

RESEARCH ARTICLE

Rainfall seasonality shapes belowground root trait dynamics in an Amazonian tropical rainforest: A test of the stress-dominance hypothesis

Oscar J. Valverde-Barrantes¹  | Laynara F. Lugli^{2,3}  | Lucia Fuchslueger^{2,4}  | Florian Hofhansl⁵  | Nathielly Martins²  | Amanda L. Cordeiro^{2,6}  | Karst Schapp^{2,7}  | Kelly M. Anderson⁸  | Sabrina Garcia² | Adriana Grandis⁹  | Carol A. Miron^{2,10}  | Katrin Fleisher¹¹  | Marcel R. Hoosbeek⁷  | Ian P. Hartley¹²  | Erick Oblitas Mendoza² | David Lapola¹³  | Carlos A. Quesada²

¹Department of Biological Sciences, Institute of Environment, International Center of Tropical Botany, Florida International University, Miami, Florida, USA; ²Coordination of Environmental Dynamics, National Institute for Amazonian Research, Manaus, Brazil; ³School of Life Sciences, Technical University of Munich, Freising, Germany; ⁴Center for Microbiology and Environmental Systems Science, University of Vienna, Vienna, Austria; ⁵International Institute for Applied Systems Analysis, Laxenburg, Austria; ⁶Department of Ecosystem Science and Sustainability, Warner College of Natural Resources, Colorado State University, Fort Collins, Colorado, USA; ⁷Soil Chemistry, Wageningen University, Wageningen, The Netherlands; ⁸Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, USA; ⁹Laboratory of Plant Physiological Ecology, Department of Botany, Institute of Biosciences, University of São Paulo, São Paulo, Brazil; ¹⁰Department of Biology, University of Hamburg, Hamburg, Germany; ¹¹Department Biogeochemical Signals, Max-Planck-Institute of Biogeochemistry, Jena, Germany; ¹²Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK and ¹³Universidade Estadual de Campinas (UNICAMP), São Paulo, Brazil

Correspondence

Oscar J. Valverde-Barrantes
Email: os.valverde33@gmail.com

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Abstract

1. The stress-dominance hypothesis (SDH) predicts that trait variation at the community level increases with the availability of limiting resources, driving spatial and temporal patterns in above-ground plant functional trait expression. Here, we test the assumption that the SDH also applies to fine roots responding to spatial and temporal fluctuations in soil resource availability.
2. We monitored fine root mass and functional root traits associated with resource acquisition, that is specific root length (SRL), specific root tip abundance (SRTA) and branching index (BI), and traits related to stress tolerance, such as root diameter (RD) and tissue density (RTD) in a Central Amazonian tree community. To test for spatial differences in root traits, we separated the uppermost organic (O-A horizon, 0–5 cm) and mineral soil (B horizon, 5–15 cm) layers, and for temporal fluctuations, we investigated the relationship of precipitation on community-level root variation over a period of 27 months.
3. In accordance with the SDH, we found that fine roots in the O-A horizon have on average 15% higher SRL, 23% higher BI, 32% higher SRTA and 15% lower RTD than those in the B horizon. Similarly, precipitation shifted the community over time to higher mean SRL, BI and SRTA ($r=0.92$, 0.84 and 0.94 , $p<0.0001$).

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respectively), although trait shifts occurred in the trimester after the rainy season onset, revealing a time-lag between rainfall patterns and community response. We also detected a positive increase in trait range for SRL and SRTA with lagged precipitation ($r=0.90$ and 0.79 , $p<0.0001$). On the other hand, traits related to stress showed a weaker negative relationship with instantaneous precipitation ($r=-0.7$ and -0.57 , $p=0.046$ and $p=0.1$ for RD and RTD, respectively).

4. Our results supported the SDH predictions that root systems will become more acquisitive in areas with more resources, and that the community will shift to more acquisitive but also broader trait dispersion as hydric stress decreases. We conclude that although higher resource availability may increase competition for acquisition, trait overdispersion seems to promote species coexistence. Our results highlight how dynamic root systems can be in response to environmental cues, cautioning the common practice of making conclusions about root traits adaptations to environmental gradients based on a single sampling observation.

KEYWORDS

Amazon, root functional traits, root plasticity, temporal variation, tropical forest

1 | INTRODUCTION

Fine roots, the most distal portions of the root system (usually <1 mm in diameter), are responsible for the uptake of soil resources, drive soil organic matter accrual in plant-dominated ecosystems and are a key factor driving mineral weathering and soil microbial dynamics (Bardgett et al., 2014; Cusack et al., 2021; Laughlin et al., 2021; McCormack et al., 2015). Despite the crucial importance of fine roots in the biogeochemical cycling of elements, few field studies have included the variation in root traits as potential drivers of ecological process, such as competition for limiting resources or species coexistence (Luo et al., 2024). Initial efforts to collate global data describing the interspecific variation in root traits point out two key dimensions (Bergmann et al., 2020). The first dimension is largely associated with the variation in specific root length (SRL, m/g), root diameter (RD, mm), the branch configuration of the root systems expressed as branching index (BI, tips/cm) and specific root tip abundance (SRTA, tips/mg). The association between these traits indicates a functional trade-off in C allocation belowground, with some species investing in a 'outsourcing' plan, showing larger cortical area, less root length and depending more on symbiotic associations for soil nutrient exploration. In contrast, those species with a 'do-it-yourself (DIY)' strategy tend to minimize symbiotic colonization and maximize root surface exposure to acquire limiting resources per relative investment of root tissue. The second dimension is interpreted as a trade-off between resource acquisition and conservation strategies, usually represented by the trade-off between root tissue density (RTD, g/cm^3) and nitrogen content in the roots. The underlying principle of this variation is that roots achieve high RTD through thicker and more stable cell walls, increasing stress tolerance but

reducing metabolic rates and thus potentially downregulating uptake capacity (Bergmann et al., 2020; Weigelt et al., 2021).

The spatial or temporal availability of soil resources could explain the dominance of alternative root traits in a community as suggested by the stress-dominance hypothesis (SDH, Grime, 1977). The SDH states that an increase in environmental stress (i.e. environmental conditions that negatively affect plant fitness) influences the distribution of functional traits within communities, and the importance of biotic competition declines as the influence of the stressor increases (Swenson & Enquist, 2007). According to the SDH, plant communities adapted to stressful conditions converge to similar stress-tolerant traits, thus exhibiting lower trait diversity skewed to the scope where trait adaptation improves the likelihood of survival. In contrast, more favourable conditions boost biotic competition for available resources, triggering higher frequency of traits positively associated with resource uptake and trait over-dispersion at the community level (i.e. wider dispersion of traits around the mean, expressed as range) as niche segregation improves species coexistence (HilleRisLambers et al., 2012; Weiher & Keddy, 1995). In other words, the SDH predicts contrasting trends in the representation of root traits in communities as resources become more readily available (Coyle et al., 2014; Figure 1).

Consistent with the SDH, studies focussing on leaf and stem traits have found that, at the community level, trait frequency is partially coupled with the apparent stress experienced by plant communities (Ackerly & Cornwell, 2007; Kraft et al., 2008; Coyle et al., 2014; Figure 1). For instance, abiotic factors such as low moisture availability or high sand content were correlated with higher frequency of low specific leaf area (SLA) or high wood density (Cornwell & Ackerly, 2009; Kooyman et al., 2010; Vleminckx et al., 2021).

