PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Fine root dynamics across pantropical rainforest ecosystems

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Abstract

Fine roots constitute a significant component of the net primary productivity (NPP) of forest ecosystems but are much less studied than aboveground NPP. Comparisons across sites and regions are also hampered by inconsistent methodologies, especially in tropical areas. Here, we present a novel dataset of fine root biomass, productivity, residence time, and allocation in tropical old-growth rainforest sites worldwide, measured using consistent methods, and examine how these variables are related to consistently determined soil and climatic characteristics. Our pantropical dataset spans intensive monitoring plots in lowland (wet, semi-deciduous, and deciduous) and montane tropical forests in South America, Africa, and Southeast Asia ($n = 47$). Large spatial variation in fine root dynamics was observed across montane and lowland forest types. In lowland forests, we found a strong positive linear relationship between fine root productivity and sand content, this relationship was even stronger when we considered the fractional allocation of total NPP to fine roots, demonstrating that understanding allocation adds explanatory power to understanding fine root productivity and total NPP. Fine root residence time was a function of multiple factors: soil sand content, soil pH, and maximum water deficit, with longest residence times in acidic, sandy, and water-stressed soils. In tropical montane forests, on the other hand, a different set of relationships prevailed, highlighting the very different nature of montane and lowland forest biomes. Root productivity was a strong positive linear function of mean annual temperature, root residence time was a strong positive function of soil nitrogen content in montane forests, and lastly decreasing soil P content increased allocation of productivity to fine roots. In contrast to the lowlands, environmental conditions were a better predictor for fine root productivity than for fractional allocation of total NPP to fine roots, suggesting that root productivity is a particularly strong driver of NPP allocation in tropical mountain regions.

KEYWORDS
allocation, biomass, fine roots, productivity, residence time, soil, turnover

1 | INTRODUCTION

Fine root biomass, productivity, and residence time are key factors in shaping both ecosystem productivity and belowground carbon dynamics. Compared to aboveground biomass stock and productivity, fine root dynamics and their controlling factors remain poorly understood, especially in tropical forest ecosystems. Previous studies show that fine root dynamics across global forest ecosystems vary: fine root biomass and productivity are higher in tropical forests than temperate and boreal forests (Finér et al., 2011; Wang et al., 2018) and residence time increases from tropical regions towards boreal forests (Finér et al., 2011; Gill & Jackson, 2000). Across old-growth Amazon forests, soil organic carbon content down to 30 cm is negatively related to soil nutrient content and fine root biomass is the

largest contributor to the soil organic carbon pool in the nutrient-poor soils (Quesada et al., 2020).

Fine roots (here defined as roots under 2 mm diameter) are the critical pathway for water and nutrient uptake, and organic carbon transport, and also act in symbiosis with fungi for uptake processes (Jackson et al., 1997; McCormack et al., 2014). Fine root biomass has been quantified in several studies for high and low soil nutrient conditions across tropical forests, using soil cores of varying diameters. In tropical lowland forest, fine root biomass increases with soil sand content (Barbosa et al., 2012; Jiménez et al., 2009; Kochsiek et al., 2013; Priess et al., 1999; Silver et al., 2000) and with precipitation at regional scale (Green et al., 2005; Ibrahim et al., 2020). Fine root biomass increases with elevation (Girardin et al., 2013; Kitayama & Aiba, 2002; Leuschner et al., 2007; Moser et al., 2010; Okada et al., 2017; Sierra

Cornejo et al., 2020) in tropical forests. Fine root biomass has also been shown to increase with decreasing mean annual temperature, soil pH, and C:N ratio in Ecuadorian montane forests (Moser et al., 2010) and with decreasing mean annual temperature and soil P availability in Bornean montane forests (Okada et al., 2017).

There are far fewer measurements of fine root productivity and dynamics because such measurements require frequent return visits to field sites, which may be time-consuming and laborious. Net primary productivity (NPP) of fine roots is defined as the new fine root biomass under 2 mm diameter accumulated per unit ground surface area per unit time. The most common technique used to quantify fine root NPP is the ingrowth core mesh (Addo-Danso et al., 2016; Marthews et al., 2014; Metcalfe et al., 2007; Vogt et al., 1998). To date, high variability of fine root productivity has been recorded for different tropical forest types, which is driven by soil properties and climatic variables (Aragão et al., 2009; Kho et al., 2013; Metcalfe et al., 2008; Moore et al., 2018; Riutta et al., 2018; Violita et al., 2016), which is driven by soil properties and climatic variables. In lowland Amazon forest, fine root productivity is influenced by soil texture (Jiménez et al., 2009; Silver et al., 2005). In montane forests, the response of fine root productivity to abiotic drivers has not shown consistent patterns across sites. In Ecuador, fine root productivity increased with decreasing temperature and increasing rainfall, elevation, and soil C:N ratio (Moser et al., 2011; Röderstein et al., 2005). However, in the Peruvian Andes, fine root productivity was high at cloud base zone, and fine root productivity increased with increasing temperature (Girardin et al., 2013). In Bornean montane forests, fine root productivity was reported to increase with increasing temperature and soil phosphorus, but decreased with increasing soil N (Okada et al., 2017).

Fine root residence time refers to how long any unit of biomass remains within the living structures of fine roots tissues, and it represents a proxy for mean fine root lifetime, weighted by root biomass, and is thereby a key determinant of soil carbon accumulation and nutrient availability from root mortality (Castanho et al., 2013; Majdi et al., 2005; Strand et al., 2008). Root residence time decreases with high root mortality, and it is the inverse of root turnover rate (Assefa et al., 2017; Friend et al., 2014; Osawa & Aizawa, 2012; Sierra Cornejo et al., 2020). Lifetime of fine roots has been reported to decrease with soil fertility in lowland Amazonian forests (Aragão et al., 2009) and in response to N soil addition (Peng et al., 2017). Several factors can contribute to increased root residence time, including root thickness as an anti-herbivore defence, water limitation, and low nutrient availability (Silver et al., 2005). In tropical montane forests, temperature has been reported to be the main driver of fine root residence time (Girardin et al., 2013; Graefe et al., 2008a, 2008b; Okada et al., 2017).

Most studies on fine root productivity do not measure aboveground productivity, and consequently, the fractional allocation to fine roots: hence, it is not clear how much inter-site variation in root productivity is caused by variation in total NPP, or by variation in the proportion of NPP that is allocated to the fine root biomass production. However, the fractional allocation of NPP to fine roots rather than the absolute fine root productivity itself may be the component which is best predicted from environmental conditions, because allocation reflects the overall strategy of the trees, such as trade-offs between investment in leaves, woody tissues, and fine roots. On the other hand, if fine roots are prioritized and less involved in the trade-offs, environment would predict root productivity better that predicted allocation to roots (Malhi et al., 2011). Soil nutrient limitation plays a key role in controlling the fractional allocation of total NPP to fine roots, with increasing allocation to fine roots on lower fertility sites and highly weathered soils (Doughty et al., 2018; Wright et al., 2011; Yavitt et al., 2011). Highly weathered lowland tropical soils are often old and associated with low pH, high concentrations of aluminium (Al), iron (Fe) oxides, and with P often being a key limiting nutrient (Laliberté et al., 2015). Fractional allocation of total NPP to fine roots is crucial for understanding how ecosystems will respond to soil disturbance and climatic variables (Green et al., 2005; Yuan & Chen, 2010).

This is one of the first analysis to date of a global tropical fine root dataset, and the first to use the exact same protocol across sites; most studies of fine root dynamics in the tropics tend to focus on a particular site or biogeographical region (e.g. Girardin et al., 2013; Okada et al., 2017; Sierra Cornejo et al., 2020), or synthesize results across studies that employ different methodologies (Moser et al., 2010; Röderstein et al., 2005). Hence, it remains unclear whether trends found in any one region are universal features of tropical forest biomes. Here, we collected and analysed a unique dataset for fine root biomass carbon stock, productivity, residence time, and fractional allocation of total NPP to fine roots from wet, semi-deciduous, deciduous, and montane old-growth forest types that span tropical regions in South America, Africa, and Southeast Asia. This global dataset is unique because (1) root dynamics data were collected to a standardized protocol across all sites; (2) soil data from all regions and sites were collected and analysed to a standardized laboratory protocol, enabling reliable cross-site comparison of the importance of soil factors; and (3) the root measurements are coupled with measurements of aboveground NPP, enabling proportional allocation to fine roots to be quantified. With these data, we address the following questions:

1. How does fine root biomass, productivity, residence time, and fractional allocation of total NPP to fine roots vary across tropical forests?
2. Are there consistent patterns in how climatic variables and physical and chemical soil properties drive fine root dynamics in tropical forests at the global scale?

2 | METHODOLOGY

2.1 | Study sites

We collected root dynamics data in 47 plots in 22 sites across three continents in lowland and montane tropical forests (MTFs). These 1-ha plots are part of the Global Ecosystem Monitoring network (GEM, Malhi et al., 2021), which uses standardize measurement protocols across all sites. The lowland forests sites are located in Bolivia, Brazil, Gabon, Ghana, Malaysia, and Peru (Table 1; Figure 1).

