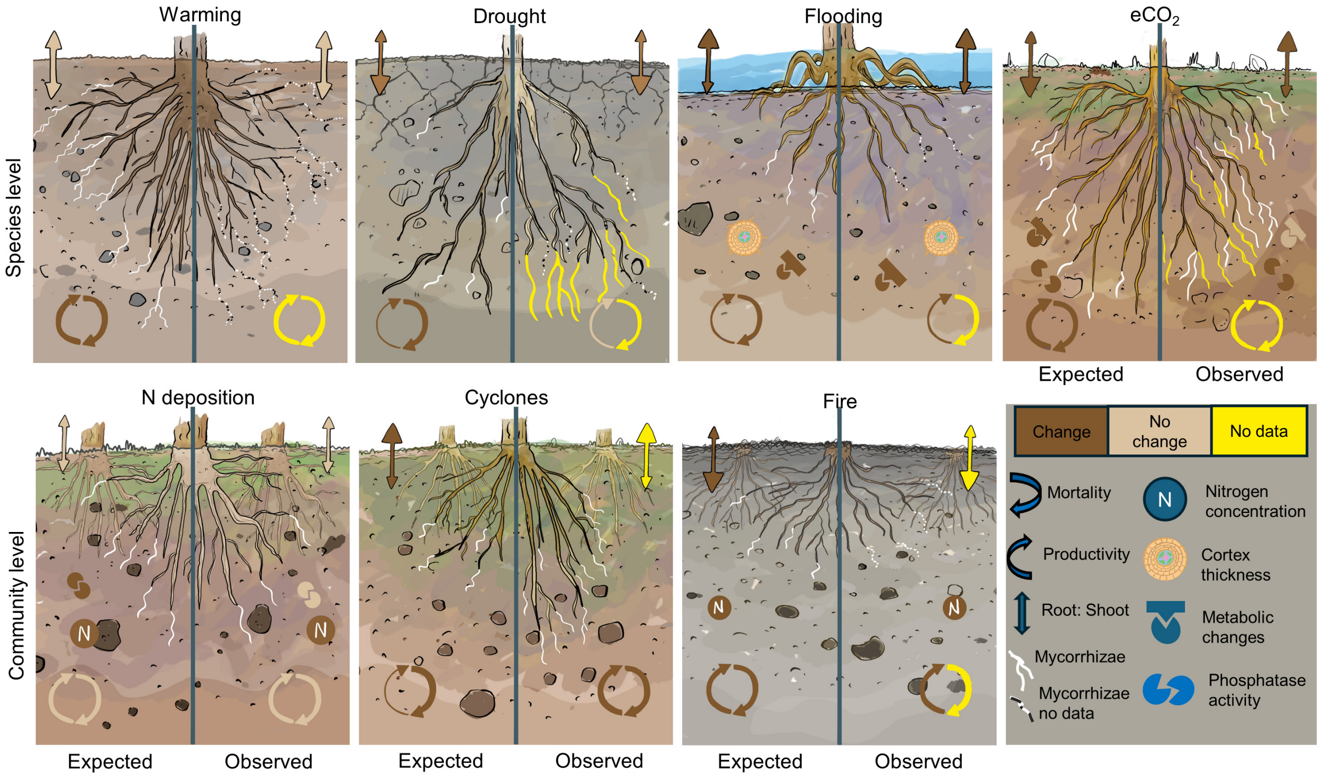


FIGURE 4 Artistic representation of expected versus observed root responses to each global change driver. Abbreviations and symbols are described in the figure legend. Root trait changes (from undisturbed conditions to either expected or observed) are differentiated by colors: Dark brown when the trait changed, light brown when there was no change, and yellow when there was no data. Mycorrhizal fungi are represented in solid white; no data on mycorrhizal fungi are represented in white dotted lines. Responses to warming, drought, flooding, and CO$_2$ are shown at the species level; responses to N deposition, cyclones, and fire are shown at the community level. The choice between displaying species or community level depends on the organism level for which more data is available for each global change driver in the SI (Tables S4–S10). Similarly, root traits represented in the figure refer to traits with more data available and summarizes the most common trend for that trait and global change driver. We chose to show expected and observed results from studies conducted in phosphorus-limited soil for N deposition since these are more predominant in tropical regions than N-scarce soils. The size and thickness of symbols represent the direction of the expected and observed responses (thicker: increase and thinner: decrease). The root system and soil types are illustrative only. Illustrator Cristian Pereyra Morales.

3.2.2 | Drought

Drought affects plant growth, reproduction, and survival by reducing C assimilation through a reduction in photosynthesis and increasing tissue desiccation with declining plant water acquisition and transportation that, in severe cases, can lead to drought-induced mortality (dos Santos et al., 2018; Powers et al., 2020). We expect drought to cause an overall decrease in root biomass and production due to plants closing their stomata to limit water loss, leading to a decline in photosynthesis and lower C assimilation and allocation to plant organs (Table S5). Tissue desiccation triggered by drought could increase root mortality, particularly of fine roots (Figure 4). We also expect the drought to cause an increase in root: shoot ratio if plants are increasing allocation to roots to increase water uptake (Figure 4); however, if the drought is too severe, this may not be possible due to a lack of photosynthate and increased root mortality. We anticipate mycorrhizal colonization to be down-regulated with drought because it is too costly to maintain this symbiosis. Additionally, drought could increase SRL and rooting depth and decrease root diameter if plants produce longer, thinner, deeper roots to increase the soil volume from which water is extracted and reach deep water sources without increasing C investment (Figure 4). Here, we report on results from experiments where soil moisture was modified with in situ throughfall exclusions and irrigation of in situ and pot experiments (Figure 2a).