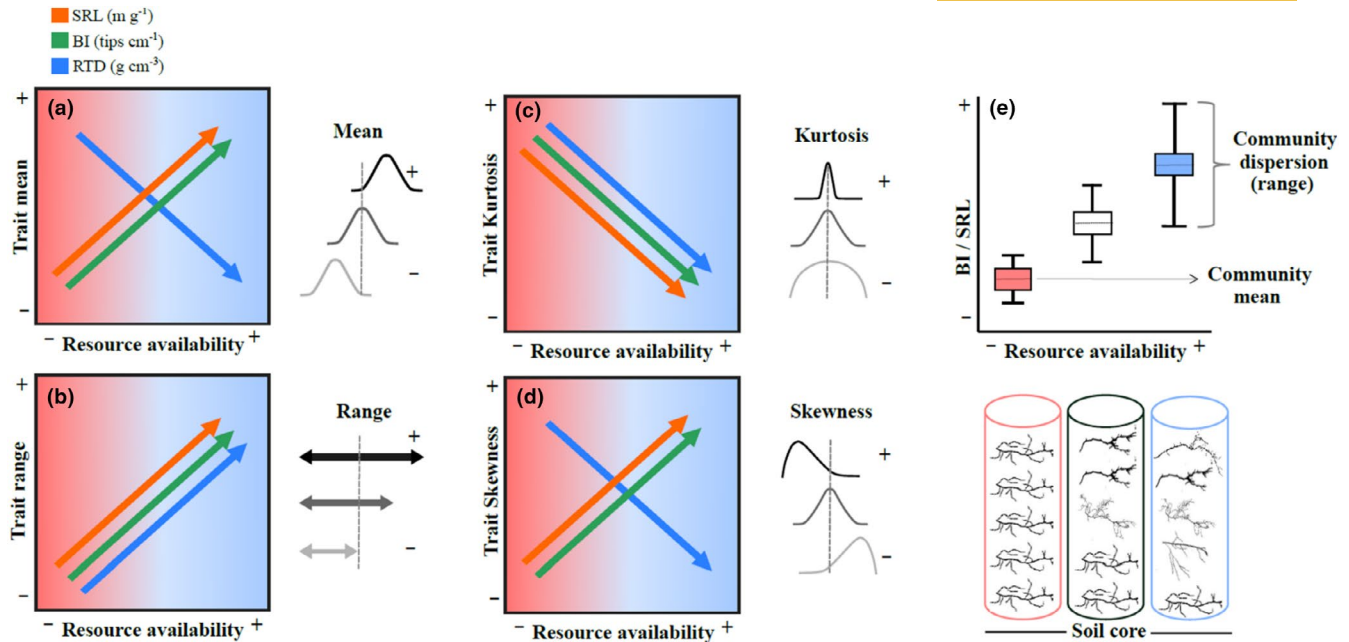


FIGURE 1 Expected shifts in root community trait values along changes in resource availability under the stress-dominance hypothesis (SDH). Variation between low and high resource availability could be interpreted as either temporal changes related to climate (e.g. precipitation) and/or variation between the upper and deeper soil layers that also vary in resource abundance. Predictions assume that environmental stress will shift the community to stress tolerant traits, with a gradual expansion to more acquisitive traits as stress decreases (panel (a) for mean and (d) for skewness). Under the SDH trait diversity is expected to decrease as stress increases, meaning narrower ranges and leptokurtic distributions (panel (b) for range and (c) for kurtosis respectively). At the core level, it is expected that root systems within cores (root neighbourhood) will shift to more acquisitive syndromes (upper panel (e), boxes representing community mean values, brackets represent community dispersion), while the neighbourhood will become more diverse, and traits more evenly distributed as resources increase (lower panel e). Red background colours represent high stress conditions, whereas blue represents lower stress conditions. SRL, specific root length; BI, branching index; RTD, root tissue density.

Similarly, global analyses have shown that the dispersion of SLA or wood density (measured as variance) is negatively correlated with latitude or elevation (Wieczynski et al., 2019), suggesting that the increase in competition under mild climatic conditions promotes trait overdispersion, encouraging a finer segregation of resource use (Yan et al., 2023).

In the case of fine roots, climate variables, such as mean annual temperature (MAT) and mean annual precipitation (MAP), were identified as potential drivers of root morphology at global scales (Holdaway et al., 2011; Valverde-Barrantes et al., 2013), subtropical (Luo et al., 2021) and tropical forests (Pierick et al., 2021; Vlemminckx et al., 2021; Weemstra et al., 2021). For instance, global studies showed unidirectional trends in RTD, SRL and RD with respect to temperature and precipitation. More specifically, they found that species with high SRL or low RTD have a higher chance of occurring in cold climates, whereas species with low SRL, large RD and high RTD were more likely to occur in dry habitats (Freschet et al., 2017; Valverde-Barrantes et al., 2016). However, they found a wide dispersion of root traits, equally abundant in warmer and wetter ecosystems, supporting the idea that instead of a trait trade-off, less stressful environments allow a wider set of root types (Laughlin et al., 2021).

In tropical forests, fine root dynamics are linked to rainfall seasonality, particularly at sites with highly weathered soils, where changes in fine root productivity can reach up to 30% between the dry and the wet season in a single year (Cordeiro et al., 2020; Cusack et al., 2021; Espeleta & Clark, 2007; Metcalfe et al., 2008). In areas located on nutrient-poor tropical forest soils, thick surface root mats are adapted to rapidly intercept nutrients leaching from the litterfall or released during decay by microorganisms (Jordan, 1985; Martins et al., 2021). In fact, several authors have suggested root morphological divergence in the tropics between species adapted to proliferate in the uppermost organic layer versus those in the mineral soil layers (Jones et al., 2011; Zeng et al., 2020) or as a plastic intraspecific response to contrasting resources (Borden et al., 2020). In these highly dynamic systems, root morphological trait syndromes may also shift with time towards more acquisitive efficiency (higher SRL, thinner RD, lower RTD) in instances of higher resource availability (Laliberté et al., 2015; Laughlin et al., 2021; Luo et al., 2021; McCormack et al., 2015; Yavitt & Wright, 2001). However, to date, most studies focussed on the description of belowground functional traits are restricted to a single sampling event, usually with no distinction between roots collected in the organic layers or the mineral

soil (Luo et al., 2021; Valverde-Barrantes et al., 2013), making impossible to evaluate how much root systems may vary along spatial or temporal scales (Metcalf et al., 2008).