TABLE 1 Characteristics of the Global Ecosystem Monitoring Network 1-hectare permanent plots across forest types of wet tropical forests (WTF), semi-deciduous tropical forests (SDTF), deciduous tropical forests (DTF), and montane tropical forests (MTF): elevation (Elev, m a.s.l.), latitude (Lat., decimal degrees), longitude (Long., decimal degrees), mean annual precipitation (MAP, mm year^{-1}), mean annual temperature (MAT, °C), potential of hydrogen (pH, H$_2$O), maximum cumulative water deficit (MCWD, mm year^{-1}), and soil properties of soil sand, clay, and silt percentage content (%), total nitrogen (N, %), total carbon–nitrogen ratio (C:N), total phosphorus (P, mg kg^{-1}), total aluminium (Al, mg kg^{-1}), calcium (Ca, mg kg^{-1}), total potassium (K, mg kg^{-1}), total magnesium (Mg, mg kg^{-1}), total sodium (Na, mg kg^{-1}), and soil cation exchange capacity (CEC, mmol+kg^{-1})

Country	Site	Plot code	Forest type	Soil type	Elev. (m asl)	Obs. period	Lat.	Long.	MAP	MAT	MCWD	Sand
Bolivia	Kenia	KEN-01	SDTF	Cambisols	384	2009–2017	−16.02	−62.73	1310	24.20	−273.52	58.05
		KEN-02	SDTF	Cambisols	384	2009–2017	−16.01	−62.74	1310	24.20	−273.52	55.48
Brazil	Caxiuana	CAX-04	WTF	Acrisols	47	2009–2016	−1.86	−51.44	2311	25.00	−463.73	83.70
		CAX-06	WTF	Acrisols	47	2009–2011	−1.72	−51.46	2311	25.00	−463.73	32.50
	Nova	NXV-01	DTF	Ferrasols	312	2014–2016	−14.70	−52.35	1530	25.20	−387.31	85.50
	Xavantina	NXV-02	DTF	Ferrasols	324	2014–2016	−14.71	−52.35	1530	25.20	−387.31	75.30
	Tanguro	TAN-01	SDTF	Ferrasols	385	2009–2011	−13.08	−52.39	1740	25.00	−412.81	45.70
		TAN-02	SDTF	Ferrasols	385	2009–2011	−13.08	−52.39	1740	25.00	−412.81	45.70
Peru	Alpahuayo	ALP-11	WTF	Gleysol	120	2010–2011	−3.95	−73.43	2689	26.60	−29.93	65.00
		ALP-12	WTF	Arenosol	150	2010–2011	−3.95	−73.43	2689	26.60	−29.93	82.00
	Jenaro	JEN-11	WTF	Acrisols	131	2014–2015	−4.88	−73.63	3100	25.20	−26.30	NA
	Herrera	JEN-12	WTF	Podzols	135	2014–2016	−4.90	−73.63	3100	25.20	−26.30	NA
	Tambopata	TAM-05	WTF	Cambisols	223	2006–2017	−12.83	−69.27	2545	24.40	−165.55	40.00
		TAM-06	WTF	Alisols	215	2006–2017	−12.84	−69.30	2545	24.40	−165.55	2.00
		TAM-09	WTF	Alisols	219	2006–2017	−12.83	−69.27	2545	24.40	−165.55	NA
	Pantiacolla	PAN-02	MTF	Cambisols	595	2013–2014	−12.65	−71.26	2366	23.50	−33.78	17.65
		PAN-03	MTF	Plinthosol	848	2013–2014	−12.64	−71.27	2835	21.90	−33.78	44.95
	Tono	TON-01	MTF	Cambisols	1000	2007–2008	−12.96	−71.57	3087	20.70	NA	27.83
	San	SPD-02	MTF	Cambisols	1527	2009–2013	−13.05	−71.54	5302	18.80	−0.16	37.51
	Pedro	SPD-01	MTF	Cambisols	1776	2009–2013	−13.05	−71.54	5302	17.40	−0.16	31.35
	Trocha	TRU-08	MTF	Cambisols	1885	2007–2008	−13.07	−71.56	2472	18.00	NA	70.01
	Union	TRU-07	MTF	Cambisols	2020	2007–2008	−13.07	−71.56	1827	17.40	NA	57.21
		TRU-04	MTF	Umbrisol	2758	2013–2014	−13.11	−71.59	2318	13.50	−0.16	13.61
		TRU-03	MTF	Umbrisol	3044	2007–2008	−13.11	−71.60	1776	11.80	NA	0.00
	Esperanza	ESP-01	MTF	Umbrisol	2863	2009–2016	−13.18	−71.59	1560	13.10	−0.33	1.37
	Wayqecha	WAY-01	MTF	Umbrisol	3045	2009–2016	−13.19	−71.59	1560	11.80	−0.33	43.65
	Acjanaco	ACJ-01	MTF	Umbrisol	3537	2013–2014	−13.15	−71.63	1980	9.00	−1.17	4.13
Ethiopia	Yayu	YAY-17	MTF	NA	1500	2015–2017	8.39	35.80	2100	26.10	−264.03	62.54
		YAY-55	MTF	NA	1327	2015–2017	8.37	35.80	2100	26.10	−245.73	36.24
Gabon	Ivindo	IVI-01	SDTF	Cambisols	578	2013–2015	−0.17	12.53	1738	23.50	−80.46	59.50
		IVI-02	SDTF	Cambisols	458	2013–2015	−0.13	12.54	1738	23.50	−80.46	46.00
	Lopé	LPG-01	SDTF	Ferrasols	406	2013–2015	−0.17	11.57	1263	25.60	−106.13	19.30
		LPG-02	SDTF	Ferrasols	302	2013–2015	−0.22	11.62	1263	25.60	−106.13	55.30
Ghana	Kogaye	KOG-02	DTF	Nitisols	229	2013–2016	7.26	−1.15	1313	26.50	−160.52	82.41
		KOG-03	DTF	Arenosol	229	2014–2016	7.26	−1.15	1313	26.50	−160.52	82.41
		KOG-04	DTF	Arenosol	197	2013–2016	7.30	−1.18	1313	26.50	−160.52	79.68
		KOG-05	DTF	NA	221	2013–2016	7.30	−1.16	1313	26.50	−160.52	76.95
		KOG-06	DTF	NA	221	2014–2016	7.30	−1.16	1313	26.50	−160.52	76.95
	Ankasa	ANK-01	WTF	Oxisols	114	2012–2017	5.27	−2.69	2050	26.70	−79.33	63.10
		ANK-02	WTF	Oxisols	114	2012–2017	5.27	−2.70	2050	26.70	−79.33	63.10
		ANK-03	WTF	Oxisols	78	2012–2017	5.27	−2.69	2050	26.70	−79.33	75.90

Silt	Clay	pH	N	C:N	P	Al	Ca	K	Mg	Na	CEC
22.82	19.13	NA	0.22	10.91	447.10	3.10	1291.00	126.60	94.60	0.70	75.90
26.27	18.25	NA	0.17	11.76		10.30	955.20	84.40	131.50	0.80	61.90
5.60	10.70	NA	0.10	13.80	37.40	10.30	1.20	1.20	0.90	0.80	1.30
13.70	53.80	NA	0.10	12.90	178.50	168.80	25.70	18.50	17.90	19.10	22.80
3.40	11.10	NA	0.10	NA	107.50	NA	19.50	39.90	7.60	NA	12.00
6.90	17.80	NA	0.10	NA	129.50	NA	50.00	46.50	27.50	NA	18.10
5.40	48.90	NA	0.20	15.90	147.00	154.40	9.00	33.70	8.10	7.70	19.50
5.40	48.90	NA	0.20	15.90	147.00	154.40	9.00	33.90	8.20	7.80	19.50
20.00	15.00	NA	0.10	11.90	110.00	249.80	20.00	29.30	9.80	2.30	30.40
16.00	2.00	NA	0.08	14.13	38.00	5.40	52.00	23.40	12.20	0.00	4.80
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
17.00	44.00	NA	0.16	9.44	256.30	382.50	6.00	35.10	12.20	2.30	44.80
52.00	46.00	NA	0.17	7.06	528.80	60.30	536.00	58.50	263.50	4.60	56.80
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
37.95	44.40	NA	0.34	10.60	709.00	231.65	5.18	16.65	5.51	NA	NA
22.65	32.40	NA	0.22	11.30	1174.80	129.28	8.52	14.43	7.68	NA	NA
32.42	39.75	3.84	0.42	12.22	751.00	NA	79.20	154.26	97.12	11.91	23.96
17.79	44.71	3.75	0.88	14.93	1630.71	683.11	183.21	154.36	317.28	28.26	42.21
26.97	41.68	3.65	1.19	18.01	1071.14	460.43	74.35	41.79	324.28	20.00	32.32
20.99	9.00	3.93	1.23	21.17	562.83	NA	75.42	95.90	38.68	26.09	45.47
26.29	16.50	4.03	0.81	17.79	495.97	NA	78.91	64.10	79.01	57.83	39.84
12.50	73.89	3.23	1.99	15.47	746.76	383.96	70.93	182.31	87.24	43.48	37.75
0.00	0.00	3.93	1.55	16.76	787.31	NA	68.93	246.41	71.60	39.13	36.07
40.00	58.63	4.17	1.48	18.82	980.82	430.90	62.38	238.10	87.90	42.52	35.25
16.50	39.85	4.00	0.88	21.23	1413.59	469.07	66.57	222.26	154.07	26.17	42.54
56.77	39.10	NA	0.94	12.83	586.93	268.07	10.83	23.52	10.07	NA	NA
22.80	14.65	6.28	0.35	11.60	989.52	0.09	824.91	79.86	244.62	2.70	63.46
27.78	35.98	6.50	0.38	12.97	1310.87	0.23	819.18	231.82	188.13	1.86	62.39
7.40	33.10	3.80	0.10	12.40	286.90	243.40	6.20	25.00	8.00	1.10	28.70
9.60	44.40	3.60	0.20	11.70	770.90	178.00	21.00	27.40	10.00	0.60	22.40
36.00	44.70	3.80	0.10	10.60	130.70	277.00	5.40	18.30	5.30	1.80	32.00
11.50	33.20	4.10	0.10	12.30	64.70	125.60	28.20	60.40	21.00	1.20	18.70
15.34	2.26	6.40	0.05	10.18	60.28	0.20	242.40	35.60	75.90	0.30	19.30
15.34	2.26	6.40	0.05	10.18	60.28	0.20	242.40	35.60	75.90	0.30	19.30
17.02	3.30	6.25	0.04	12.21	65.97	1.00	209.70	27.80	69.60	0.60	17.00
18.71	4.34	6.09	0.03	14.25	71.65	1.80	177.00	19.90	63.30	0.90	14.80
18.71	4.34	6.09	0.03	14.25	71.65	1.80	177.00	19.90	63.30	0.90	14.80
15.30	21.60	4.70	0.10	12.80	126.00	164.40	6.50	17.80	19.10	7.40	20.90
15.30	21.60	4.70	0.10	12.80	126.00	164.40	6.50	17.80	19.10	7.40	20.90
11.40	12.80	4.80	0.10	12.70	88.20	126.70	33.70	22.20	27.60	6.20	18.90

TABLE 1 (Continued)