Experimental manipulation of soil moisture, contrary to expected, did not elicit changes in root biomass and root biomass production at the species level (Ohashi et al., 2015; Figure 4, Table S5), with some studies still finding an increase in root: shoot ratio (Barton & Shiels, 2020; Smith-Martin et al., 2019), or no changes (Schumacher et al., 2008). No studies examined root mortality or mycorrhizal colonization at the species level (Figure 2b). At the community level, however, the impacts of drought on root system traits can vary considerably (Table S5). For example, three throughfall exclusion experiments in east-central Amazonia in Brazil (Davidson et al., 2008; Nepstad et al., 2002), southern China (Deng et al., 2018), and a Bornean tropical forest in Malaysia (Ohashi et al., 2015) found no differences in fine root (<2 mm in diameter) biomass between the drought treatment and control plots. However, a reduction in root biomass was found in two other throughfall experiments in a rainforest in southwest China (Zhou et al., 2019) and a premontane forest in Indonesia (Moser et al., 2014), as well as in studies reporting recurrent droughts in wet forests in Puerto Rico (Beard et al., 2005). Moser et al. (2014) also found an increase in fine root necromass by 250% in dry plots, mainly at the 0–40 cm soil depth in Indonesia. Furthermore, fine root growth, length, and surface area were consistently lower in droughted plots compared with controls after 5 years of throughfall exclusion in a lowland forest in Brazil (Metcalfe et al., 2008). Interestingly, long-term exposure to experimental drought increased root growth when water was more available, possibly to compensate for low annual growth rates. In contrast, root growth in a throughfall exclusion experiment in a premontane forest in Indonesia (Moser et al., 2014) and a Bornean tropical forest in Malaysia (Ohashi et al., 2015) showed no responses. The divergence in results reported here (Figure 3; Table S5) emphasizes the importance of considering multiple factors, such as species versus community traits, developmental stage, soil depths where roots were collected, and the duration and intensity of drought exposure when interpreting these trends (Table S5).

Drought can also shift C allocation between aboveground and belowground components of tropical forests. At the community level, Doughty et al. (2015) found that during the 2005 drought in the Amazon Basin, there was less C allocated to fine root productivity right after the drought and more C allocated to the canopy, suggesting a mechanism to replace lost and damaged leaves to increase photosynthesis. Experimental drought in a lowland dipterocarp forest in Malaysia caused higher seedling mortality due to root damage by herbivory (Bebber et al., 2002), while in a greenhouse experiment, drought led to higher biomass allocation to roots in seedlings of tropical tree species in Ghana (Amissah et al., 2015), Hawaii (Barton & Shiels, 2020), and during seasonal water stress in Australia (Thomas, Eamus, et al., 2000). Nevertheless, species did not consistently change root: shoot ratios under experimentally drier conditions in a greenhouse experiment in Seychelles (Schumacher et al., 2008), in Hawaii (Barton & Shiels, 2020), and from a common garden experiment with lianas in Panama (Smith-Martin et al., 2019). For example, Smith-Martin et al. (2019) found that only trees had higher root: shoot ratios in the dry plots versus the wet ones, but there was no difference in lianas. Such diverse responses in C allocation during drought periods offer valuable insights into the plasticity of responses from different species and communities.

Regarding root morphology patterns, a greenhouse study found no changes in SRL but higher total root length per unit of plant biomass in response to drought (Amissah et al., 2015). On the contrary, in a throughfall exclusion experiment in a lowland forest in the Amazon, there was an increase in SRL and SRA in response to 1 year of drought (Metcalfe et al., 2008). Adjusting root morphology instead of root growth (Weemstra et al., 2020) or producing new roots from C that has been stored in the tree for some time (Trumbore et al., 2006) could increase soil resource uptake with no extra C cost, being important strategies for coping with drier conditions when photosynthates are not abundant. Species with shallow roots are probably more vulnerable to decreased soil moisture in wetter forests than deep-rooted species in seasonal tropical forests (Markesteijn & Poorter, 2009). However, Smith-Martin et al. (2019) found no difference in the maximum rooting depth of lianas and trees between the dry and wet plots in a 4-year irrigation common garden experiment. Rooting depth will be particularly important if tropical trees do not adapt to changes in soil moisture, as already observed in a multi-year irrigation experiment in a seasonal tropical forest in Panama (Yavitt & Wright, 2001). However, if the drought is not too extreme to kill the plants, species with shallow roots might recover faster after drought (Cao, 2000), perhaps because shallow roots are better positioned to access rainwater. Nonetheless, if and how root traits in different soil depths might adapt to longer, drier periods should be evaluated in longer-term experiments.

Few studies have measured root chemistry and physiological changes in response to drought (Figure 2a,b). In a greenhouse experiment in Brazil, seedlings from native and invasive species showed reduced root potassium (K) concentrations under 4 months of drought but no significant differences in phosphorus (P) and N root content (Barros et al., 2020). A 6-year throughfall experiment in southwest China found that belowground autotrophic respiration declined by 35%, accompanied by reduced fine root biomass (Zhou et al., 2019). Using a greenhouse experiment studying six species of Panamanian trees, Wolfe and Goldstein (2017) found that species that survived the drought had lower lateral-root surface area and relatively lower water content in roots than those that were vulnerable to the drought treatment, potentially aiming to reduce water loss. Although the opposite may be true, producing roots that can store water may promote plant survival under drought (Poorter & Markesteijn, 2008); however, little is known about the importance of such root adaptation in tropical forests. Root hydraulic conductance increased in the intermediate stages of wilting in a tree seedling drought experiment conducted in Panama (Tyree et al., 2003); yet, it is unclear why this occurred, and there are very few studies on root hydraulics in general. Due to the close link between soil water and nutrient uptake by roots, drought could also affect fine root trait expression due to multiple resource limitations (Cusack et al., 2021). Further studies should account for the interaction among these factors to improve our understanding of such mixed responses.

3.2.3 | Flooding

Flooding makes soil conditions hypoxic or anoxic, which is usually accompanied by increased levels of CO_2, anaerobic decomposition, and a reduction in the soil redox potential followed by an accumulation of potentially toxic compounds (Joly & Crawford, 1982; Wittmann, 2011). These conditions generally lead to a decreased root: shoot ratio as C allocation is prioritized to stem growth to enhance photosynthetic efficiency to survive under flooding, and phloem translocation to roots decreases (Yang & Li, 2016; Figure 4). Consequently, root production is reduced, mortality increases in anaerobic conditions, and total fine root biomass is reduced (Lopez & Kursar, 2003; Sauter, 2013; Figure 4). In some frequently flooded ecosystems, such as riparian and coastal areas, plants exhibit morphological, anatomical, and physiological adaptations to avoid oxygen deficiency (Yamamoto et al., 1995), such as aerenchyma tissue, greater root porosity, formation of adventitious roots and/or hypertrophic lenticels, pneumatophores, the induction of fermentative enzymes, as well as the production of elevated levels of antioxidant compounds (Cheng et al., 2015; Wang & Cao, 2012; Wittmann, 2011).