In this study, we quantified spatial and seasonal fluctuations of fine root morphological traits in a mature Amazonian tropical rainforest. Using the predictions of the SDH (see Figure 1 for details), we expected community level root trait shifts towards more acquisitive traits, such as lower RTD and higher SRL, and a wider distribution of trait values at the community level in response to higher precipitation. More specifically, we hypothesized that (i) root trait values positively associated with acquisition (high SRL and proliferation of root tips) will prevail in times when environmental stressors diminish, and biotic competition is more intense (Figure 1a). Consequently, we predicted (i.a) higher abundance of roots systems with an acquisition syndrome (higher SRL, SRTA and BI) in roots on the surface layer (0–5 cm) compared to the mineral horizon (5–15 cm) and (i.b) a negative relationship between SRL, SRTA and BI and conservative traits (high RTD and RD) over time, supporting the idea of a coordinated shift in foraging strategies as seasons change. We expected (ii) a shift in root functional traits at the community level as rainfall increases, such that mean community values for acquisition traits should increase, whereas conservative traits would decrease (Figure 1a). Moreover, we expected a coordinated increase in trait variation (increases in range), platykurtic distribution (flatter distribution) and negative skewness (bias representation of higher values) in traits associated with acquisition rates as precipitation increase (Figure 1b–d). Finally, (iii.a) we expected that the distribution of root traits within soil cores (in the following referred to as root neighbourhoods) should be more even (platykurtic distribution, higher range) than expected by chance during the rainy season, supporting the idea of higher trait displacement because of stronger biotic competition at small spatial scales (Figure 1d,e). Moreover, (iii.b) the proportion

of soil cores showing evidence of competitive displacement and more acquisitive traits should increase as soil conditions improve (Figure 1d,e, Luo et al., 2021; Pacala & Tilman, 1994), thus mirroring a shift to platykurtic distribution and negative skewness as rainfall increases.

2 | METHODS

2.1 | Site description

The study was carried out in the Cuieiras Reserve at ZF2, ca. 60 km north of Manaus, Amazonas, Brazil (latitude S 2°35' 40", longitude W 60°12' 28") as part of the initiative to study the ecosystem response of mature tropical forest to elevated CO₂ levels (permissions by the Brazilian Ministry of Science, Technology, Innovation and Communications (Grant BR-T1284), the Brazil's Coordination for the Improvement of Higher Education Personnel (CAPES-Grant 23038.007722/2014-77), and the Amazonas Research Foundation (FAPEAM-Grant 2649/2014)). The vegetation is an old growth lowland rainforest with a 40-m-tall canopy dominated by the families Fabaceae, Sapotaceae, Burseraceae and Lecythidaceae (da Silva et al., 2011; Higuchi et al., 1998). The mean air temperature is 26°C, and the mean annual precipitation is 2400 mm (Araújo et al., 2002; Figure 2). Soils are classified as Geric Ferralsols with a pH of 3.9 on average (Quesada et al., 2010). Nutrient availability in the mineral soil is low, particularly for P, with available P varying from 7 to 16 mg kg⁻¹ (Schaap et al., 2021). The precipitation during the study period was obtained from a meteorological station located 2 km from the study site (Tower K34, Cordeiro et al., 2020). During the studied period, precipitation followed the climate seasonality of the area (Cordeiro et al., 2020; Fontes et al., 2018; Figure 2) and increased from March to May

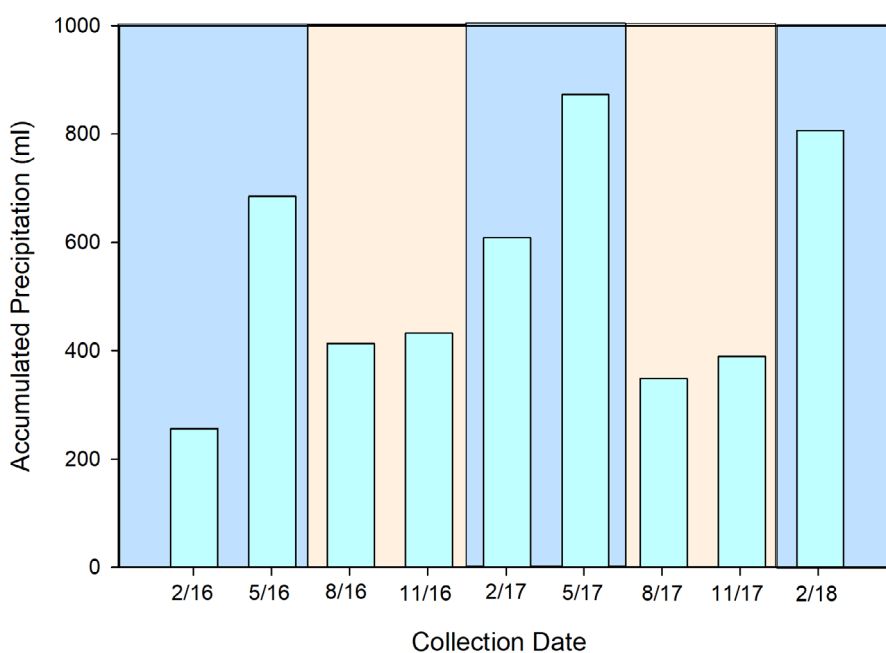


FIGURE 2 Reported precipitation and litterfall rates in the study area. The blue and grey shaded areas represent the wet (January–April) and dry seasons (July–October), bars indicate accumulated precipitation between sampling intervals.

2016 and from January to May 2017. Dry periods occurred from September to December 2016 and more markedly from July to November 2017. For this study, accumulated precipitation was estimated as the total amount of rain recorded in the 3 months before the soil cores were sampled.

2.2 | Soil and root collection

To measure changes in root morphology over time, soils were sampled sequentially from 18 locations along a 500 m transect between February 2016 and February 2018 every three months (9 sampling dates). Each location was separated by a gap of approximately 30 m, with three cores collected per location, 10 m away from each other and perpendicular to the main transect, thus amounting to a total of 54 cores per sampling date. After removing loose senescent leaves from the topsoil, cores were taken with a custom-made steel soil corer (10 cm in diameter) down to 15 cm soil depth. Each sample was sealed in a plastic bag and taken to the laboratory. In the laboratory, samples were separated into two different soil layers: the organic horizon—including the surface mat of roots, litter and humus (0–5 cm)—and the mineral horizon (5–15 cm), hereafter named the O-A and B horizons, respectively. Soil cores were left in water overnight and sieved in a 2 mm mesh, while entire roots were carefully separated and classified as dead or alive based on the elasticity and colour of the root system (Valverde-Barrantes et al., 2013). Roots were classified as live or dead based on friability, colour, and the presence of a stele following Meinen et al. (2009). Live fine roots <1 mm in diameter were classified using an electronic calliper and pooled for biomass assessment. A subset of fine roots was randomly selected for morphological analysis. We defined our sampling unit within cores as fine root clusters ~10 cm in length, which generally included two to three orders of non-lignified roots attached to a woodier central segment, hereafter referred to as fine root sample. On average, 7 ± 2 fine root samples were extracted from each core (~20% of the total biomass) for scanning. After scanning, all samples were oven-dried for 48 h at 65°C to constant weight (Valverde-Barrantes et al., 2013). Fine root biomass encompasses all fine roots, including those used for morphological analysis.

2.3 | Root morphological trait measurements

Each selected fine root sample was scanned using a high-resolution flatbed scanner (600 DPI resolution, 256-level grayscale, TIFF format; Epson Scanner Perfection V700 Photo, USA) and analysed using the WinRhizo software (2007 Pro version, Instrument Regent, Quebec, Canada, details in Appendix S1) following Bouma et al. (2000). From the image analysis, we extracted the total length, and total number of tips per root sample. Using the dry mass per root sample, we calculated SRL, SRTA and BI as the trait positively associated with root acquisition function. In addition, using volume estimations from the software, we estimated RTD as the trait positively associated

with stress tolerance, and average root diameter from the images as RD, representing the tradeoff between mycorrhizal dependency and soil exploratory ability (Leuschner et al., 2004; Meinen et al., 2009).