Country	Site	Plot code	Forest type	Soil type	Elev. (m asl)	Obs. period	Lat.	Long.	MAP	MAT	MCWD	Sand
	Bobiri	BOB-01	SDTF	Ultisols	235	2013–2016	6.70	−1.32	1345	26.10	−204.78	55.47
		BOB-02	SDTF	Ultisols	235	2013–2017	6.75	−1.34	1345	26.10	−204.78	46.75
Malaysia	Danum	DAN-04	WTF	Orthic	225	2015–2017	4.95	117.80	2977	26.50	−31.07	36.53
	Valley	DAN-05	WTF	Acrisols	235	2015–2017	4.95	117.79	2977	26.50	−31.07	34.14
	Maliau	MLA-01	WTF	Podzols	318	2012–2017	4.75	116.97	3154	25.70	−29.01	43.50
	Basin	MLA-02	WTF	Podzols	326	2012–2017	4.75	116.95	3154	25.70	−29.01	19.00
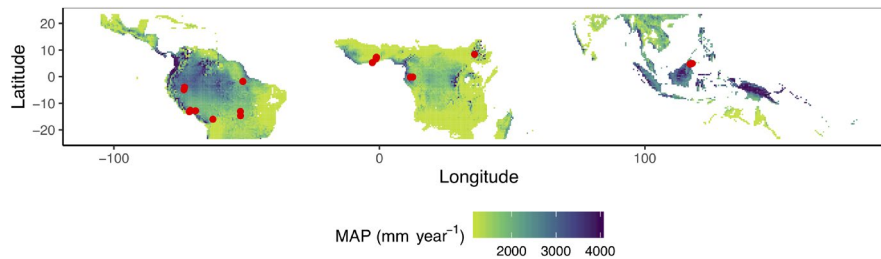
FIGURE 1 The Global Ecosystem Monitoring Network (GEM) permanent plot locations across forest types of wet, semi-deciduous, deciduous, and montane tropical forests. Colours indicate mean annual precipitation (MAP) and red dots show the study sites

They span a rainfall gradient from 1310 and 3154 mm year^{-1}, and were classified into wet tropical forests (WTF), semi-deciduous tropical forests (SDTF), and deciduous tropical forests (DTF) based on their seasonal patterns in rainfall (Feng et al., 2013; Rifai et al., 2018). The MTFs study sites are located across an elevation gradient that ranges between 595 and 3537 m a.s.l. in Peru and Ethiopia (Table 1).

In Peru, the lowland plots (n = 7) are located in Tambopata National Reserve, Allpahuayo-Mishana National Reserve (ALP), Manu National Park, and Jenaro Herrera Local Conservation Area (JEN), and the montane plots (n=12) are located in or adjacent to Manu National Park. The Peruvian plots are part of Amazon Forest Inventory Network (RAINFOR), Andes Biodiversity and Ecosystem Research Group (ABERG), GEM, and Instituto de Investigaciones de la Amazonia Peruana (IIAP) projects (del Aguila-Pasquel et al., 2014; Malhi et al., 2017).

In Bolivia, the two plots are located in SDTFs of private properties at the Hacienda Kenia (KEN) in Guarayos Province, Santa Cruz (Araujo-Murakami et al., 2014). In the Brazilian Amazon, two plots are located in WTF of Caxiuanã National Forest Reserve (CAX), Pará, eastern Brazilian Amazon (da Costa et al., 2014), two in the privately owned Fazenda Tanguro of Mato Grosso State (TAN), dry forest near the southern boundary of the Amazon rainforest (Rocha et al., 2014), and two in Nova Xavantina (NXV), cerrado and cerradão transitional forest near the Bacaba Municipality Reserve, Nova Xavantina (Gvozdevaite et al., 2018).

In Ghana, three evergreen plots are located in the Ankasa Conservation Area (ANK), two semi-deciduous plots are located in the Bobiri Forest Reserve (BOB), and five plots are located in dry forest and mesic savanna in the Kogyae Strict Nature Reserve

(KOG; Moore et al., 2018). In Gabon, two plots are located in Ivindo National Park (IVI), and two plots are located in Lopé National Park (LPG; Rifai et al., 2018). In Ethiopia, two plots are located at transitional montane rainforest of Yayu Forest Coffee Biosphere Reserve (YAY), as part of the Exploring the Ecosystems Limits to Poverty Alleviation in African forest-agriculture Landscapes (ECOLIMITS) project (Morel, Hirons, et al., 2019).

In Sabah, Malaysian Borneo, two plots are located in the Maliau Basin Conservation Area (MLA) and two in the Danum Valley Conservation Area (DAN). These plots are part of intensive monitoring of the Stability of Altered Forest Ecosystem (SAFE) programme (Ewers et al., 2011; Riutta et al., 2018). The Danum plots are within the 50 ha CTFS-ForestGEO monitoring plot.

2.2 | Measurements of fine root dynamics

Total fine root biomass carbon stock (Cstock$_{fr}$) was recorded from four (YAY-17, YAY-55), nine (ANK-01, ANK-02, ANK-03, TRU-03, TRU-07, TRU-08, and TON-01), or 16 (all other sites) soil cores per plot. A post hole digger shovel was used to collect soil cores with a diameter of 12 cm and depth of 30 cm from which all roots were extracted. The coring holes and the newly root-free soil were then used for installing root ingrowth cores. The cylindrical ingrowth cores of 12 cm diameter and 40 cm length were made of plastic wire mesh of 1.5 cm space cloth, which allowed the regrowth of roots and the movement of soil macrofauna into the core. The ingrowth cores were installed into the holes down to 30 cm depth, with the top 10 cm of the core sticking out of the soil. Each core was filled with its native soil and the soil vertical profile and bulk

Silt	Clay	pH	N	C:N	P	Al	Ca	K	Mg	Na	CEC
26.80	17.70	6.70	0.10	9.40	210.40	1.40	620.10	54.80	127.50	0.90	46.00
24.50	28.80	7.90	0.20	11.80	320.00	2.00	948.40	29.20	164.70	0.90	46.00
40.94	22.52	5.55	0.11	9.15	447.01	3.22	590.20	20.58	398.25	24.73	64.18
42.02	23.84	4.51	0.13	8.06	217.59	253.27	87.62	68.70	165.10	6.22	48.12
33.90	22.60	4.20	0.10	5.50	171.70	436.40	15.30	62.90	45.50	1.80	36.40
57.90	23.10	4.40	0.10	6.40	74.20	186.10	205.10	59.60	214.20	15.40	43.20

density maintained as natural as possible. The cores were harvested every 3 months to quantify *fine root productivity* (NPP$_{fr}$) and reinstalled again in the same hole. Roots were manually collected from the cores, following the GEM protocol (Marthews et al., 2014; Metcalfe et al., 2007). Fine roots in each core were extracted for a period of 40 min (4 × 10 min) and the total root mass in the sample was estimated from a cumulative root mass over time curve, up to 120 min (Girardin et al., 2013). The 40-min fine root technique extraction has been used for fine root dynamic studies in Africa (Moore et al., 2018), Southeast Asia (Kho et al., 2013; Riutta et al., 2018), and Amazon basin (Aragão et al., 2009; Girardin et al., 2013; Metcalfe et al., 2008). This process allows the roots search period to have a reasonable time limit in the field while considering that a small fraction of the fine roots is likely to remain uncollected (Metcalfe et al., 2007; Riutta et al., 2018). Collected roots were cleaned using water and fine sieves to avoid loss of fine roots during the rinsing process, and were oven-dried at 70°C until constant mass. Fine roots (≤2 mm diameter) were separated and weighed to determine the total fine root C stock (Aragão et al., 2009; Metcalfe et al., 2008). To assess fine root C stock (Mg C ha^{-1}) and productivity (Mg C ha^{-1} year^{-1}), dry mass was converted into carbon units by assuming a carbon content of 45%. We mined the Fine-Root Ecology Database (FRED; roots.ornl.gov; Iversen et al., 2017) and calculated the average fine root carbon content of broadleaved species, 45% with standard error of 0.12%, n = 1771. To be consistent with other studies within the GEM network (Malhi et al., 2021 and references therein), we express fine root stock and productivity in units of carbon, rather than dry mass. We estimated the fine root C stock and productivity down to 30 cm soil depth in all plots.

Fine root carbon residence time (RT$_{fr}$) was calculated dividing the average Cstock$_{fr}$ by annual NPP$_{fr}$ (Girardin et al., 2010). *Fractional allocation of total NPP to fine root productivity* (Allocation$_{fr}$) was assessed by dividing the NPP$_{fr}$ recorded in this study by total ecosystem NPP (NPP$_{total}$) measured in each plot in previous studies (Araujo-Murakami et al., 2014; del Aguila-Pasquel et al., 2014; Girardin et al., 2014; Huaraca Huasco et al., 2014; Malhi et al., 2017; Moore et al., 2018; Riutta et al., 2018). NPP$_{total}$ was the sum of canopy productivity (estimated from canopy litterfall), wood productivity (stem and coarse wood productivity of stems ≥10 cm diameter at breast height, based on allometric equations), and fine root productivity (Malhi et al., 2009).

2.3 | Soil properties and climatic variables

Soils data (Table 1) were collected from all sites to a consistent RAINFOR protocol (Quesada et al., 2009) and analysed to a common and cross-calibrated protocol either at the INPA soil laboratory in Manaus, Brazil (for samples from Brazil, Bolivia, and Peru sites) or at the University of Leeds (samples from all other sites). Mean annual precipitation (MAP) and temperature (MAT) were calculated using data from automatic weather stations installed close to each plot (Table 1). The mean maximum cumulative water deficit (MCWD) was calculated from precipitation data as the peak of dry season water deficit during the root sampling period, following Aragão et al. (2007), assuming an invariant evapotranspiration rate of 1200 mm year^{-1}.

2.4 | Statistical analyses

To examine the drivers of fine root dynamics across the 47 plots, we applied generalized additive models (GAMs) separately for lowland and montane forests, with soil properties and climatic variables as explanatory factors, using *mgcv* package for R (Wood, 2011). First, to reduce dimensionality and to identify the most orthogonal soil properties, we conducted a principal component analysis (PCA) of soil variables for lowland and montane forests with the measurements of total concentration of soil texture (sand, silt, and clay), pH, nitrogen (N), carbon–nitrogen ratio (C:N), phosphorus (P), aluminium (Al), calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), and soil cation exchange capacity. The PCA was conducted with the *factoextra* package for R (Kassambara & Mundt, 2020) and the variables with the highest loadings on the first four PCA axes were selected as potential explanatory variables in the regression models for fine root dynamics. Soil sand content (%), pH, P, and K were selected for lowland forest, and P, N, soil clay content (%), and K for montane forests (Table S1; Figure S1). In addition, the available climatic variables MAP, MCWD, and MAT were selected as potential explanatory variables for multiple regression for lowland and montane forests.