Few studies have measured root responses to flooding in tropical forests, all of them being at the species level (Figure 2b; Table S6). Most studies have measured root responses to flooding in flood-tolerant species, which seem more flexible in their response to flooding than those from non-flooded areas. For example, the root: shoot ratio of flood-tolerant species in a floodplain tropical forest increased during prolonged flooding (Lucas et al., 2013). Other studies have also shown physiological and anatomical adaptations to flooding in flood-tolerant species (Lopez & Kursar, 2003; Ow et al., 2019; Silva et al., 2010). Overall, studies have shown that, as expected, flooding reduced root biomass (Pisicchio et al., 2010), root: shoot ratio (Moungsrimuangdee et al., 2020), root productivity (Lopez & Kursar, 2003; Silva et al., 2010) and rooting depth (Lopez & Kursar, 2003) from tropical trees (Figure 4).

Root physiological responses to flooding include a change in the metabolic rates of specific compounds that guarantee enough ATP (adenosine triphosphate) production (Ribeiro et al., 2022). Experimental freshwater flooding has shown effects on root metabolomes and alcohol dehydrogenase activity (ADH), a key enzyme related to plant anaerobic metabolism, within flood-tolerant and drought-tolerant populations of *Guazuma ulmifolia* (Ribeiro et al., 2022). In response to flooding stress, both populations exhibited a significant increase in stress-associated root metabolites, including lactate, alanine, and gamma-aminobutyric acid, aiming to enhance photosynthesis and activate antioxidant enzymes, with only flood-adapted individuals increasing the concentration of five other root amino acids related to stress signaling (cysteine, glycine, serine, threonine, and proline; Ribeiro et al., 2022). Furthermore, the roots of flood-adapted individuals returned to normal metabolic levels faster than drought-adapted individuals (Ribeiro et al., 2022).

In Singapore, three tropical urban species decreased N uptake in response to experimental flooding but recovered after long-term flooding (Ow et al., 2019). *Melaleuca cajuputi*, a tropical tree species adapted to flooding, responded by moving from glycolysis within its root system to enhancing alcohol fermentation, an anaerobic pathway for energy production in flooded conditions (Yamanoshita et al., 2005). Finally, a study from a tropical floodplain in central Amazon found that a tree species adapted to flooding, *Salix martiana*, presented a lower resistance to gas exchange due to suberized hypodermis compared with *Tabernaemontana juruana*, allowing the former to have greater oxygen content in the root cortex under oxygen stress (De Simone et al., 2002). Such fast responses of metabolic and physiological root traits and recovery to pre-flooding conditions suggest coordinated regulatory mechanisms for flood tolerance that may give flood-tolerant species an adaptive advantage under increased flooding intensity and frequency (Lopez & Kursar, 2003; Ow et al., 2019; Silva et al., 2010).

A study in a semi-deciduous seasonal forest in Brazil found that with flooding, *Heliocarpus popayanensis* decreased its root cortex thickness (Pisicchio et al., 2010), while another study in the same country but in a riparian forest found that *Parapiptadenia rigida* increased cortex thickness, the diameter of cortical cells, and cortical porosity (Silva et al., 2010). In response to flooding, the latter species also developed hypertrophied lenticels, superficial and adventitious roots, and root aerenchyma, which confer these trees the advantage of tolerating oxygen deficiency (Silva et al., 2010). Flooding can also affect the mechanisms by which symbiosis with microorganisms can start. For instance, in species growing under hydroponic conditions, the intracellular invasion of roots by N-fixing bacteria took place at lateral-root bases, while under aerated conditions, it was via root hairs (Bomfeti et al., 2013; Goormachtig et al., 2004) with such versatile infection plasticity allowing efficient nodulation in flooded and non-flooded conditions in tropical species. Although the studies in this review show that low oxygen conditions of flooded soils directly affect root traits related to anatomy (Figure 3a,b), such as aerenchyma formation and root porosity, other traits, such as hydraulic conductivity and gas exchange, that might better reflect plant adaptations in such conditions were little studied. Another critical uncertainty lies in the responses of tree species in ecosystems predicted to experience unprecedented flooding due to climate change (Lucas et al., 2013).

3.2.4 | Cyclones

The aftermath of a cyclone in the vegetation can be very extreme, causing total defoliation in canopy species, uprooting trees, and depositing large amounts of debris onto the forest floor (Walker et al., 1991), which in turn influences the understory temperature, and moisture, and soil biogeochemistry (Shiels & González, 2014). Depending on the cyclone's intensity, the canopy loss can, in the short term, considerably decrease C allocation to the roots at the species level, reducing root production and total fine root biomass (Figure 4; Silver & Vogt, 1993). Due to the physical disturbance aboveground, fine and coarse root mortality is expected to increase, and mycorrhizal colonization is expected to decrease shortly after the disturbance. Differences in coarse root traits such as morphology, architecture, and anatomy can determine which trees will resist uprooting during a cyclone disturbance, but fine root traits can also be important in tree recovery after the disturbance (Marler, 2001). However, the mid to longer-term effects of a cyclone and the canopy opening include a shift in the plant community (Alonso-Rodríguez et al., 2022; Yaffar, Wood, et al., 2021), where acquisitive species thrive until the canopy closes again. Thus, changes in root morphological trait expression are expected, for instance, thinner and longer roots (Yaffar, Wood, et al., 2021). This can result in greater root production and biomass at the community level if conditions are favorable (Yaffar, Wood, et al., 2021).

Most of the information about the effect of cyclones in tropical forests comes from community-level studies (Figure 2b; Table S7). In congruence with our expectations, all studies we reviewed reported an immediate decline in fine root biomass following a cyclone disturbance due to physical disturbance and defoliation. Root biomass declined 40% after 2 months of a simulated hurricane disturbance (Silver & Vogt, 1993) and 200-fold 2 months after Hurricane Hugo passed through these sites due to root mortality increase (Beard et al., 2005; Parrotta & Lodge, 1991). It took over 10 years to recover root biomass after this hurricane due to root physical disturbance, changes in non-structural carbohydrates (NSC) in coarse roots, and moisture stress (Beard et al., 2005; Parrotta & Lodge, 1991), and recovery was slower for plots with aboveground removal (Teh et al., 2009). Similarly, Herbert et al. (1999) measured 48% root mortality and 2 years for root biomass recovery after Hurricane Iniki in a forest of Kauai, Hawaii. Contrary to previous studies, in a warming experiment in Puerto Rico that was interrupted by consecutive hurricanes Irma and Maria, root biomass and production increased 10 months after the hurricane disturbances in 2017, likely due to the change in forest composition where the understory flourished after canopy openness (Yaffar, Wood, et al., 2021). Such pre-warming conditions also decreased fine root production compared with control plots post-hurricanes (Yaffar, Wood, et al., 2021). Furthermore, rooting depth did not change after Hurricanes Irma and Maria in this same study (Yaffar, Wood, et al., 2021).