2.4 | Statistical analysis

We applied the following complementary statistical analysis for testing each of the hypotheses proposed for evaluating the observed belowground phenological responses to different environmental cues. Our first objective was to examine (i.a) how trait syndromes varied between the soil horizons and (i.b) how coordinated was the variation in root functional traits across the two investigated layers. We used a repeated-measurements ANOVA approach to test for changes in root traits by depth and over time (*lmer* function, *lme4* package, Bates et al., 2015). For each ANOVA we selected the traits as response variables, sampling depth \times date as factors, and sampling location nested in date as the error term. To examine coordination in root functional traits over time, we compared how acquisition traits (SRL, SRTA and BI) correlated with traits associated with stress tolerance (RD and RTD, Hogan et al., 2020). Due to the low number of observations ($n=9$), significant results were double-checked using a permutation correlation test score with 999 simulations (Chihara & Hesterberg, 2022, *permCorrTest* function, *CarlentonStats* package).

To test (ii) the expected coordinated changes in trait mean, range, and kurtosis in the community among sampling dates, we first performed permutation correlations between mean, range and kurtosis trait values of the community over time (*permCorrTest* function, *CarlentonStats* package). Then, we tested whether changes in morphology were associated with environmental factors by correlating community mean values for each trait per date with the accumulated rainfall in the 3 months before the soil core sampling (hereafter instantaneous precipitation) and with the amount of litterfall accumulated between collection dates (0–3 months), using permutation correlation tests. Since responses to environmental factors at the community could be delayed with respect to the onset of the season (Espeleta & Clark, 2007), we repeated the analyses using the precipitation data from the previous trimester (3–6 months) preceding the collection, hereafter lagged precipitation.

Finally, we tested (iii.a) whether root neighbourhoods showed evidence of trait displacement seasonally, by assessing the relative signal of competitive trait displacement in each soil core (Kraft et al., 2008; Stubbs & Bastow Wilson, 2004). First, we calculated the observed kurtosis, skewness and range values in each core, using all the fine root morphological information at the core level (i.e. both soil layers combined). To create a null distribution for each soil core under the assumption of assembly by chance, we randomly selected fine root samples from all observations, holding the number of samples constant with those measured in each core. Then, we calculated all statistical moments for each randomly generated root neighbourhood and compared them with the observed values. This process was repeated 999 times for each soil core, and then we estimated the P-value for each neighbourhood as the proportion of times that the simulated momentum was lower

than the observed value (Stubbs & Bastow Wilson, 2004). Finally, to use the cumulative evidence across the entire forest stand to test the null hypothesis of no difference between the observed and randomly assembled neighbourhoods, we converted p -values from all cores studied into corresponding Z -values and combined them according to Stouffer's method to generate a combined p -value (Whitlock, 2005). Finally, to test the hypothesis of increasing trait displacement as the rainy season lingers (iii.b) we correlated the proportion of cores that showed evidence of overdispersion with precipitation patterns, using permutation correlations to test for significant relationships between variables. All statistical analyses were performed with the statistical software R (version 4.3.1, R Core Team, 2023).

3 | RESULTS

3.1 | Dominating root trait syndromes differ between soil layers

As expected from hypothesis (i.a), fine roots in the O-A horizon showed more acquisitive trait syndromes than those in the B horizon. An acquisitive trait like SRTA was on average $32.2 \pm 4.9\%$ (Mean \pm SE) higher in the uppermost than in the mineral soil layer, independently of the season. Similar trends were observed for BI and SRL ($23.1 \pm 3.4\%$ and $14.7 \pm 4.5\%$ higher in the uppermost layer, respectively). In contrast, O-A horizon roots were $15.03 \pm 3.5\%$ less dense (RTD) compared to the B horizon (Figure 3). Only RD did not show significant differences between layers (Figure 3b). We found that temporal changes were mirrored between layers, with no significant interactions between soil depth and time for any trait (Tables S1 and S2, Figure S1). For biomass and morphological traits, temporal variation was the main factor explaining phenological shifts. Total fine root biomass ranged between 162 ± 44 and $385 \pm 106 \text{ g m}^{-2}$ (Figure 3f), with consistently $\sim 60\%$ higher root biomass in the O-A horizon than the B horizon, and variation in biomass between layers was positively correlated over time (Pearson's correlation $r=0.8$, $p<0.001$, $n=9$, Figure S1).

For hypothesis (i.b), acquisition-related traits correlated negatively with stress tolerance traits (Figure 4). However, the trend was only significant for the relationship between RD and SRTA ($r=-0.71$, $p=0.04$) and RD and SRL ($r=-0.83$, $p=0.008$), which have been reported to have a strong mathematical interdependence (Ostonen et al., 2007; but see Kramer-Walter et al., 2016). RTD was also related negatively to SRL and SRTA, but the trends were marginally significant (Pearson correlation $r=-0.52$, $p=0.04$; $r=-0.71$, $p=0.04$ for SRL and SRTA respectively). Branching intensity showed no relationship with either SRTA or SRL (Figure 4a,d).

3.2 | Correlations between trait means and other statistical moments

Mean SRL, BI and SRTA had significant positive correlations with their respective range (Pearson correlation $r=0.92$, 0.84 and 0.94 ,

$p<0.0001$ respectively, Table S1), supporting the SDH prediction that community-level mean values would correlate positively with the range (hypothesis ii), indicating an increase in trait diversity as conditions become less stressful with the onset of the rainy season. However, we did not find the same patterns for trait evenness. Mean BI showed a weak positive correlation between the mean and kurtosis over time ($r=0.65$, $p=0.06$), whereas SRL and SRTA showed no relationship with their respective kurtosis ($r=0.14$ and 0.02 , $p>0.05$, Table S1). Thus, suggesting little support to the idea that traits are more evenly distributed as the community shifts to more acquisitive root types. The exception to this pattern was RTD, which showed a significant negative relationship between mean community and the respective range and kurtosis ($r=-0.64$ and -0.79 respectively, $p<0.0001$, Table S1), supporting the hypothesis (ii) that as roots decrease in RTD at the community level, the community range would increase.

None of the changes in mean root trait values were associated with leaf litterfall production, so we excluded litterfall from further analysis. In contrast, we found that mean community trait values changed with rainfall. Changes in mean values of SRL and SRTA were not directly associated with instantaneous precipitation ($r=-0.12$ and -0.45 , $p=0.8$, and 0.2 , respectively), but with the lagged trimester ($r=0.92$ and 0.73 , $p<0.001$ respectively, Figure 5). Similarly, the ranges of SRL and SRTA ($r=0.90$ and 0.79 , $p<0.0001$) were also positively correlated with the lagged accumulated precipitation. The exception for this pattern was the range of BI that was negatively associated with instantaneous precipitation ($r=-0.68$, $p=0.04$). For acquisition traits neither skewness or kurtosis showed a significant trend with precipitation patterns, except for SRL and SRTA kurtosis showing marginal negative relationships with instantaneous precipitation ($r=-0.62$ and -0.58 , $p=0.08$ and 0.082), and between SRL skewness and instantaneous precipitation ($r=-0.59$, $p=0.1$).