The analyses were carried out with multiple regression models, to understand which combination of explanatory variables best explained each fine root dynamics component (Cstock$_{fr}$, NPP$_{fr}$, RT$_{fr}$, and Allocation$_{fr}$). Cstock$_{fr}$, NPP$_{fr}$, and RT$_{fr}$ were modelled using Gamma distribution (values are positive, variance increases with increasing mean) with a log link function. Allocation$_{fr}$ was modelled

with the Beta distribution and logit link function (Allocation$_{fr}$ is always greater than 0 and less than 1).

Akaike's information criterion (AIC$_c$) for small samples ($n < 40$) was used to compare the models, the minimum AIC$_c$ was selected as the best-fit estimator, and the models were examined by *MuMIn* package (Barton & Barton, 2015). All statistical analyses were conducted with R statistical software, version 3.6.0.

3 | RESULTS

3.1 | Fine root biomass carbon

High variability in fine root C stock was recorded across the lowland forest types of wet, semi-deciduous, and deciduous (Figure 2a), and along the MTF ecosystems (Figure 2b). The highest fine root C stock

was recorded for a wet eastern Amazonian forest (CAX-06), and the lowest C stock was recorded for a wet Malaysian Bornean rainforest (DAN-04). Across the lowland forests, the total fine root C stock varied by more than an order of magnitude between 0.85 ± 0.13 and 24.29 ± 3.84 Mg C ha^{-1}. In montane forests, high variation of fine root C stock was recorded with elevation that ranged between 2.10 ± 0.18 Mg C ha^{-1} (595 m a.s.l.) and 6.25 ± 0.94 Mg C ha^{-1} (2020 m a.s.l.). We estimated a total pantropical fine root C stock average of 5.57 ± 0.64 Mg C ha^{-1}.

Cstock$_{fr}$ was a good predictor of NPP$_{fr}$ across lowland forests, but was not a good predictor of NPP$_{fr}$ in montane forests (Figure 3). The GAM models revealed that Cstock$_{fr}$ in lowland forests was best explained by total K soil content (Figure 4a; Table 2). In montane forests, the best model for Cstock$_{fr}$ included soil clay content with positive and marginally significant effects of P and MCWD (Figure 4g–i; Table 2).
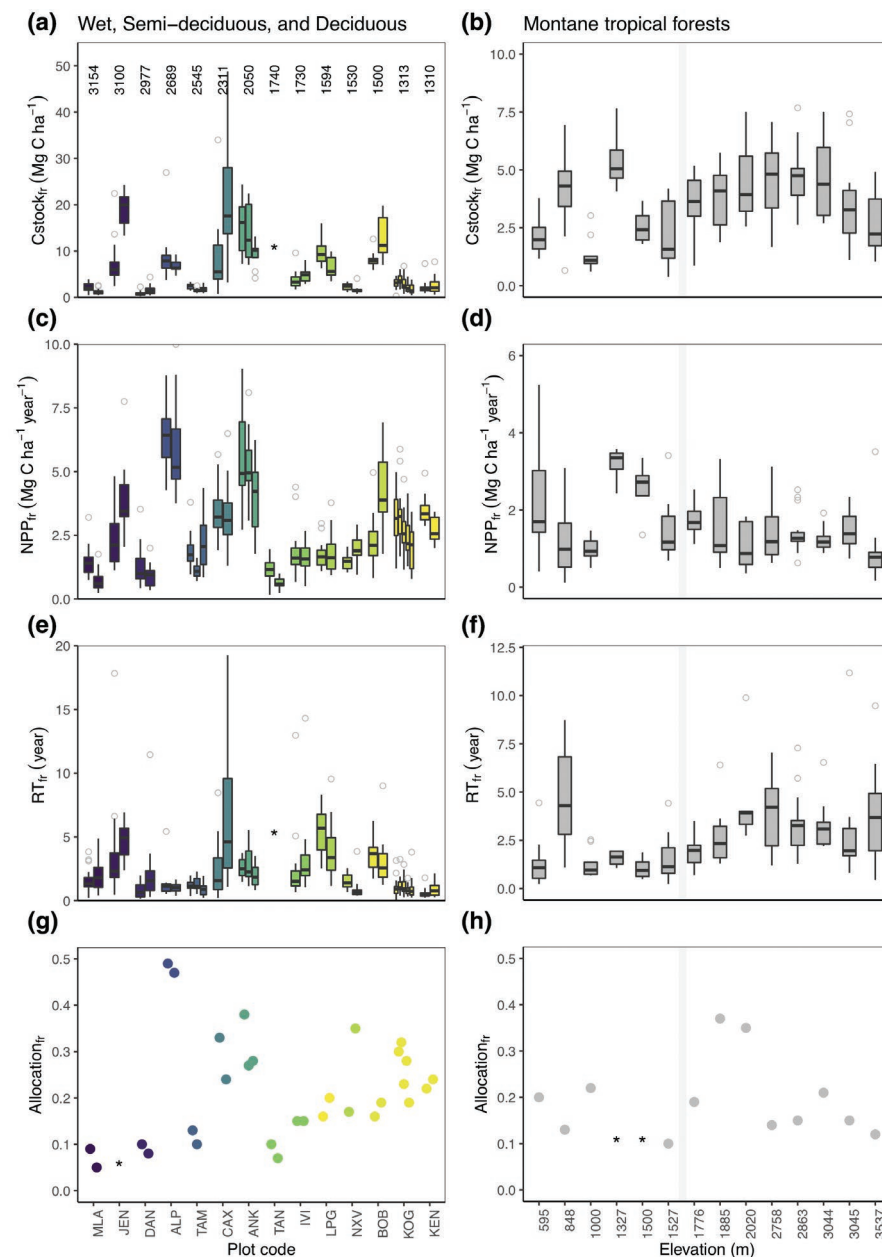

FIGURE 2 Variation in lowland (left) and montane (right) tropical forests of (a, b) total fine root carbon stock (Cstock$_{fr}$), (c, d) fine root net primary productivity (NPP$_{fr}$), (e, f) fine root residence time (RT$_{fr}$), and (g, h) the fractional carbon allocation of total ecosystem NPP to fine roots (Allocation$_{fr}$). Wet (3154–2050 mm year^{-1}), semi-deciduous, and deciduous (1740–1310 mm year^{-1}) lowland forests (left panels) are ordered from highest (left) to lowest (right) mean annual precipitation (mm year^{-1}), which is shown on the upper x-axis. The montane tropical forests (right panels) are ordered from lowest to highest elevations and grey shaded area indicates the cloud base at 1600 m a.s.l. (consistent with Malhi et al., 2017). Forest type designations of the plots followed Rifai et al., (2018). Note the different y-axis scales for lowland and montane forests. In some tropical forests, some aspects of fine root dynamics data were not recorded and missing data are denoted with an asterisk (*). For the list of the plots and their characteristics, see Table 1

FIGURE 3 Relationships between fine root carbon stock (Cstock_fr) and net primary productivity (NPP_fr) in (a) wet, semi-deciduous, and deciduous lowland tropical forests, coloured by mean annual precipitation (MAP) and (b) montane tropical forests (MTF) by elevation. The slope of dot dash (RT = 4), dotted (RT = 3), and dashed (RT = 2) lines through the origin indicate fine root residence times (RT = Cstock_fr/NPP_fr). The error bars show the standard error of the mean. Continent legend shows the African (AFR), South American (SA), and Southeast Asian (SEA) study sites
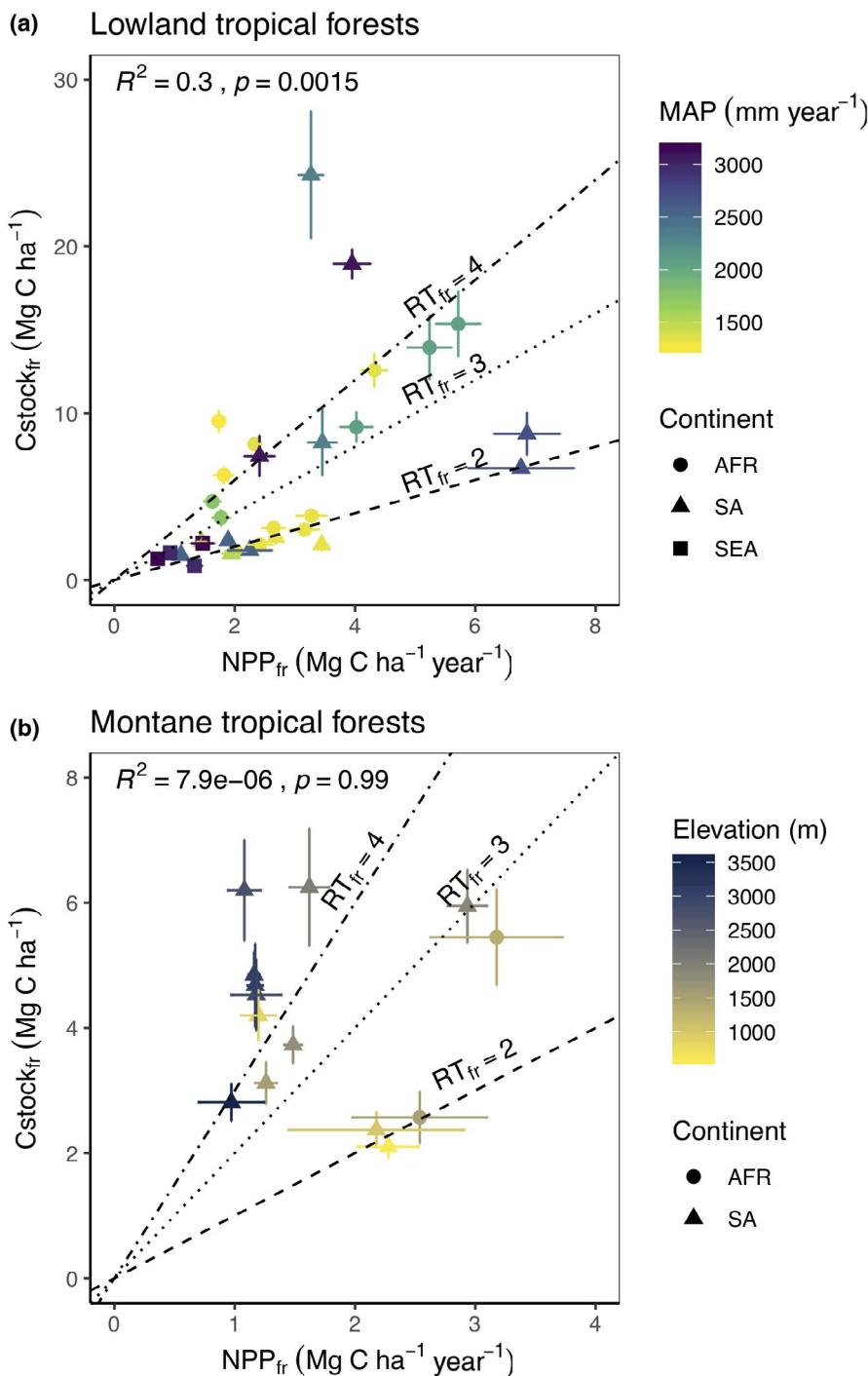
3.2 | Fine root NPP