Multiple interactions between cyclone disturbance and other environmental or anthropogenic disturbances can affect root functional traits directly through wind force, anoxic conditions, or salt stress (Blood et al., 1991; Parrotta & Lodge, 1991) or indirectly through changes in soil nutrient availability, photosynthesis rates, and C allocation rates (Herbert et al., 1999; Parrotta & Lodge, 1991; Teh et al., 2009; Vargas et al., 2009; Yaffar, Wood, et al., 2021). For example, drier conditions after Hurricane Hugo delayed root recovery (Beard et al., 2005; Parrotta & Lodge, 1991), and soil P fertilization hastened root recovery after Hurricane Iniki (Herbert et al., 1999). Furthermore, Vargas et al. (2009) showed that plants allocated stored C to the production of new fine roots after canopy defoliation from Hurricane Wilma in Mexico, where the increased age of the C allocated for new roots increased with forest age in seasonally dry forests, suggesting plant adaptation to recover from cyclone disturbances.

On root morphological responses to cyclones, no apparent changes have been found for root length, diameter, branching ratio, and intensity at the species level after Hurricanes Irma and Maria (Yaffar, Defrenne, et al., 2021), but see Lodge et al. (2016). At the community level, SRL increased, and root diameter decreased after 10 months of Hurricanes Irma and Maria, showing the changes in plant community composition (Yaffar, Wood, et al., 2021). Root P and K concentration decreased after experimental aboveground biomass removal, with an even sharper decrease in root P after Hurricane Hugo (Silver & Vogt, 1993). However, no differences in root P concentration from different species in Puerto Rico were found after Hurricanes Irma and Maria (Yaffar, Defrenne, et al., 2021). Such contrasting responses can be attributed to the differences in environmental conditions after the hurricanes, the time of root measurements after the disturbance, and the root order selection for measurements.

Only a few studies measured root physiology and microbial association in response to cyclones (Figure 2a,b). Root phosphatase enzyme activity decreased 6 months after hurricanes Irma and Maria, but this response was unrelated to increased soil available P at the sites (Yaffar, Defrenne, et al., 2021). Vargas et al. (2010) measured root AMF colonization before and after Hurricane Wilma in Mexico and found that contrary to our expectations, AMF colonization increased post-hurricane, possibly to capitalize on the pulse in nutrient availability and the use of old NSC pools invested in maintaining and increasing the root length colonized by AM fungi (Vargas et al., 2009). As cyclone severity increases (Knutson et al., 2020), it is essential to have long-term measurements of the community and species-specific responses, especially from root traits such as root architecture, morphology, and root-microbial association that are more likely to respond to the effects of cyclones.

3.2.5 | Nitrogen deposition

Expected N deposition can increase soil ammonium and nitrate concentrations while lowering pH in urban-proximate tropical forests (Cusack et al., 2015). Root response can vary depending on local soil N status. For example, in N-scarce soils, such as those found in less-weathered soils or early successional and montane tropical forests, N deposition could relieve N limitation to plant growth and shift plant biomass allocation away from root biomass and root production (Cusack et al., 2011; Gower & Vitousek, 1989; Liu et al., 2020). In N-rich soils, which are typical of strongly weathered soils in the majority of lowland tropical forests (Holzman, 2008), N deposition may cause indirect effects on roots via decreased soil pH and mobilization of scarce rock-derived nutrients like P and base cations (Cusack et al., 2016). If N deposition triggers higher P or cation availability, root biomass might decrease as a sign of alleviation of nutrient limitation, or contrarily, if the limitation of those elements is exacerbated, root biomass could increase, and traits would change to facilitate uptake of the limiting resources. For instance, root phosphatase activity in P-limited environments is expected to increase with N addition to increase P mineralization (Houlton et al., 2008). Nonetheless, the multiple effects of N deposition on N availability, soil pH, and mobilization/leaching of rock-derived nutrients can produce interacting and conflicting impacts, such that there could be no net effects on tropical forest root characteristics (Figure 4). Only a few studies have simulated N deposition by applying fertilizers in amounts compared with atmospheric deposition (Mo et al., 2015;

Zhu et al., 2022). In this review, we extend our scope to encompass in situ and pot N fertilization experiments (Figure 2a). While these experiments partially simulate N deposition by applying fertilizers onto the soil surface, they may not fully capture the impacts on canopy processes and throughfall, which are typical of atmospheric deposition.

Overall, N fertilization experiments in the tropics have shown that forest ecosystems vary substantially in plant growth responses to added N (Table S8; Wright, 2019; Wright et al., 2018). For example, N additions increased root productivity in N-limited montane forests in Panama (Adamek et al., 2011) but did not affect root biomass stocks in these same forests (Adamek et al., 2011; Andersen et al., 2010) nor in mixed pine and evergreen forests in China (Zhu et al., 2013). N addition in N-limited soils in Hawaii increased root biomass (Ostertag, 2001), while it decreased both root biomass and necromass in premontane, N-rich forests in Puerto Rico (Cusack et al., 2011). However, N addition did not result in changes in root biomass or production in P-limited forests in Colombia (Quinto Mosquera & Moreno Hurtado, 2022), Brazil (Lugli et al., 2021), and Hawaii (Ostertag, 2001), or in high-N and high-P lowland tropical wet forests in Costa Rica (Alvarez-Clare et al., 2013) and Panama (Wurzburger & Wright, 2015; Yavitt et al., 2011). These mixed results of N addition across tropical forests highlight that soils with different baseline N status, soil pH, and leaching effects of N can render contrasting effects of N addition on roots.