As hypothesized (ii), traits associated with stress tolerance, RD and RTD, correlated negatively with instantaneous precipitation, although only significantly for RD ($r=-0.7$ and -0.57 , $p=0.046$ and 0.17 respectively). The range of RD and RTD ($r=-0.72$ and -0.56 , $p=0.026$ and 0.13 respectively) and kurtosis ($r=-0.77$ and -0.55 , $p=0.014$ and 0.14 respectively, Figure 5) correlated negatively with instantaneous precipitation. Overall, the results supported the hypothesis (ii) that the mean and range of acquisitive traits will increase, and stress-tolerant mean traits would decrease with the increase in precipitation (Figure 5).

3.3 | Trait dispersion within root neighbourhoods

We also assessed the relative signal of competitive trait displacement within each soil core (i.e. root neighbourhood). Supporting our hypothesis (iii.a), our findings indicate trait displacement, i.e. negative kurtosis values, among root neighbourhoods. Within root neighbourhoods two out of the five traits investigated showed significant evidence of a more even distribution than expected by chance. More specifically, the distribution of SRL and SRTA showed more negative kurtosis values within 40% of the cores collected over 27 months

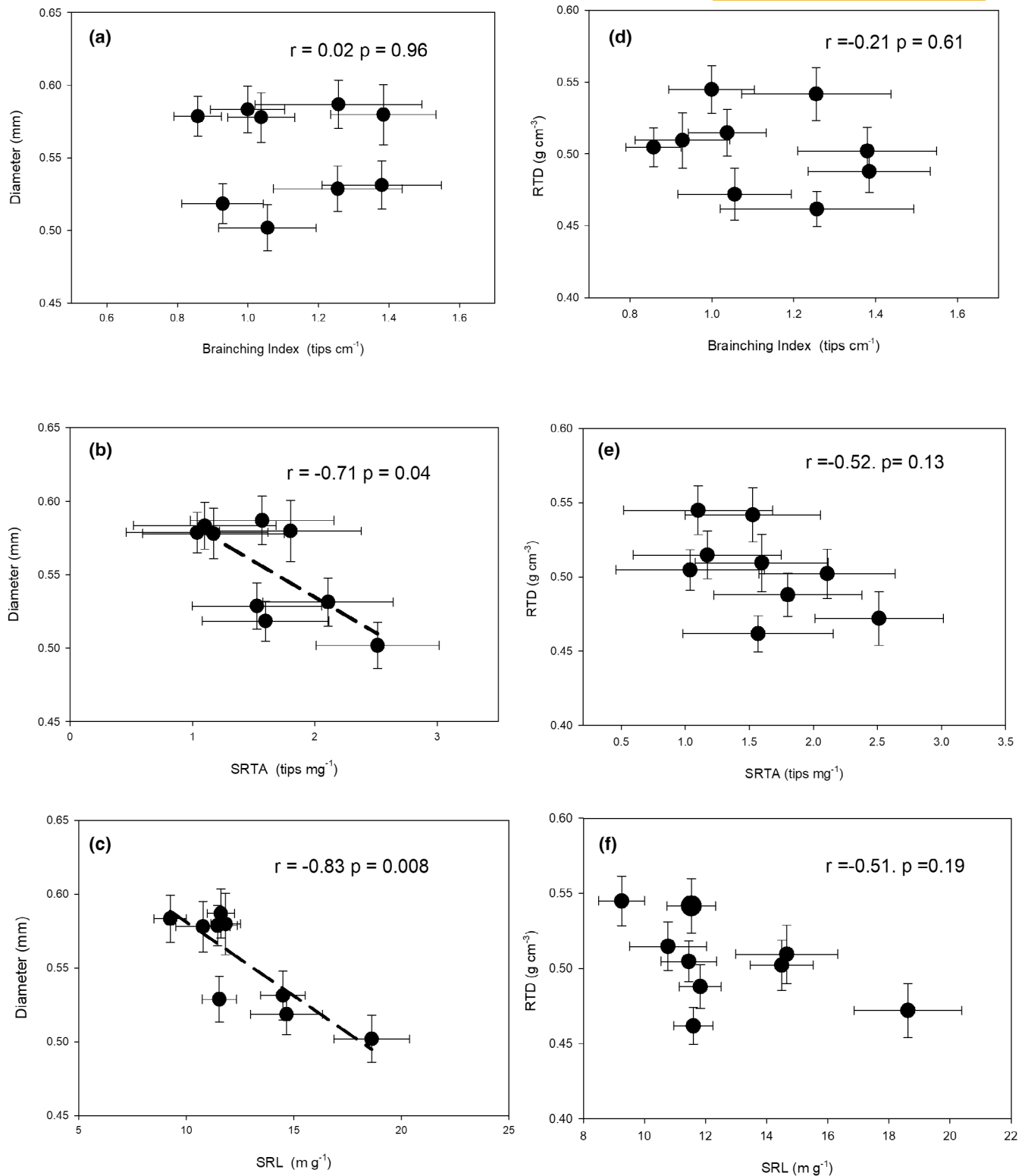


FIGURE 3 Relationship between fine root functional traits associated with stress tolerance (Average Diameter, right panels; RTD, left panels) and traits associated with resource acquisition (BI, panels (a and d), SRTA, panels (b and e); SRL, panels (c and f)). Bars represent standard errors around the mean for each variable.

(varying from 17% to 56% and 28% to 53% among dates from SRL and SRTA respectively, $p=0.03$ and 0.04). The other traits also showed negative kurtosis values but the proportion of cores with significantly lower values was less abundant (18%, 15%, and 14%; $p=0.11$,

0.06 , 0.12 for BI, RTD and D, respectively, [Table S3](#)). Skewness was consistently positive (skewed to conservative traits) across dates and a higher proportion of cores showed more positive skewness than expected by chance for all traits, except RTD ([Table S1](#)). On