We recorded high variation in NPP_fr across the lowland forests (Figure 2c). Highest NPP_fr was reported on an Amazonian white sand soil forest (ALP-11), and the lowest NPP_fr was recorded for a Malaysian Bornean forest (MLA-02). The highest NPP_fr was recorded for a semi-deciduous West African forest (BOB-02) and the lowest average was recorded for a semi-deciduous Amazon forest (TAN-02). NPP_fr across the lowland forest types ranged between 0.64 ± 0.07 and 6.86 ± 0.56 Mg C ha^{-1} year^{-1}. The mean annual average of NPP_fr along the montane forests varied between

0.97 ± 0.27 and 3.18 ± 0.55 Mg C ha^{-1} year^{-1} and tended to decrease with increasing elevation (Figure 2d). Highest NPP_fr estimates were recorded in an eastern African montane forest (1327 m a.s.l.) and the lowest on an Andean upper montane forest (3500 m a.s.l.). The total average of NPP_fr across the pantropical forest was 2.43 ± 0.23 Mg C ha^{-1} year^{-1}.

In the multiple GAM models, lowland forest NPP_fr was best explained through a positive relationship to soil sand content only (Figure 4b; Tables 2 and 3). In montane forests, NPP_fr was best explained by MAT, with a positive relationship (Figure 4j; Table 2).
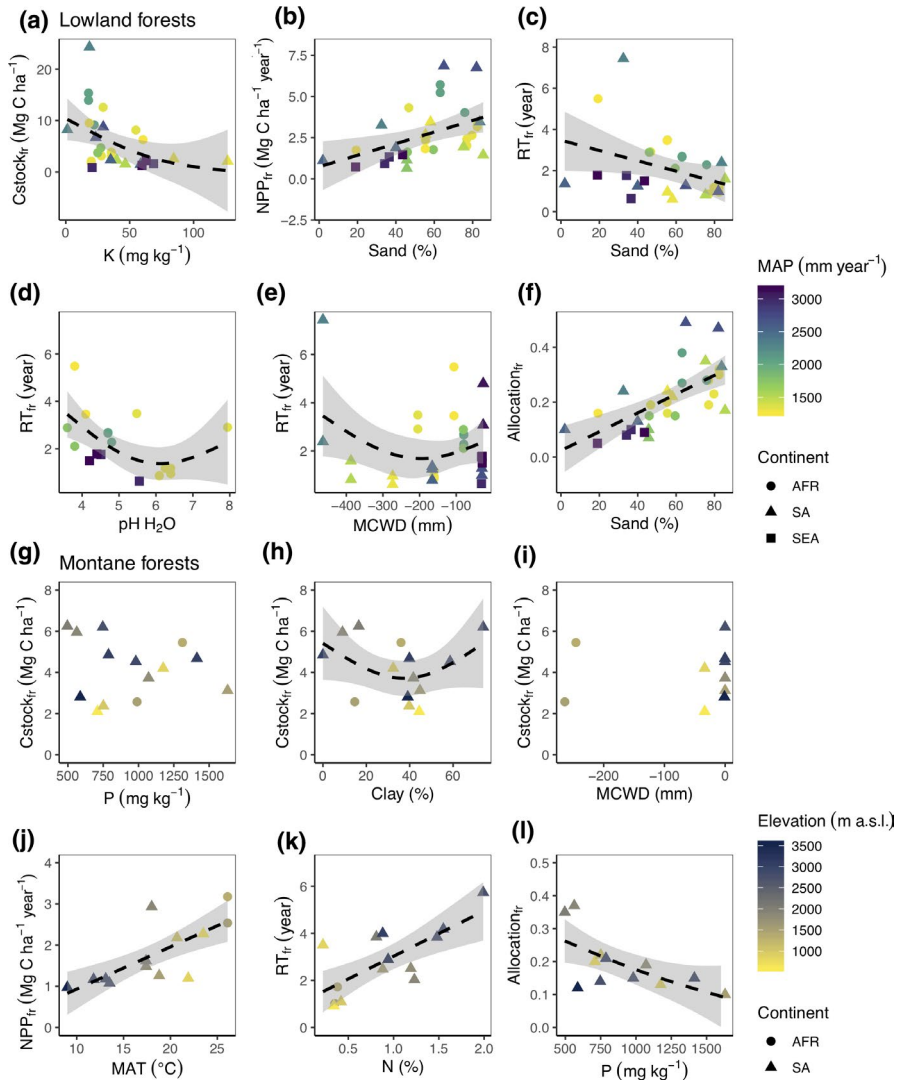
FIGURE 4 Generalized additive model (GAM) predictions of fine root biomass (Cstock$_{fr}$), net primary productivity (NPP$_{fr}$), residence time (RT$_{fr}$), and allocation for lowland tropical forests (a–f) and for montane tropical forests (g–l) in relation to total soil potassium (K, mg kg^{-1}), soil phosphorus (P, mg kg^{-1}), nitrogen (N, %) mean annual temperature (MAT, °C), potential of hydrogen (pH H$_2$O), maximum cumulative water deficit (MCWD, mm year^{-1}), soil clay texture content (%), and soil sand texture content (%). For model coefficients, see Table 2. Dashed lines indicate the GAM model predictions and grey bands show the 95% confidence interval for each model prediction. Soil data are integrated over 0–30 cm depth. Continent legend shows the African (AFR), South American (SA), and Southeast Asian (SEA) Global Ecosystems Monitoring study sites

3.3 | Fine root residence time

Residence time varied between 6 months (KEN-01) and 7 years (CAX-06) across the lowland forest sites, and between 9 months (595 m a.s.l.) and 5 years (2758 m a.s.l.) along the montane forests (Figure 2e,f). The highest and lowest fine root residence time was recorded in lowland wet and semi-deciduous forests of the Amazon region. Little variation of RT$_{fr}$ was recorded on montane forests. Across the elevation gradient, RT$_{fr}$ increased with increasing elevation and decreasing mean annual temperature. The lowest residence time was recorded in a montane forest and the highest average RT$_{fr}$ was recorded in an upper montane forest of the Peruvian Andean transect. Figure 3 shows the linear relationship between fine root C stock and productivity across lowland and montane forest ecosystems, to illustrate how the variability in residence time is driven by its two components (RT$_{fr}$ = Cstock$_{fr}$/NPP$_{fr}$). The high fine root residence time was associated with high root C stock across lowland and MTFs, with a positive and significant relationship in lowland forests. The pantropical average of root residence time was 2.35 ± 0.22 years.

The relationship between environmental variables and residence time was less clear. We found that soil pH was closely associated with RT$_{fr}$ in lowland forests, with RT$_{fr}$ increasing in both more basic and more acidic soils. Soil sand content and MCWD also have some explanatory power (Figure 4; Table 2). In montane forests, RT$_{fr}$ was associated most with total soil N content (Figure 4k; Table 2).

3.4 | Fractional NPP allocation to fine roots

Fractional allocation of total NPP to fine roots varied between 5 ± 1% and 49 ± 5% across the lowland forests, and between 10 ± 1% and 37 ± 4% in montane forests (Figure 2g). The highest proportional root allocation was recorded for a wet Amazon lowland forest (ALP-11) and lowest for a Malaysian Bornean wet rainforest (MLA-02). In addition, root allocation tended to increase from cloud base zone to upper montane forest and then decreased on tree line forests (3537 m a.s.l.) and highest root allocation was recorded at 2020 m a.s.l. (Figure 2h). The pantropical average proportion of productivity allocated to fine roots was 21 ± 2%.

TABLE 2 Summary of generalized additive models (GAMs), for fine root carbon stock (Cstock$_{fr}$, Mg C ha^{-1}), fine root net primary productivity (NPP$_{fr}$, Mg C ha^{-1} year^{-1}), residence time (RT$_{fr}$, year), and NPP allocation to fine roots (Allocation$_{fr}$), with climatic variables of mean annual temperature (MAT, °C), and soil properties of soil sand content (Sand, %), potassium (K, mg kg^{-1}), phosphorus (P, mg kg^{-1}), nitrogen (N, %), maximum cumulative water deficit (MCWD, mm year^{-1}), and potential hydrogen (pH H$_2$O, %) as explanatory variables. Standard error (SE), deviance explained (DE), root mean square error (RMSE), significance of the model coefficients p values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'NS' 1), and Akaike information criterion (AIC). The best model (lowest AIC) for each response variable is presented here, for full model, see Table S2

Forest types	Response variables	Explanatory variables	Estimate	SE	p	DE (%)	RMSE	AIC
Lowland forests (wet, semi-deciduous, deciduous)	Cstock$_{fr}$	Intercept	2.425728	0.262749	***	24.70	5.32107	156.773
		K (mg kg^{-1})	−0.01664	0.005657	**			
	NPP$_{fr}$	Intercept	0.159532	0.280278	*	27.40	1.668431	108.548
		Sand (%)	0.015856	0.004654	**			
	RT$_{fr}$	Intercept	2.644315	0.545779	***	56.90	0.6477272	52.4028
		Sand (%)	−0.014561	0.00597	*			
		pH H$_2$O (%)	−0.422804	0.133904	**			
		MCWD (mm)	−0.009831	0.002936	**			
	Allocation$_{fr}$	Intercept	−2.47168	0.2895	***	50.60	0.0916062	−57.6311
		Sand (%)	0.02263	0.00453	***			
Montane forests (MTF)	Cstock$_{fr}$	Intercept	0.0606716	0.5108584	NS	54.30	0.9018852	51.6039
		P (mg kg^{-1})	0.0004674	0.0002748	NS			
		Clay (%)	0.0191156	0.0074311	*			
		MCWD (mm)	−0.0013453	0.001084	NS			
	NPP$_{fr}$	Intercept	−0.36622	0.28799	NS	50.60	0.5563	26.9086
		MAT	0.05285	0.01552	**			
	RT$_{fr}$	Intercept	0.4211	0.2437	NS	40.10	0.9098165	48.7975
		N (%)	0.6272	0.2341	*			
	Allocation$_{fr}$	Intercept	−0.4573069	0.341369	NS	38.20	0.06978606	−22.8033
		P (mg kg^{-1})	−0.0009314	0.0003831	*			