Across several studies in the Americas, there has been no response of root morphological traits with N additions. For example, root length or SRL did not change in most studies in low-P fertility forests (Table S8; e.g., Blair & Perfecto, 2008; Lugli et al., 2021; Wurzburger & Wright, 2015). Moreover, root diameter, SRA, and RTD in P-limited central Amazon forests did not change with N addition (Lugli et al., 2021), nor did root tips per length in a low-P lowland tropical forest in Panama (Woods et al., 2018). Some N-addition studies found increased fine root N content, including N-rich tropical forests in China and Puerto Rico (Cusack et al., 2011; Mo et al., 2015; Zhu et al., 2022) and N-poor secondary forests and plantations in China (Zhu et al., 2022). In a pot experiment in Panama, Batterman, Wurzburger, et al. (2013) also found that N addition increased N content in roots in plants growing in naturally low-P soils. However, other studies found no responses in root N content to N addition in high-N forests (Alvarez-Clare & Mack, 2015; Lugli et al., 2021; Wang et al., 2019; Wurzburger & Wright, 2015) and in N-poor forests in China (Zhu et al., 2013). No changes in C concentrations in roots were observed in P-poor tropical forests/species (Batterman, Wurzburger, et al., 2013; Lugli et al., 2021), while C:N decreased in N-rich tropical forests and N-poor tropical plantations in China (Zhu et al., 2022). Root P concentrations, in general, did not change with N addition (Alvarez-Clare & Mack, 2015; Lugli et al., 2021; Mo et al., 2015; Zhu et al., 2013) but decreased with simulated N-deposition levels in N-rich tropical primary forests in China (Zhu et al., 2022) and potted plants growing in low-P soils in Panama (Batterman, Wurzburger, & Hedin, 2013). Thus, root morphology typically has not changed with N additions, but fine root N content has had mixed responses across tropical forests (Figures 3a and 4).

In agreement with the expected stimulation of root phosphatase activity, N fertilization in Hawaii increased root phosphatase production across soils ranging from N-limited and fertile to P-limited (Treseder & Vitousek, 2001). However, studies conducted in primary and secondary humid forests in China (Ao et al., 2022), P-limited primary and secondary forests in Borneo (Yokoyama et al., 2017), and an Amazonian tropical forest (Lugli et al., 2021) reported no change in root phosphatase activity when N was added. Other physiological traits, like root respiration in a montane forest in Peru (NP co-limitation), decreased with N addition (Fisher et al., 2013), while N uptake decreased in P-limited forests in Hawaii, and P uptake did not change in all the Hawaiian study sites across a range in soil fertility (Treseder & Vitousek, 2001). Thus, while most studies have found no change in root physiology with N addition, there is some indication that N addition could shift roots toward more P acquisition, lower root respiration, and/or decreased N uptake in some P-scarce tropical forests.

For microbial associations, most studies found decreased colonization rates of AMF when N was added, as in Hawaiian P-limited forests (Treseder & Vitousek, 2001), in *Inga punctata* (Batterman, Wurzburger, et al., 2013) and in NP co-limited montane forests in Ecuador (Camenzind et al., 2014). However, some studies found no change in AMF colonization with N addition in P-limited forests in the Amazon (Lugli et al., 2021) and N-limited forests in Hawaii (Treseder & Vitousek, 2001). Another study found that the response varied with elevation in Ecuador (Cárate-Tandalla et al., 2018). Interestingly, nodule formation and N fixation rates in roots decreased with N addition, independently of background soil fertility across some Costa Rican and Panamanian forests (Batterman, Hedin, et al., 2013; McCulloch & Porder, 2021; Waring et al., 2019). Thus, as with other effects of N addition, responses of root symbionts varied across sites and were not always in accordance with baseline soil fertility. Overall, while N fertilization is the global change type of experiment with the most root trait observations in our review, there is still generally poor replication across sites with similar baseline fertility and elevation, and there are under-measured root traits related to anatomy and architecture.

3.2.6 | Increasing atmospheric carbon dioxide concentration

The increasing concentration of CO_2 in the atmosphere is fundamentally different from the other global change drivers discussed here. Rather than being episodic and geographically variable, CO_2 is increasing gradually and uniformly across the Earth. Although increasing global atmospheric CO_2 concentration is the main driver of global climate changes, its effects on fine roots are likely to be indirect responses: the direct effects of CO_2 occur only in leaves, with changes in roots being secondary or tertiary responses to changes in C allocation or interactions with water or nutrient economies.

Although there have been few studies of elevated CO_2 responses in tropical trees (Cernusak et al., 2013; da Silva Fortirer et al., 2023) or forests, the relative response of root growth or root: shoot ratio to equivalent CO_2 was inconsistent, often varying with soil nutrient status (Figure 4; Table S9). Therefore, hypotheses can be proposed based on many studies of temperate regions while recognizing that responses in tropical ecosystems will be shaped by the overriding influence of soils and climate. Competing model-driven hypotheses for the AmazonFACE experiment (https://amazonface.inpa.gov.br/) in central Amazonia in Brazil include a greater stimulation of net primary productivity (NPP) than observed in temperate forests due to greater CO_2 stimulation of photosynthesis in warmer temperatures (Hickler et al., 2008) or, alternatively, reduced NPP response because of the nutrient limitation in nutrient-poor tropical soils (Fleischer et al., 2019; Yang et al., 2019). If C assimilation and NPP increase—the primary mechanism of CO_2 response—an increase in the allocation of C belowground can be expected, supporting possible increases in root production and biomass, deeper root distribution, and increased root activity, including exudation and enzymatic activity. Testing these predictions in CO_2 enrichment experiments should be a high priority because of the interactions of root systems on soil biogeochemical cycling and their feedback on the NPP response (Iversen et al., 2012). Responses to elevated CO_2 of root morphology within the same species and root order are less likely, and since tropical roots are already heavily colonized by AMF, no changes in mycorrhizal colonization at the root level are expected. Testing these predictions will require carefully separating individual tree responses from community-level responses, which can be difficult in highly diverse tropical forests. Below, we focus on experiments and model projections from subtropical and warm temperate forests, and guided by these and the few studies from tropical species (Figure 2a,b), we highlight critical questions concerning root responses to eCO_2 in the tropics.