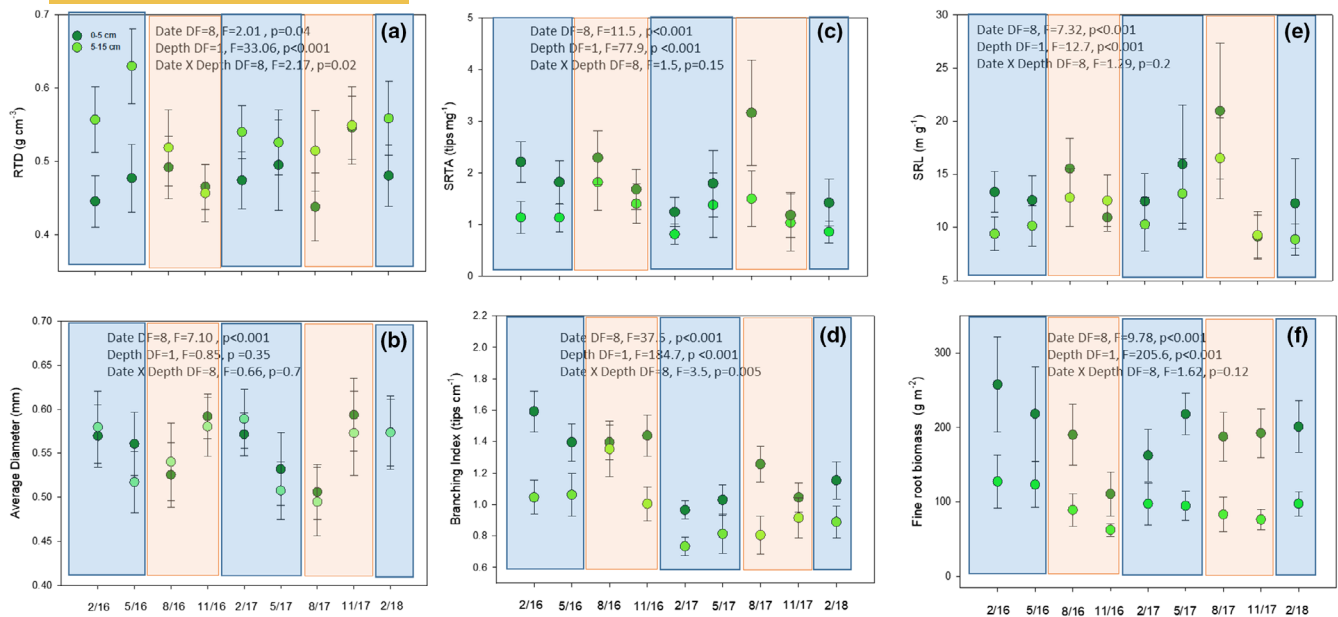


FIGURE 4 Root trait phenology at two different depths (0–5 and 5–15 cm) in a tropical rainforest in Central Amazon. Bars represent 95% CI. Left panels represent traits associated with root stress tolerance: Root tissue density (a), and average diameter (b). Central and upper right panel represent traits positively associated with resource acquisition: Specific root tips abundance (SRTA, c), branching index (d) and specific root length (e). Bottom right panel (f) represents changes in biomass over time. The blue and grey shaded areas represent the wet and dry seasons respectively.

average 54% and 57% of cores (for SRL and SRTA, respectively) showed evidence of positive skewness ($p < 0.001$), whereas for RD and BI the average was 34% and 28%, respectively ($p = 0.01$). We did not find evidence that root neighbourhoods showed wider ranges than those expected stochastically for any trait (Table S3).

As expected from the SDH, (iii.b) the frequency of cores with positive skewness increased as precipitation declined for RD ($r = -0.75$, $p = 0.006$), SRTA ($r = -0.67$, $p = 0.03$) and SRL ($r = -0.63$, $p = 0.04$), which suggests a shift to more conservative traits, as conditions got drier. Similarly, the proportion of cores with a platykurtic distribution, i.e. indicating trait clustering, increased as rainfall decreased, although not significantly (Figure 6, Table S3). Finally, we found no evidence that the neighbourhood ranges changed substantially with precipitation at any time (Figure 6).

4 | DISCUSSION

Our study demonstrates that morphological adaptations in tropical fine roots reflect shifts in plant community competition in response to seasonal fluctuations in resource availability as predicted by the SDH. Our data indicate that at the community level, root traits reflect an adjustment to drier conditions by becoming shorter, and thicker, with fewer tips. In contrast, as moisture increases, the associated release of nutrients from decomposing litter promotes longer, thinner and more branched root systems. Moreover, we observed an increase in root functional trait diversity with precipitation, suggesting an increase in niche segregation during the rainy season (Paradiso et al., 2019). However, the response was not

instantaneous. We observed a lagged response of belowground root traits to environmental cues, which indicate a temporal adjustment of the plant community to climate seasonality.

4.1 | Spatial variation in fine root functional traits

Our results suggest a decrease in absorptive capabilities and an increase in traits associated with stress tolerance with soil depth, supporting the hypothesis (i.a) that alternative trait syndromes are more frequent at different soil layers. Similar trends have been reported for both temperate (Liu et al., 2009; Wang et al., 2013) and tropical communities (Cordeiro et al., 2020). These findings could result from either strong plasticity of some species in the community, or a high specialization of species with contrasting morphological characteristics proliferating at different depths. Supporting the case of plasticity, multiple studies have shown that certain plant species can substantially alter root morphology along the soil profile (Trocha et al., 2017; Zadworny et al., 2016). Some subtropical and tropical tree species showed higher tip proliferation, branching, and absorptive surface area when exposed to nutrient patches (Liu et al., 2015), different nutrients (Borden et al., 2020), or in the litter layer (Martins et al., 2021; Miyatani et al., 2018; Pregitzer et al., 1993). These studies suggest that plastic responses are an important driver of community-level trait variation (Burton et al., 2017; Read et al., 2017; Weemstra et al., 2021).

On the other hand, the idea that species can spatially segregate their root systems has been proposed repeatedly (Bennett et al., 2002; Leuschner et al., 2004), including studies conducted in tropical ecosystems (Jones et al., 2011; Schimann et al., 2008; Zeng et al., 2020). The