TABLE 3 The regression linear models for fine root carbon stock (Cstock$_{fr}$, Mg C ha^{-1}), fine root net primary productivity (NPP$_{fr}$, Mg C ha^{-1} year^{-1}), residence time (RT$_{fr}$, year), and NPP allocation to fine roots (Allocation$_{fr}$), with climatic variables of mean annual temperature (MAT, °C), and soil properties of soil sand content (Sand, %), potassium (K, mg kg^{-1}), phosphorus (P, mg kg^{-1}), and nitrogen (N, %)

Forest types	Response variables	Explanatory variables	Estimate	SE	T-value	p	R^2
Lowland forests (Wet, Semi-deciduous, Deciduous)	Cstock$_{fr}$	Intercept	10.270422	1.935823	5.305456	0.000015	0.14
		K (mg kg^{-1})	−0.097197	0.041679	−2.332028	0.027715	
	NPP$_{fr}$	Intercept	0.809491	0.864430	0.936445	0.357051	0.18
		Sand (%)	0.039080	0.014353	2.722848	0.011014	
	RT$_{fr}$	Intercept	3.476324	0.755731	4.599946	0.000097	0.10
		Sand (%)	−0.025037	0.012362	−2.025319	0.053215	
	Allocation$_{fr}$	Intercept	0.023466	0.048756	0.481301	0.634043	0.43
		Sand (%)	0.003863	0.000810	4.771527	0.000052	
Montane forests (MTF)	NPP$_{fr}$	Intercept	−0.105399	0.536073	−0.196613	0.847421	0.53
		MAT (°C)	0.113993	0.028894	3.945215	0.001945	
	RT$_{fr}$	Intercept	1.096767	0.548030	2.001289	0.068500	0.49
		N (%)	1.928536	0.526337	3.664068	0.003242	
	Allocation$_{fr}$	Intercept	0.365703	0.064382	5.680221	0.000204	0.32
		P (mg kg^{-1})	−0.000165	0.000066	−2.484225	0.032308	

Allocation$_{fr}$ was a function of soil sandiness in lowland forests and GAM analysis revealed that fine root allocation was best explained by soil sand content with a positive relationship (Figure 4f; Tables 2 and 3). In montane forests, fine root allocation was best explained by soil P content (Figure 4l; Tables 2 and 3). One of the clearest results of this analysis is that Allocation$_{fr}$ of NPP to fine roots is associated with soil sand content in lowland forests. This strong relationship does not hold in montane forests plots, where NPP$_{fr}$ is a function of mean annual temperature.

4 | DISCUSSION

4.1 | Fine root dynamics variation across tropical rainforest

Fine root dynamics varied from wet to deciduous lowland forests, but in montane forests fine root C stock and residence time increased with increasing elevation and fine root productivity increased with decreasing elevation (Figure 3). Table 4 presents estimates of fine root C stock, productivity, residence time, and fractional allocation available in the current literature in tropical forests. We found clear trends across lowland tropical forests of highest fine root productivity, residence time, and carbon allocation in sites with high soil sand content (this study; Cavelier, 1992; Jiménez et al., 2009; Metcalfe et al., 2008; Noguchi et al., 2014; Pavlis & Jeník, 2000; Silver et al., 2000). However, the Bornean wet forests had the lowest NPP$_{fr}$ averages for lowland plots, and these rates are similar to previous studies (Green et al., 2005; Kho et al., 2013; Kochsiek et al., 2013).

In MTFs, the trends of fine root dynamics are more complex. Fine root C stock increased with increasing elevation in tropical montane regions of Costa Rica, Ecuador, Ethiopia, Indonesia, Peru, Malaysia, Rwanda, and Venezuela (this study; Assefa et al., 2017; Hertel et al., 2009; Ibrahima et al., 2010; Leuschner et al., 2007; Moser et al., 2010; Okada et al., 2017; Priess et al., 1999). We also found high root C stocks in the nutrient-poor sites at the cloud base zone with low soil P. Root residence time increased with elevation, responding to the high soil organic matter and N content while fine root productivity decreased with elevation.

Fine root residence time in both lowland and montane forests also depends on the proportion of the smaller-diameter, shorter-lived absorptive roots and the larger-diameter, longer-lived transport roots; their size difference is species-specific (Joslin et al., 2006; McCormack et al., 2015; Wang et al., 2019) and likely to vary among soil types (Cusack & Turner, 2020; Ibrahima et al., 2010; Telles et al., 2003). Therefore, the mean residence time in each site is influenced by the species composition and the relative proportion and size distribution of the different root types, which we do not quantify in this study.

Soil texture played a key role in fractional allocation of total NPP to fine roots across lowland forests; allocation was higher in sandy soils than in clay, which may reflect the decrease in carbon allocation to stem and canopy productivity (Aragão et al., 2009; Kochsiek et al., 2013; Metcalfe et al., 2008). Allocation to fine roots also increased with decreasing soil P and N content (Pregitzer et al., 1995; Wright et al., 2011).

Malhi et al. (2011) estimated average tropical forest NPP allocation of 34% to canopy, 39% to woody tissue, and 27% to fine roots, with a considerable variation across sites and regions. In Southeast Asia, NPP allocation to fine roots ranged between 10% and 14% for old-growth lowland dipterocarp forests (Kho et al., 2013; Riutta et al., 2018), and between 6% and 30% in Kinabalu montane forests (Okada et al., 2017). This small fractional allocation to fine roots in South East Asia may be due to the ectomycorrhizal symbionts of the dipterocarp trees, which enhance nutrient uptake (Brearley., 2012; Robinson et al., 2020). In West African forests allocation to fine roots ranged between 22% and 33% (Moore et al., 2018; Morel, Adu Sasu, et al., 2019), similar rates were reported for a previous Amazon basin study (Malhi et al., 2017). According to previous studies and this study, allocation to fine roots in lowland and montane forests across the tropics is driven by soil texture and nutrient content. Understanding belowground processes is particularly important for understanding the functioning of tropical forests on poor soils, where the fractional allocation of total NPP to fine roots is high.

Is allocation a better predictor of NPP$_{fr}$ than absolute values of NPP$_{fr}$? The GEM approach of quantifying total NPP (instead of studying root productivity in isolation) provide a unique opportunity to quantify allocation of NPP between components. This allows us to distinguish if root productivity is low because of low overall NPP, or because a smaller proportion of the total NPP is allocated fine root production. In lowland forests, our results indicate that allocation is more predictable than root productivity alone, and that the sand content is the strongest driver of NPP allocation to roots (Figure 4; Table 3). Sandy soils are more penetrable by fine roots but also have less water retention, and therefore the fractional allocation of total NPP to fine roots appears to be a clear priority at the expense of aboveground productivity. In montane forests, on the other hand, NPP$_{fr}$ appears to be better predicted than Allocation$_{fr}$. This suggests that in montane forests fine root productivity rates are directly determined or limited by environmental conditions, and do not exhibit resource allocation trade-offs against aboveground components of NPP. This suggests that root productivity may be a particularly high priority in montane systems that is not subject to allocation trade-offs.

4.2 | The effect of soil chemical properties on fine root dynamics

One remarkable result of our study is that climate variables hardly feature as explanatory variables for fine root dynamics. Instead, soil texture and chemistry dominate as explanatory factors. Soil nutrient content and texture are key drivers of fine root dynamics across the tropical forests monitored by the GEM network. In particular,

TABLE 4 Fine root carbon stock (Cstock$_{fr}$; Mg C ha^{-1}), net primary productivity (NPP$_{fr}$; Mg C ha^{-1} year^{-1}), residence time (RT$_{fr}$; year), and fractional NPP allocation to fine roots (Allocation$_{fr}$) recorded by forest types of wet (WTF), semi-deciduous (SDTF), deciduous (DTF), and montane (MTF) tropical forests ecosystems

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	Cstock$_{fr}$ (Mg C ha^{-1})	NPP$_{fr}$ (Mg C ha^{-1} year^{-1})	RT$_{fr}$ (year)	Allocation$_{fr}$	Reference
Colombia	Logged forest 18 years old, low terraces	WTF		20	5.19				Rev. in Jiménez et al. (2009)
Colombia	Logged forest of 25 years old, low terraces	WTF		20	4.55				Rev. in Jiménez et al. (2009)
Colombia	Logged forest of 37 years old, low terraces	WTF		20	6.83				Rev. in Jiménez et al. (2009)
Colombia	Old forests in low terraces	WTF		20	12.40				Rev. in Jiménez et al. (2009)
Colombia	Terra firme clay loam forest (Plinthosol)	WTF	105	20	2.46	2.45	1.01		Jiménez et al. (2009)
Colombia	Terra firme clay loam forest (Plinthosol)	WTF	110	20	2.95	1.85	1.60		Jiménez et al. (2009)
Colombia	Loamy sand forest	WTF	130	20	8.86	6.00	1.48		Jiménez et al. (2009)
Colombia	Old-growth forest	WTF	160	20	12.39				Pavlis and Jenik (2000)
Brazil	CAX-04	WTF	47	30	7.43	3.46	2.39	0.33	Present study
Brazil	CAX-06	WTF	47	30	21.86	3.27	7.44	0.24	Present study
Brazil	Lower slope in baixio	WTF	120	40	8.02				Noguchi et al. (2014)
Brazil	Mid-slope	WTF	120	40	4.25				Noguchi et al. (2014)
Brazil	Upper-slope	WTF	120	40	3.52				Noguchi et al. (2014)
Brazil	Sand plot	WTF	50	30	5.67	1.80	3.15		Metcalfe et al. (2008)
Brazil	Dry plot	WTF	50	30	4.05	1.35	3.00		Metcalfe et al. (2008)
Brazil	Clay plot	WTF	50	30	6.08	1.80	3.38		Metcalfe et al. (2008)
Brazil	Fertile plot	WTF	50	30	4.46	3.15	1.41		Metcalfe et al. (2008)
Brazil	Sandy soil	WTF		10	1.82				Silver et al. (2000)
Brazil	Clay soil	WTF		10	0.77				Silver et al. (2000)
Ghana	ANK-01	WTF	114	30	13.81	5.72	2.68	0.38	Present study
Ghana	ANK-02	WTF	114	30	12.55	5.24	2.66	0.27	Present study
Ghana	ANK-03	WTF	78	30	8.25	4.02	2.28	0.28	Present study
Ivory Coast	Old-growth forest (Banco P.)	WTF		30	5.10				Rev. in Cavelier (1992)
Ivory Coast	Old-growth forest (Banco T.)	WTF		30	4.46				Rev. in Cavelier (1992)
Ivory Coast	Old-growth forest (Yapo)	WTF		30	5.02				Rev. in Cavelier (1992)
Malaysia (Borneo)	Dipterocarp forest	WTF	200	15	0.69				Green et al. (2005)
Malaysia (Borneo)	DAN-04	WTF		30	0.76	1.34	0.63	0.10	Present study
Malaysia (Borneo)	DAN-05	WTF		30	1.46	0.93	1.76	0.08	Present study