Until now, very few experiments have aimed to document tropical species-level responses to eCO_2, and the absence of large-scale fertilization experiments in tropical forests precludes any understanding of community responses. Agreeing with our expectations, tropical species-level pot studies have found increased coarse and fine root biomass and total length under eCO_2 (Arnone & Körner, 1995; Reef et al., 2016; Reekie & Bazzaz, 1989). Nonetheless, root:shoot ratios responses were absent or tended to decline with eCO_2 (Arnone & Körner, 1995; Reef et al., 2016; Reekie & Bazzaz, 1989), which suggests either a whole-plant increase in biomass or an even greater stimulation of C allocation aboveground. Fine root productivity is an essential component of forest NPP (Huaraca Huasco et al., 2021), and its expected increase in response to eCO_2 has been observed in temperate forest eCO_2 experiments (Matamala & Schlesinger, 2000; Norby et al., 2004), although no data from tropical species/forests are available. However, evidence from the warm temperate, P-limited Eucalyptus woodland EucFACE site has shown only a minor increase in fine root biomass and turnover in the top 30 cm of soil with eCO_2, despite a significant increase in C flux belowground (Jiang et al., 2020), with root biomass instead temporally tied to water availability (Piñeiro et al., 2022). Although root mass and productivity measurements in tropical forests are often confined to the soil's top 30 cm (or less), this approach will likely miss a significant fraction of roots, such as the case of fine roots growing up to 1 m depth in central Amazonia (Cordeiro et al., 2020). In temperate forests, eCO_2 has often been associated with deeper root distributions (Iversen, 2010), which can provide increased access to limiting nutrients and water, and increased input of C to deeper soil (Iversen et al., 2012). In addition, fine roots on the surface and in the litter layer are a unique feature of wet tropical forests growing in highly weathered soils (Herrera et al., 1978; Martins et al., 2021; Stark & Jordan, 1978). Since recycling plant organic matter is an essential source of nutrients in tropical forests, the role of roots growing in more superficial soil layers should be addressed.

The type of root-mycorrhizal interactions may also modulate responses to eCO_2. In a meta-analysis gathering data from eCO_2 experiments in different parts of the globe, Terrer et al. (2016) showed that plant species associated with ectomycorrhizal (ECM) fungi increased their above and belowground biomass in eCO_2 regardless of N availability, whereas the CO_2 response of AMF-associated plants was limited by low N availability (Terrer et al., 2016). Tropical forests typically associated with P limitation and dominated by AMF could potentially show enhanced biomass under eCO_2 (Terrer et al., 2016). This speculation sets forth a worthwhile hypothesis and leaves open the question of responses of ECM-dominated tropical forests, such as Dipterocarp forests. Effects of eCO_2 on mycorrhizal colonization and hyphal growth have been studied in many temperate tree species and forests (e.g., Mohan et al., 2014; O'Neill et al., 1987; Treseder, 2004), but much less so in the tropics. Seedlings of the shade-tolerant tropical tree *Beilschmiedia pendula* had greater AMF colonization in eCO_2 than in ambient controls (Lovelock et al., 1996). Nasto et al. (2019) attributed the increased AMF colonization of tropical tree seedlings in eCO_2 to a greater metabolic capacity to acquire P. In addition to AMF, several studies found higher N fixation activity in tropical tree seedlings grown in eCO_2 (Nasto et al., 2019; Thomas, Bashkin, et al., 2000; Trierweiler et al., 2018). In old tropical soils, the association between N_2-fixing bacteria and trees is widespread (Houlton et al., 2008). Despite the potential mechanisms behind N_2-fixers allowing for greater N investment in mycorrhizal association and/or exudation of P-related enzymes (Nasto et al., 2017), studies have failed to find support for this hypothesis at the individual and species level in tropical forests (Batterman et al., 2018; Batterman, Wurzburger, et al., 2013; Nasto et al., 2014; Soper et al., 2019), suggesting that the interactions between soil N and P availability, especially in changing climate, warrants further study.

Interactions between eCO_2 and nutrient availability have been key to evaluating ecosystem response to eCO_2 (Zaehle et al., 2014). Many tropical forests are more likely to be limited by P rather than by N (Cunha et al., 2022); models representing Central Amazon forests project a diminished response to eCO_2 when P limitation is factored in (Fleischer et al., 2019). However, some of these limitations might be alleviated if there are mechanisms whereby eCO_2 increases P availability (Reichert et al., 2022). For example, the potential extra

C assimilated by plants could be either invested in exchange for nutrients or protection against pathogens via AMF (Nasto et al., 2019) and could trigger positive priming (Nottingham et al., 2012; Phillips et al., 2012). Experiments with seedlings of four species of tropical trees grown in eCO_2 indicated that phosphatase activity was stimulated in some species but not in others (Nasto et al., 2019). Hence, future work could test the hypothesis that forests exposed to eCO_2 in situ (especially in an intact forest Free Air CO2 Enrichment-FACE experiment) increase root phosphatase activity at the ecosystem level, as the whole forest responds to increasing competition and demand for soil P. The quality of the root tissue produced under eCO_2 could also affect ecosystem-level litter decomposition and nutrient cycling. Increased CO_2 concentrations (800 ppm) elicited changes in root tissue quality, resulting in higher root P concentrations in a study with seedlings of *Avicennia germinans*, a tropical mangrove tree species (Reef et al., 2016). Although FACE experiments in temperate forests have provided valuable information on forest responses to future climate (Norby & Zak, 2011) and have informed ecosystem models (Medlyn et al., 2015), to date, no FACE experiment has been conducted in the tropics. The AmazonFACE experiment (https://amazonface.inpa.gov.br/), currently under development in central Amazon in Brazil, will help to fill such a significant gap.

3.2.7 | Fire

Fires not only kill and damage trees aboveground but burn belowground biomass as well. In places where fires are common, native species typically exhibit a relatively large biomass investment into roots (Boonman et al., 2020; Durigan et al., 2012; Fidelis et al., 2013) compared with other species from less fire-prone environments to survive fires (Tomlinson et al., 2012), tolerate dry seasons (Durigan et al., 2012), or store NSC for resprouting (Boonman et al., 2020; Durigan et al., 2012; Hoffmann et al., 2004; Schutz et al., 2009). At the community level, the initial decline in root biomass is followed by increasing investment in belowground productivity in post-fire recovery phases (Durigan et al., 2012; Uhl & Jordan, 1984). Fire immediate and short-term effects on root traits include a reduction in belowground biomass and heightened root mortality (Asbjornsen et al., 2005; Delitti et al., 2001; Uhl & Jordan, 1984). As photosynthetic aboveground organs are lost to fires, short-term carbon investments into root production and mycorrhizal colonization are expected to decline. However, in the long run, subsequent fire events may shift community composition from a woody forest into a more herbaceous-dominated ecosystem state reflecting root traits that promote post-fire regrowth, such as a greater root:shoot ratio, SRL, root productivity, and concentrations of NSCs (Figure 4; Archibald et al., 2019; Issifu et al., 2021; Paula & Pausas, 2011).