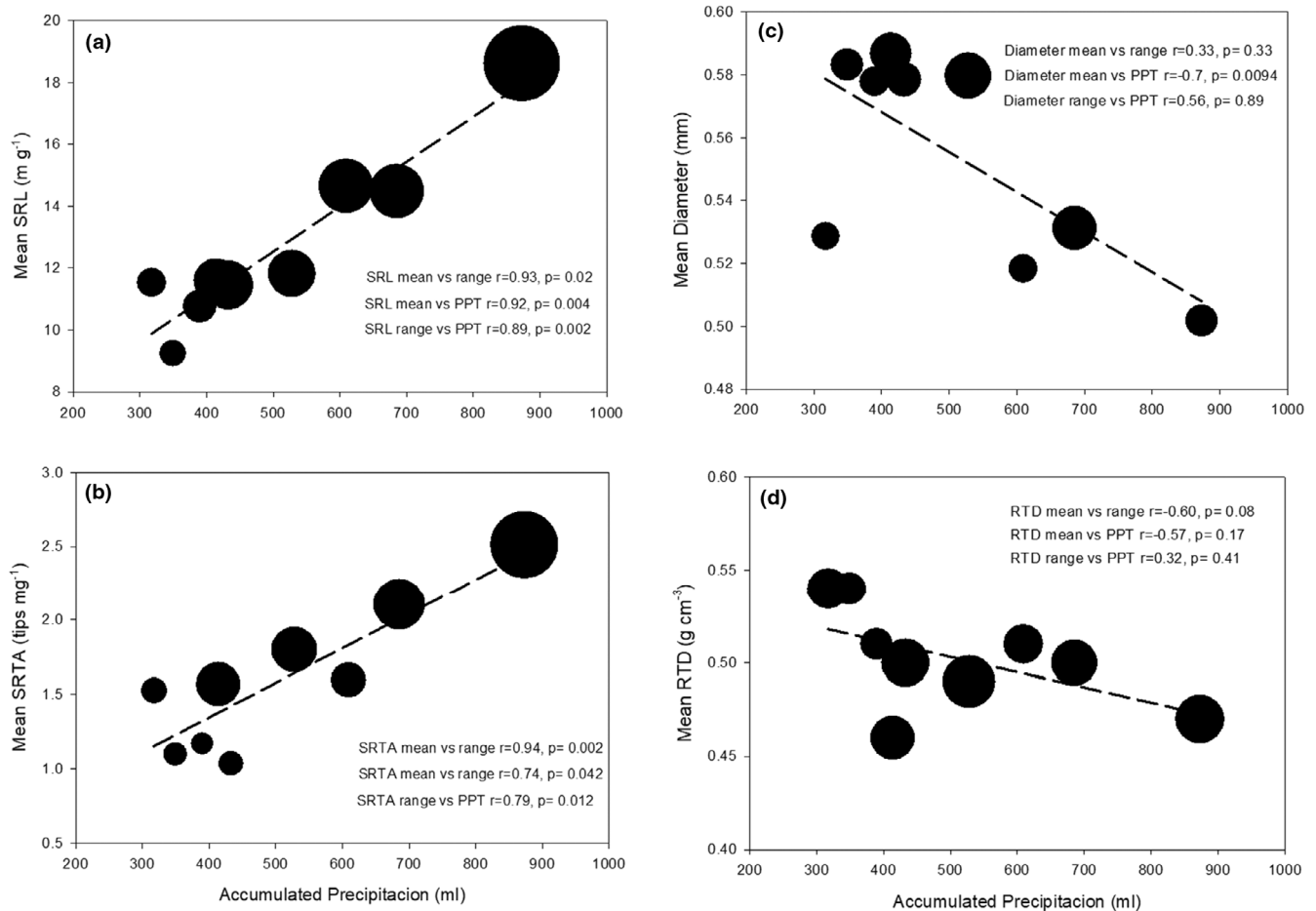


FIGURE 5 Effect of precipitation on community level root functional traits in a tropical rainforest in Central Amazon. The right panels show the relationship between the accumulated precipitation the trimester before sampling and community mean values for two traits associated with resource acquisition (SRL, panel (a) and SRTA, panel (b)). The left panels show the same relationship for two traits associated with stress tolerance (average diameter, panel (c) and RTD, panel (d)). The size of the circles is proportional to trait range at each sampling point.

clear pattern in root segregation along soil profiles that we observed in this study is in line with findings reporting root trait divergence between organic and mineral soil layers (Mommer et al., 2010; Zeng et al., 2020). We postulated that this pattern could be even more pronounced in nutrient-depleted Amazonian tropical forests, where nutrients can be recycled directly from leaf decomposition in the litter layer (Martins et al., 2021), thus promoting strong resource competition in the soil uppermost layer. We acknowledge, however, that the lack of a specific identification of root systems prevents us from drawing more robust conclusions. Further studies using molecular techniques targeting root identity are crucial to discern potential specific spatial patterns we were unable to detect in this study (Luo et al., 2021).

4.2 | Temporal changes in belowground functional traits

In contrast to our hypothesis (i.b) we found a relatively independent variation between traits associated with uptake capacity (SRL, SRTA, BI) and those usually associated with stress tolerance (RD, RTD). Although the mathematical limitations associated with the collinearity

between SRL, RD, and RTD (Ostonen et al., 2007) may put a cautionary remark on our conclusion, this trend is in line with the observed independence found among species at global levels (Bergmann et al., 2020; Erktan et al., 2018; Laughlin et al., 2021), and within communities in Amazonian forests (Vleminckx et al., 2021). This universal pattern suggests a general ability of plants to control acquisition traits independently from root tissue construction costs (Kong et al., 2019; Reichert et al., 2022). Thus, it is plausible that plants can alter tissue investment without altering surface or diameter (Kong et al., 2014, 2019; Valverde-Barrantes et al., 2016, 2020; Colombi et al., 2022) or modify their investment on symbiotic associations over time (Atkinson et al., 2003). For example, studies have reported RTD to be negatively associated with herbivory and pathogen infection risk (Laliberté et al., 2015), enzymatic production (Lugli et al., 2020), or root respiration rates (Makita et al., 2012). Likewise, RTD is commonly reported to have a negative relationship with root nitrogen content (Bergmann et al., 2020; Kong et al., 2019), implying a decrease in physiological activity as trees form more robust and denser roots (Jia et al., 2013; Makita et al., 2015; Paradiso et al., 2019). However, these studies also indicate that neither SRL nor RTD should be used as proxies for root physiological activity. Further studies are necessary to disentangle

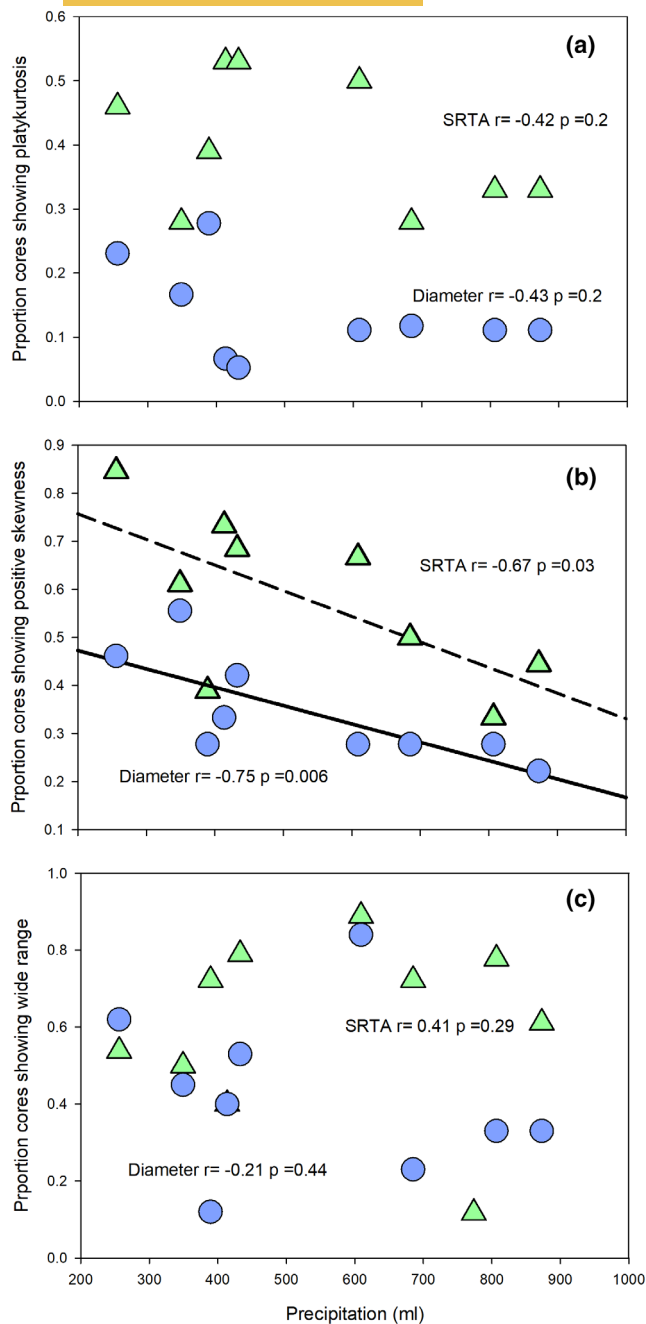


FIGURE 6 Proportion of cores showing evidence of core platykurtosis, representing even distribution in root neighbourhoods (panel a); positive core skewness, representing shifts to more conservative traits (panel b), and core range, representing trait overdispersion (panel c). Symbols represent the proportion of root neighbourhoods that showed momentum values that were higher than expected by chance. Triangles represent SRTA and circles represent RD.

how chemical and anatomical modifications in roots may influence physiological processes belowground.