(Continues)

TABLE 4 (Continued)

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	$Cstock_{fr}$ (Mg C ha^{-1})	NPP_{fr} (Mg C ha^{-1} year^{-1})	RT_{fr} (year)	$Allocation_{fr}$	Reference
Malaysia (Borneo)	MLA-01	WTF		30	1.98	1.47	1.50	0.09	Present study
Malaysia (Borneo)	MLA-02	WTF		30	1.15	0.72	1.79	0.05	Present study
Peru	ALP-11	WTF	120	30	7.89	6.86	1.28	0.49	Present study
Peru	ALP-12	WTF	150	30	6.04	6.76	0.99	0.47	Present study
Peru	JEN-11	WTF	131	30	6.68	2.41	3.07		Present study
Peru	JEN-12	WTF	135	30	17.06	3.95	4.80		Present study
Peru	TAM-05	WTF	223	30	2.12	1.89	1.25	0.13	Present study
Peru	TAM-06	WTF	215	30	1.35	1.11	1.36	0.10	Present study
Peru	TAM-09	WTF	219	30	1.60	2.25	0.79		Present study
Republic of the Congo	Gallery forests	WTF	540	40	3.81				Ifo et al. (2015)
Republic of the Congo	Hill-slope forest	WTF	540	40	1.74				Ifoet al. (2015)
Brazil	TAN-01	SDTF	385	30		1.14		0.10	Present study
Brazil	TAN-02	SDTF	385	30		0.64		0.07	Present study
Bolivia	KEN-01	SDTF	384	30	2.12	3.45	0.61	0.22	Present study
Bolivia	KEN-02	SDTF	384	30	2.57	2.68	0.96	0.24	Present study
Gabon	IVI-01	SDTF	578	30	3.74	1.77	2.11	0.15	Present study
Gabon	IVI-02	SDTF	458	30	4.71	1.63	2.90	0.15	Present study
Gabon	LPG-01	SDTF	406	30	9.53	1.74	5.47	0.16	Present study
Gabon	LPG-02	SDTF	302	30	6.29	1.82	3.46	0.20	Present study
Ghana	BOB-01	SDTF	235	30	8.15	2.33	3.50	0.16	Present study
Ghana	BOB-02	SDTF	235	30	12.58	4.32	2.91	0.19	Present study
Ghana	Old growth forest	SDTF	268	30	0.64				Addo-Danso et al. (2018)
Ghana	Logged over forest	SDTF	276	30	1.37				Addo-Danso et al. (2018)
Ghana	SDTF (Upper slope)	SDTF		30	1.71				Rev. in Cavelier (1992)
Ghana	SDTF (Middle slope)	SDTF		30	4.59				Rev. in Cavelier (1992)
Ghana	SDTF (Bottom slope)	SDTF		30	1.53				Rev. in Cavelier (1992)
Brazil	NXV-01	DTF	312	30	2.30	1.45	1.59	0.17	Present study

(Continues)

TABLE 4 (Continued)

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	Cstock$_{fr}$ (Mg C ha^{-1})	NPP$_{fr}$ (Mg C ha^{-1} year^{-1})	RT$_{fr}$ (year)	Allocation$_{fr}$	Reference
Brazil	NXV-02	DTF	324	30	1.59	1.94	0.82	0.35	Present study
Ghana	KOG-02	DTF	229	30	3.02	3.16	0.95	0.30	Present study
Ghana	KOG-03	DTF	229	30	3.86	3.28	1.18	0.32	Present study
Ghana	KOG-04	DTF	197	30	3.13	2.65	1.19	0.23	Present study
Ghana	KOG-05	DTF	221	30	2.12	2.42	0.87	0.28	Present study
Ghana	KOG-06	DTF	221	30	1.74	2.02	0.86	0.19	Present study
Ecuador	Lower montane forest	MTF	1050	25	1.22	1.63	0.75		Moser et al. (2010)
Ecuador	Lower montane forest	MTF	1540	25	2.52	4.08	0.62		Moser et al. (2010)
Ecuador	Lower montane forest	MTF	1890	25	2.79	3.16	0.88		Moser et al. (2010)
Ecuador	Upper montane forest	MTF	2380	25	2.84	2.75	1.03		Moser et al. (2010)
Ecuador	Upper montane forest	MTF	3060	25	4.86	1.67	2.92		Moser et al. (2010)
Ecuador	Lower montane forest	MTF	1900	110	4.01				Soethe et al. (2007)
Ecuador	Upper montane forest	MTF	2400	110	3.28				Soethe et al. (2007)
Ecuador	Upper montane forest	MTF	3000	110	6.76				Soethe et al. (2007)
Ecuador	Lower montane forest	MTF	1892	20		2.28			Röderstein et al. (2005)
Ecuador	Upper montane forest	MTF	2380	20		5.52			Röderstein et al. (2005)
Ecuador	Upper montane forest	MTF	3059	20		5.23			Röderstein et al. (2005)
Ecuador	Lower montane forest	MTF	1050	30	1.21				Leuschener et al. (2007)
Ecuador	Upper montane forest	MTF	3060	30	5.07				Leuschener et al. (2007)
Ethiopia	Lower montane forest	MTF	1500	30	2.57	2.538	1.01		Present study
Ethiopia	Lower montane forest	MTF	1327	30	5.45	3.177	1.72		Present study
Indonesia	Pre-montane forest	MTF	1000	20	2.16				Hertel et al. (2009)
Malaysia (Borneo)	Sedimentary montane forest	MTF	700	30	2.52				Kitayama and Aiba (2002)
Malaysia (Borneo)	Sedimentary montane forest	MTF	1700	30	4.28				Kitayama and Aiba (2002)
Malaysia (Borneo)	Sedimentary montane forest	MTF	2700	30	4.32				Kitayama and Aiba (2002)
Malaysia (Borneo)	Sedimentary montane forest	MTF	3100	30	4.59				Kitayama and Aiba (2002)
Malaysia (Borneo)	Ultrabasic montane forest	MTF	700	30	2.34				Kitayama and Aiba (2002)

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TABLE 4 (Continued)

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	Cstock$_{fr}$ (Mg C ha^{-1})	NPP$_{fr}$ (Mg C ha^{-1} year^{-1})	RT$_{fr}$ (year)	Allocation$_{fr}$	Reference
Malaysia (Borneo)	Ultrabasic montane forest	MTF	1700	30	4.05				Kitayama and Aiba (2002)
Malaysia (Borneo)	Ultrabasic montane forest	MTF	2700	30	4.32				Kitayama and Aiba (2002)
Malaysia (Borneo)	Ultrabasic montane forest	MTF	3100	30	6.48				Kitayama and Aiba (2002)
Malaysia (Borneo)	Very short heath forest	MTF	1000	15	6.39				Miyamoto et al. (2016)
Malaysia (Borneo)	Short heath forest	MTF	1000	15	5.63				Miyamoto et al. (2016)
Malaysia (Borneo)	Mix dipterocarp transition forest	MTF	1000	15	4.01				Miyamoto et al. (2016)
Malaysia (Borneo)	Small crow heath forest	MTF	500	15	2.79				Miyamoto et al. (2016)
Malaysia (Borneo)	Large crown heath forest	MTF	500	15	2.57				Miyamoto et al. (2016)
Malaysia (Borneo)	Mixed dipterocarp forest	MTF	500	15	1.71				Miyamoto et al. (2016)
Malaysia (Borneo)	Sedimentary site	MTF	700	15	1.88	0.62	3.01	0.06	Okada et al. (2017)
Malaysia (Borneo)	Sedimentary site	MTF	1700	15	2.50	0.72	3.45	0.12	Okada et al. (2017)
Malaysia (Borneo)	Sedimentary site	MTF	2700	15	3.43	0.89	3.86	0.19	Okada et al. (2017)
Malaysia (Borneo)	Sedimentary site	MTF	3100	15	3.69	0.32	11.44	0.08	Okada et al. (2017)
Malaysia (Borneo)	Ultrabasic site	MTF	700	15	2.03	1.02	1.99	0.11	Okada et al. (2017)
Malaysia (Borneo)	Ultrabasic site	MTF	1700	15	4.28	0.66	6.50	0.14	Okada et al. (2017)
Malaysia (Borneo)	Ultrabasic site	MTF	2700	15	2.89	0.39	7.46	0.11	Okada et al. (2017)
Malaysia (Borneo)	Ultrabasic site	MTF	3100	15	3.06	0.38	8.13	0.30	Okada et al. (2017)
Malaysia (Borneo)	Quaternary site	MTF	1700	15	1.87	1.03	1.82	0.14	Okada et al. (2017)

(Continues)

TABLE 4 (Continued)

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	$Cstock_{fr}$ (Mg C ha^{-1})	NPP_{fr} (Mg C ha^{-1} year^{-1})	RT_{fr} (year)	$Allocation_{fr}$	Reference
Peru	Pre-montane forest	MTF	595	30	2.10	2.28	0.92	0.2	Present study
Peru	Pre-montane forest	MTF	848	30	4.20	1.20	3.51	0.13	Present study
Peru	Pre-montane forest	MTF	1000	30	2.37	2.18	1.09	0.22	Present study
Peru	Lower montane forest	MTF	1527	30	3.12	1.26	2.48	0.1	Present study
Peru	Lower montane forest	MTF	1776	30	3.73	1.49	2.51	0.19	Present study
Peru	Lower montane forest	MTF	1885	30	5.95	2.93	2.03	0.37	Present study
Peru	Lower montane forest	MTF	2020	30	6.25	1.62	3.85	0.35	Present study
Peru	Upper montane forest	MTF	2758	30	6.20	1.08	5.74	0.14	Present study
Peru	Upper montane forest	MTF	3044	30	4.85	1.16	4.18	0.21	Present study
Peru	Upper montane forest	MTF	2863	30	4.53	1.18	3.84	0.15	Present study
Peru	Upper montane forest	MTF	3045	30	4.68	1.17	4.00	0.15	Present study
Peru	Upper montane forest	MTF	3537	30	2.81	0.97	2.89	0.12	Present study
Venezuela	High forest (Ferralsol)	MTF	1200	20	5.13	2.81	1.83		Priess et al. (1999)
Venezuela	Medium forest (Ferralsol)	MTF	1201	20	5.49	2.75	1.99		Priess et al. (1999)
Venezuela	Low forest (Ferralsol)	MTF	1202	20	4.33	3.78	1.15		Priess et al. (1999)
Venezuela	Terra firme forest	MTF		30	6.21				Rev. in Jiménez et al. (2009)
Venezuela	Bana	MTF		30	7.07				Rev. in Jiménez et al. (2009)
Venezuela	Transitional forest Caatinga/Bana (Podzol)	MTF		30	7.07				Rev. in Jiménez et al. (2009)
Venezuela	Caatinga	MTF		30	8.06				Rev. in Jiménez et al. (2009)
Venezuela	Transitional forest TF/Caating (Podzol)	MTF		30	17.78				Rev. in Jiménez et al. (2009)

we identified soil sand content and N, P, and K concentration as the main soil properties that drive fine root dynamics across the tropics.