Only one study has examined how fires influence the root traits of surviving plant species, so we focus here on observations of community-level changes in root traits associated with transitions from forests to more herbaceous-dominated landscapes (Figures 2b and 4; Table S10). As expected, fires have been observed to reduce root biomass and drive root mortality in the short term (<5 years post-fire; Table S10) in a variety of tropical ecosystems, including a montane cloud forest in Mexico (Asbjornsen et al., 2005), a lowland forest in Venezuelan Amazon (Uhl & Jordan, 1984), the Brazilian cerrado (Delitti et al., 2001), and in the Western Ghats of India (Sundarapandian & Swamy, 1996). Only one study found that root biomass and C concentrations of roots <5 mm in diameter did not vary significantly with stand age in a fire recovery chronosequence in western Mexico (Quintero-Gradilla et al., 2020). Such differences might be due to the time elapsed post-fire and the communities examined in post-fire environmental conditions (Asbjornsen et al., 2005; Issifu et al., 2021). Responses of fine root productivity to fire also varied, with no responses detected in savannas and semi-deciduous forests in Brazil (Loiola et al., 2015) and higher productivity in moist forests in India (Sundarapandian & Swamy, 1996). We also note a significant research gap in the indirect effects of fire on root systems via altering mycorrhizal networks (Cairney & Bastias, 2007), for which no such data exists to our knowledge. We expect mycorrhizal colonization should decline due to the disruption of fire on belowground root biomass and the lack of photosynthate investment from burnt aboveground organs to sustain root symbiont associations.

The effect of fires can impact root tissue quality, though a lack of studies exists on this topic. A common observation from fire-prone environments is the enhancement of root NSCs used to stimulate the regrowth of burnt plant organs (Hood et al., 2018; Issifu et al., 2021). A study from a northern Australian savanna demonstrated that unburnt plots had three times the wet season soil respiration as burnt plots, mainly due to significant differences in root-derived respiration (Richards et al., 2012). This might suggest that fires indirectly impact root C and nutrient dynamics belowground, though further studies, especially at the species level, are required to conclusively determine if and how different species can cope with this global change driver in tropical forests. Although we expected that changes in plant community would favor species with root acquisitive traits (e.g., higher SRL), no data on root morphology or root anatomical traits were available (Figure 2a,b). As more fire events start to enter non-fire-prone ecosystems, the resilience of non-adapted forests might be compromised as they may lack root traits that promote fire resistance or tolerance (Cardoso et al., 2016; Hoffmann et al., 2004). Hence, it is imperative that we identify relevant root traits for assessing future species' capacity to adapt to fire events.

3.3 | General patterns and moving forward

This review highlights the inherent diversity in root trait responses to global change drivers. In summary, root traits across different categories were responsive to global change drivers, although the presence and direction of changes were specific to the different drivers. Additionally, our findings indicate that the probability of responses to global change drivers remains consistent across root trait categories. However, we acknowledge the potential for broader datasets in the future to unveil novel patterns not captured in this study, especially if less commonly measured traits are included.

While N deposition (using N fertilization experiments as proxies) was the global change with most measurements in tropical regions, it was the one where root traits were least responsive, potentially due to other limiting environmental resources (e.g., P). From these few responses, we found stimulation of phosphatase enzyme exudation and decline in AMF and N_2-fixing symbiosis, suggesting that less studied physiological root traits and microbial associations could be more prone to responses than other commonly measured traits. Drought was also among the global change drivers stimulating fewer changes in root traits, but in general, we found increased root:shoot ratio at the same time as increasing total root length, potentially increasing water uptake as greater soil volume is explored. Despite the gradual and almost uniform increase in warming and CO_2 around the globe, these were the least studied global change drivers, together with fire. From these few studies, roots from tropical species seemed very responsive to eCO_2 and warming, with generally increased root biomass. Microbial association (mycorrhizal fungi and N_2-fixing bacteria) also increased with eCO_2, likely to increase soil resource acquisition to support plant growth. The abrupt changes in environmental conditions after flooding, cyclones, and fire also translate into root dynamics and trait expression changes. With flooding, we noted responses related to root physiology and chemistry and changes in rooting depth distribution to overcome anoxic conditions. Yet, these changes were different for flood-adapted species compared with non-adapted species, showing more flexibility of root traits on species that are frequently affected by floods. The plant community change following fire and cyclones generally decreases root biomass but increases productivity and investment in acquisitive morphological traits or association with arbuscular mycorrhizal fungi, as more acquisitive plants are established in the newly disturbed habitats.

Among the potential variables and mechanisms explaining such diversity in root responses to global change, we list the scale of measurement (species vs. community level studies; measurements at the root order versus total root system), differences in experimental timeframe and treatment intensity, and the potential interactions between global changes and other limiting environmental resources. The high taxonomic and functional diversity within tropical forests (Gatti et al., 2022) is reflected in the variety of responses found in root trait expression across studies and the frequent disagreement between expected and observed patterns (Figure 4). Incorporating functional grouping or syndromes based on root trait characteristics (Dallstream et al., 2022) would be relevant to simplifying the immense species diversity in tropical forests (i.e., Rius et al., 2023). Furthermore, understanding whole-plant responses to global changes could shed light on compensatory mechanisms between above and belowground plant tissues, where, for instance, the lack of or weak changes in some root traits could be counterbalanced by changes at the leaf level and vice-versa. Understanding changes in root:shoot allocation and the expression of root traits related to resource acquisition and use will likely be essential to predict the forest's role as future C sinks. In that sense, the outcomes of community-level and species-level responses can differ, with community-level information potentially representing the trait responses from the most dominant species. In addition, understanding these responses across different soil depths and the interaction between roots, microbes, and environmental properties will strengthen the link between root traits and their functions. This will likely move the focus of this research field away from only commonly studied characteristics (e.g., root biomass and production) and into physiological, chemical and anatomical traits that are likely to respond faster to environmental changes.

Many challenges exist in conducting large-scale ecosystem experimental manipulation, and at the same time, there are limitations in extrapolating information derived from plant-level studies. For instance, differences in experiment duration can affect trait responses, but many manipulation experiments are not funded for more extended periods. Therefore, most studies tend to capture plant trait plasticity rather than species turnover, except for fire and cyclone studies, which are episodic and destructive global change drivers that generally result in the establishment of new species. Moreover, in a multi-factor world where global change drivers co-occur and other environmental resources are simultaneously limiting, factorial experimental approaches can be helpful in understanding root responses, although the interpretation of results remains challenging (Norby & Luo, 2004). For example, episodic disturbances such as cyclones, fires, and flooding decrease root biomass, and under elevated CO_2 and warming, the C losses from tropical soils could be even more significant. Furthermore, due to the tendency of stronger P rather than N limitation in many tropical forests (Cunha et al., 2022; Lugli et al., 2021; Wright, 2019), understanding differences in soil nutrient availability will help us predict which regions will be most affected by increased N deposition either directly or indirectly and how this might interact with other global changes (e.g., eCO_2, drought). Therefore, modeling approaches are of great value in overcoming empirical limitations in predicting root responses to diverse climate change scenarios (Cusack et al., 2024; Norby & Luo, 2004).