Our results highlight the importance of accounting for temporal variability in belowground plant functional traits. In the past, studies have reported low or no association between soil conditions and root trait distributions across local scales in temperate (Holdaway et al., 2011; Valverde-Barrantes et al., 2013), subtropical

(Luo et al., 2021), and tropical forests (Pierick et al., 2021; Weemstra et al., 2021). We assume that the lack of association could be partially explained by the lack of information about temporal fluctuations in root traits. Here, for our hypothesis (ii) we demonstrated that over time not only mean values can change substantially, but also other aspects like trait dispersion or evenness could provide key information about the temporal dynamics of root traits in response to seasonal resource pulses in forest communities (Vleminckx et al., 2021). For instance, we found that trait dispersion for SRTA and SRL exhibited a stronger positive response to precipitation than the respective mean trait. Hence, rather than complete shifts in the plant community, it seems that responses to resource availability can be idiosyncratic, suggesting multiple adaptations to numerous soil stressors among coexisting species competing for water and nutrients (Joslin et al., 2000; Lugli et al., 2020; Paradiso et al., 2019; Weemstra et al., 2021). Studies conducted in temperate and subtropical forests reported that tree species with thinner, and more branched root systems tend to modify their morphology more than species with thick-root systems, in response to resource pulses (Eissenstat et al., 2015; Liu et al., 2015). Therefore, changes in trait dispersion may correspond with pulses in root proliferation among species with thin root systems that experience high mortality during the dry season, whereas thick-rooted species remain more stable throughout the year. In future, identification of individual and coexisting species might allow discerning trait variation associated with interspecific differences and intraspecific plasticity (Hofhansl et al., 2021), as well as how temporal changes in root proliferation may explain the competitive displacement patterns reported in this study.

4.3 | The root economic space promoting species coexistence

Over the last decade, the number of studies highlighting the remarkable diversity of root traits in terrestrial ecosystems increased substantially (see Laughlin et al., 2021 for a review). Nevertheless, there is still a lack in studies on root trait diversity and how this mediates belowground competition among coexisting plant species. Our hypothesis (iii) stated that morphological variance could represent species-specific responses to resource availability along both spatial and temporal gradients, adding a further dimension to niche segregation among coexisting species. A descriptive root morphology study conducted in Andean tropical forests found similar trait ranges (Pierick et al., 2021) along altitudinal gradients. Here, we found that the overdispersion of root traits within neighbourhoods was common, thus suggesting that alternative strategies represented by contrasting morphologies may enhance resource use in these communities (Comas & Eissenstat, 2009; Holdaway et al., 2011; Luo et al., 2021). Our results align with the commonly observed trait overdispersion in root neighbourhoods as reported for other forest biomes globally (Luo et al., 2021; Pierick et al., 2021; Valverde-Barrantes et al., 2015; 2021). We propose that this evidence indicates a strong root niche segregation process shaping coexistence within plant communities,

warranting future studies elucidating how belowground interactions promotes diversity in tropical ecosystems.

Finally, the observed lagged response of root proliferation in response to foregoing precipitation events suggests that root morphology is indirectly controlled by soil moisture conditions. Assuming a rapid response to the chemical cues from organic material decomposition by microorganisms (Buscardo et al., 2018, 2021; Hodge, 2004; Schaap et al., 2021), we initially expected an increase in traits associated with nutrient interception and acquisition in the onset of the rainy season. However, the response was delayed, suggesting either a lag-time in the response between microbial activity and nutrient release, competition for resources with microbes, or a slow physiological shift in C allocation between above- and below-ground organs (Kuzyakov & Xu, 2013; Malhi et al., 2004). In fact, some studies found that after an initial strong proliferation of soil microorganism with resource pulses, plants tend to proliferate roots over medium to long term interactions, which could explain the initial delay in root growth (Kuzyakov & Xu, 2013). Moreover, root mortality tends to be higher at the end of the rainy season, when soils are highly saturated (Luizão et al., 2007) and pathogen loads build up (Kivlin & Hawkes, 2016). Thus, it is possible that trees require time to get enough reserves to induce new roots after moisture is reestablished in the soil (Espeleta & Clark, 2007). Further studies linking tree C allocation, root phenology, and soil microbial dynamics will add important evidence to the hypothesis posed in this study.

5 | CONCLUSIONS

Our study highlights an important temporal association between climatic conditions and functional trait dynamics, which might be crucial for developing more accurate mechanistic models when projecting climate-driven shifts in community structure and nutrient cycling. Further insight into root dynamics, complemented with root identification and leaf phenology, will foster our understanding of the complex interactions between trees and their environment in tropical forest ecosystems. By fully accounting for individual-level trait variation and productivity patterns within communities, these studies will strengthen our understanding of broad ecological patterns across space and time, a prerequisite for projecting ecosystem functioning and forest stability under future climatic scenarios.

AUTHOR CONTRIBUTIONS

David Lapola, Lucia Fuchslueger, Florian Hofhansl, Oscar J. Valverde-Barrantes, Kelly M. Anderson and Carlos A. Quesada designed the study. Erick Oblitas, Florian Hofhansl, Oscar J. Valverde-Barrantes, Karst Schapp and Adriana Grandis coordinated the field work including soil core collection, sampling processing and root scanning, with help from Laynara F. Lugli, Sabrina Garcia, Amanda L. Cordeiro, Carol A. Miron and Nathielly Martins. Oscar J. Valverde-Barrantes, Laynara F. Lugli, Lucia Fuchslueger and Florian Hofhansl wrote the manuscript with significant contributions of Marcel Hoosbeek, Ian P. Hartley, and Katrin Fleisher.

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CONFLICT OF INTEREST STATEMENT

All authors approve the final version of the manuscript and declare no conflict of interest. Florian Hofhansl is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0k6djhb0>.

ORCID

Oscar J. Valverde-Barrantes  <https://orcid.org/0000-0002-7327-7647>

Laynara F. Lugli  <https://orcid.org/0000-0001-8404-4841>

Lucia Fuchslueger  <https://orcid.org/0000-0002-9615-4439>

Florian Hofhansl  <https://orcid.org/0000-0003-0073-0946>

Nathielly Martins  <https://orcid.org/0000-0002-2501-747X>

Amanda L. Cordeiro  <https://orcid.org/0000-0001-7226-0133>

Karst Schapp  <https://orcid.org/0000-0003-1627-9029>

Kelly M. Anderson  <https://orcid.org/0000-0002-1460-9904>

Adriana Grandis  <https://orcid.org/0000-0002-8416-3733>

Carol A. Miron  <https://orcid.org/0000-0001-8276-030X>

Katrin Fleisher  <https://orcid.org/0000-0002-9093-9526>

Marcel R. Hoosbeek  <https://orcid.org/0000-0003-0617-0089>

Ian P. Hartley  <https://orcid.org/0000-0002-9183-6617>

David Lapola  <https://orcid.org/0000-0002-2654-7835>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Mean and statistical momentums for five fine root functional traits across two years of sequential coring in a primary tropical forest in Central Amazon ($n = 36$ cores per date).

Table S2. Analysis of variance results describing temporal and depth variation in root traits in a mature tropical rainforest in Central Amazon.

Table S3. Mean and statistical moments (kurtosis, range, and skewness) in the distribution of functional root traits along time in a tropical rainforest in Central Amazon.

Figure S1. Correlation between belowground functional traits at different depths.

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