Since the frequency and strength of some climate change drivers reported here are expected to increase and become more widespread, studying the less affected ecosystems might help us establish how resilient forests would be. The heterogeneity of tropical forests makes it critical to examine how responses to different global changes vary among tropical regions using consistent methods. We also note a lack of data from the paleotropics, and we anticipate that background differences in root trait expression compared with other tropical regions (Addo-Danso et al., 2020) might result in different forest response trajectories due to global change. The plasticity of plant root traits, their ability to sustain such changes, and future species turnover (favoring species with more adapted traits) are crucial in determining the consequences of climate change in forest ecosystems. Ultimately, this information becomes vital in developing robust mitigation and adaptation strategies for tropical regions.

AUTHOR CONTRIBUTIONS

Daniela Yaffar: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Laynara F. Lugli:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; supervision; validation; visualization; writing – original draft; writing – review and editing. **Michelle Y. Wong:** Conceptualization; data curation; methodology; resources; writing – original draft; writing – review and editing. **Richard J. Norby:** Resources; supervision; validation; writing – original draft; writing – review and editing. **Shalom D. Addo-Danso:** Data curation; formal analysis; investigation; methodology; validation; writing – original draft; writing – review and editing. **Marie Arnaud:** Conceptualization; data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Amanda L. Cordeiro:** Conceptualization; data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Lee H. Dietterich:** Data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Milton H. Diaz-Toribio:** Data curation; methodology; resources; writing – original draft; writing – review and editing. **Ming Y. Lee:** Data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Om Prakash Ghimire:** Data curation; investigation; methodology; validation; writing – review and editing. **Chris M. Smith-Martin:** Data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Laura Toro:** Data curation; investigation; methodology; resources; writing – original draft; writing – review and editing. **Kelly Andersen:** Validation; writing – review and editing. **Lindsay A. McCulloch:** Investigation; validation; writing – review and editing. **Ina C. Meier:** Validation; writing – review and editing. **Jennifer S. Powers:** Writing – review and editing. **Mareli Sanchez-Julia:** Methodology; validation; writing – review and editing. **Fiona M. Soper:** Validation; writing – review and editing. **Daniela F. Cusack:** Conceptualization; formal analysis; resources; software; writing – review and editing.

AFFILIATIONS

[1]Environmental Science Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA
[2]Functional Forest Ecology, University of Hamburg, Hamburg, Germany
[3]School of Life Sciences, Technical University of Munich, Freising, Germany
[4]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA
[5]Cary Institute of Ecosystem Studies, Millbrook, New York, USA
[6]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, USA
[7]Forest and Climate Change Division, CSIR-Forestry Research Institute of Ghana, Kumasi, Ghana
[8]Sorbonne Université, CNRS, INRAE, Institute of Ecology and Environmental Sciences (IEES), Paris, France
[9]School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK
[10]Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, Colorado, USA
[11]Department of Biology, Haverford College, Haverford, Pennsylvania, USA
[12]Jardín Botánico Francisco Javier Clavijero, Instituto de Ecología, A.C. Xalapa, Veracruz, Mexico
[13]Asian School of the Environment, Nanyang Technological University, Singapore, Singapore
[14]Department of Plant and Environmental Sciences, Clemson University, Clemson, South Carolina, USA
[15]Department of Plant and Microbial Biology, University of Minnesota, St. Paul, Minnesota, USA
[16]Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, Missouri, USA
[17]Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama
[18]Department of Integrative Biology, University of South Florida, Tampa, Florida, USA
[19]Department of Biology and Bieler School of Environment, McGill University, Montreal, Qubec, Canada

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the SI and in the NGEE-T Archive: https://doi.org/10.15486/ngt/2382698.

ORCID

Daniela Yaffar https://orcid.org/0000-0002-8090-7096
Laynara F. Lugli https://orcid.org/0000-0001-8404-4841
Michelle Y. Wong https://orcid.org/0000-0002-7830-8035
Richard J. Norby https://orcid.org/0000-0002-0238-9828

Shalom D. Addo-Danso https://orcid.org/0000-0001-5074-1673
Marie Arnaud https://orcid.org/0000-0003-4001-6499
Amanda L. Cordeiro https://orcid.org/0000-0001-7226-0133
Lee H. Dietterich https://orcid.org/0000-0003-4465-5845
Milton H. Diaz-Toribio https://orcid.org/0000-0003-1675-2699
Ming Y. Lee https://orcid.org/0000-0002-4538-9342
Om Prakash Ghimire https://orcid.org/0009-0005-7206-2352
Chris M. Smith-Martin https://orcid.org/0000-0002-6557-1432
Laura Toro https://orcid.org/0000-0002-0550-3294
Kelly Andersen https://orcid.org/0000-0002-1460-9904
Lindsay A. McCulloch https://orcid.org/0000-0001-6868-2632
Ina C. Meier https://orcid.org/0000-0001-6500-7519
Jennifer S. Powers https://orcid.org/0000-0003-3451-4803
Mareli Sanchez-Julia https://orcid.org/0009-0001-3193-8259
Fiona M. Soper https://orcid.org/0000-0002-9910-9377
Daniela F. Cusack https://orcid.org/0000-0003-4681-7449

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Cusack, D. F., Christoffersen, B., Smith-Martin, C. M., Andersen, K. M., Cordeiro, A. L., Fleischer, K., Wright, S. J., Guerrero-Ramírez, N. R., Lugli, L. F., McCulloch, L. A., Sanchez-Julia, M., Batterman, S. A., Dallstream, C., Fortunel, C., Toro, L., Fuchslueger, L., Wong, M. Y., Yaffar, D., Fisher, J. B., … Norby, R. J. (2024). Toward a coordinated understanding of hydro-biogeochemical root functions in tropical forests for application in vegetation models. *New Phytologist*, *242*(2), 351–371. https://doi.org/10.1111/nph.19561

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SUPPORTING INFORMATION

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