Decreasing total soil K was correlated with increased fine root C stock across the lowland forest types. This was related to K limitation in our study sites, whereby ecosystems with high soil sand content are more K limited and, therefore, have higher root C stock. Such ecosystems need to store more K in their root systems, and forage deeper to access K stores in the soil (Sardans & Peñuelas, 2015; Soethe et al., 2007). This is confirmed by long-term soil fertilization experiments in lowland WTFs in Panama that showed a decline in root C stock in response to elevated K (Cusack et al., 2018; Yavitt et al., 2011). Also, the addition of K reduced fine root C stock at the community level, reduced allocation to roots, and increased tree height growth rates (Wright et al., 2011). Hence, we conclude that soil sand content and K are negatively correlated across the lowland forests, and lowland tropical tree species have to invest more energy to increase the fractional allocation to roots in sandy soil forests.

Soil N content was positively correlated with fine root residence time in montane forests. Our calculated variation in root residence time in the montane forests is more strongly driven by the variation in root C stock than by the variation in root productivity (Figure 2b). Some studies reported that soil N deficiency is expected to increase fine root C stock and longevity, and soil N availability decreased from 1050 to 3060 m a.s.l. due to decreasing N mineralization and concentration of inorganic sources (Graefe et al., 2010; Moser et al., 2011). Nitrogen inputs to the soil depend on the symbiotic N fixation rates of N fixing tree species, and high N use efficiency is associated with tropical white sand and montane forests with low rates of N circulation (Hedin et al., 2009; Menge et al., 2019; Pajares & Bohannan, 2016). Overall, our montane forest results support the constant allocation hypothesis of Hendricks et al. (1993) that root residence time increases with increasing N soil availability.

We identified P as a key determinant of the fractional allocation of total NPP to fine roots in montane forests. Phosphorus is the most limiting soil nutrient component in tropical forests after N and K (Laliberté et al., 2015; Lugli et al., 2019; Quesada et al., 2009). Fine root C stock, longevity, and total length increased in response to P deficiency in montane forests in Malaysian Borneo (Kitayama, 2013; Okada et al., 2017; Ushio et al., 2015). The limiting P supply means that at the plot level, morphological traits that facilitate P uptake are favoured on soils of low P (Addo-Danso et al., 2020), which could be due to the plasticity of the species traits or due to the community shift. Plants also develop rhizosphere and mycorrhizal fungi symbioses in response to persistent P deficiency (Raghothama & Karthikeyan, 2005). Between 1885 and 2020 m a.s.l. (cloud base range), we recorded the highest fractional allocation to fine roots that ranged between 39% and 41%, rates comparable to those found in lower montane forest with low P availability in the South American Andes (Moser et al., 2011). Ushio et al. (2015) suggested that high allocation to fine roots in mid-elevation montane forests is an adaptation to soils with low P availability by increasing specific

root surface and longevity. Diffusion of P in nutrient-poor tropical soils is particularly slow because high concentration of Al, iron oxides, and hydroxide drive the fast absorption of P (Laliberté et al., 2015; Ushio et al., 2015). Also, fertilization experiment revealed that litterfall content of P and N is lower on WTF above 1500 m a.s.l. (Tanner et al., 1998).

Sand content of the soil was the main determinant of fine root productivity, residence time, and fractional allocation of total NPP to fine roots across lowland rainforest ecosystems. Sandy soil forests assign more biomass, length, and surface area to fine roots through faster growth and greater investment in root dynamics. This is probably due to the lower nutrient and water-holding capacity of the sandy soils, compared with clay soils (Kochsiek et al., 2013; Nepstad et al., 1994). Soil respiration in sandy soils is higher than in clay soils, which may be an indicator of high fine root productivity and allocation across tropical lowland forests (Silver et al., 2005; Sotta et al., 2006). Root decay rates are also lower in sandy soils than in clay soils due to water and nutrient limitation and lower decomposer diversity (Silver et al., 2005). According to our results and previous studies, forests with high soil sand content have high fractional allocation of total NPP to fine roots, as a response to low nutrient availability in lowland forest soils (Aragão et al., 2009; Jiménez et al., 2009; Kochsiek et al., 2013; Quesada et al., 2012; Silver et al., 2000; Yavitt et al., 2011). On sandy soils, most lowland tropical wet forests produce litter low in N and on clay soil, low in P (Cavelier, 1992; Tanner et al., 1998).

Soil clay content was another significant predictor of fine root C stock in montane forests in our study. In previous studies, soil clay content and root biomass were significant predictors of soil carbon stock in humid tropical forests in Panama (Cusack et al., 2018), and clay content had a positive correlation with soil organic carbon concentration (Quesada et al., 2020) and with old soil carbon stock (Telles et al., 2003) in lowland forests in the Amazon. Root mortality and root exudates constitute the majority of the organic carbon inputs into the soil (Girardin et al., 2013; Graefe et al., 2008a, 2008b; Zimmermann et al., 2009), with recent inputs detected even in the subsoil (>30 cm depth; Balesdent et al., 2018). Approximately 50% of soil carbon exceeds the age of 100 years in the top 30 cm layer in the tropics (Balesdent et al., 2018). The persistence of these organic carbon inputs in the soil over time is strongly linked to adsorption and soil texture (Lehmann & Kleber, 2015), with clay minerals being important in the retention and stabilization of soil organic carbon (Singh et al., 2018).

Soil pH emerged as the second soil property after soil sand texture that drives root residence time in lowland forests, residence time increasing with increasing soil acidity (Figure 4d). Two previous studies in tropical forests reported that soil acidity was negatively correlated with fine root biomass, and high fine root productivity originated from the necessity of plants to uptake nutrients in strongly acidic soils (Hertel et al., 2009; Priess et al., 1999). High soil acidity across lowland old-growth forests may also increase the soil aluminium content (see the soil PCA analysis in Figure S1 and Table S1); therefore, the lower fine root

biomass and longer residence time in low pH soils may also be due to the increased Al toxicity. Al is known for its negative effect on root tips and root elongation in mineral soil, which reduces the growth of roots (Delhaize et al., 2012; Gupta et al., 2013; Rout et al., 2001). The negative effect of the Al stress on root morphology has been demonstrated on tree seedlings in tropical montane forests (Rehmus et al., 2014) and should be explored on fine root trait studies across a wider range of tropical forests.

4.3 | The effect of climatic variables on fine root dynamics

Our analyses revealed that MAT and MCWD are related to fine root dynamics across the tropical forests, although these drivers were not as strong as soil texture and chemistry. MAT had a positive effect on fine root productivity in montane forests. A similar effect was reported on root NPP in Ecuadorian and Bornean montane forests (Moser et al., 2010; Okada et al., 2017). In previous studies, decreasing temperature increased root residence time, resulting in a decrease in fine root decomposition, mineralization, and nitrification with increasing elevation in poorly developed and high acidity montane forests (Graefe et al., 2008b; Reich et al., 2014; Sierra Cornejo et al., 2020). The tropical montane trees respond by producing more fine roots to uptake nutrients in low-nutrient soils and MAT drives the fine root productivity in montane forests.

Most of the fine root dynamics studies across lowland forests recorded a positive relationship between precipitation and fine root biomass and productivity at a regional scale (Cusack et al., 2018; Green et al., 2005; Kho et al., 2013; Violita et al., 2016). In western Ghana, root biomass study along a precipitation gradient from dry to wet lowland forests revealed that Cstock$_{fr}$ increased with increasing MAP (Ibrahim et al., 2020). We did not find any significant pan-tropical relationships for precipitation and fine root dynamics. Yet, the annual MCWD slightly increased fine root residence time across lowland forests.

4.4 | Methodological considerations

Soil cores and ingrowth cores are a widely applied methods that provide direct estimates of root biomass and productivity, we acknowledge the uncertainties and limitations associated with these methods. First, the sampling depth is limited, in our case 30 cm, which leads to an underestimate of fine root biomass and productivity. The reported proportions of the fine root biomass in the top 30 cm soil layer out of total biomass range between 42% and 57% in tropical forests (Jackson et al., 1997), some new studies reported 46% in Amazon forests (Cordeiro et al., 2020) and ~44% in Africa (Ibrahima et al., 2010). The data on the depth profile of fine root productivity are more limited, with 60% within the top 30 cm reported for Central Amazon (Cordeiro et al., 2020). Residence time within the top 30 cm compared with the whole soil profile is also

likely to be an underestimate, as the life span of the deeper fine roots exceeds that of shallower roots (Cordeiro et al., 2020). Second, the ingrowth core method may underestimate productivity, particularly in systems where root turnover is high (Hendricks et al., 2006; Katayama et al., 2019). We collect both living and dead roots from the ingrowth cores (the dead roots would have been alive within the 3-month interval, as we start with root-free soil), and our collection interval, 3 months, is relatively short, which decreases this bias. Katayama et al. (2019) estimated that approximately 7% of the fine roots decomposed fully within a 3-month period in a Bornean forest. Third, the installation of the core causes disturbance, which causes additional noise in the data, and possibly an over-estimate in the short-term root production due to reduced competition in the initially root-free soil and the proliferation of adventitious roots due to the root severing at the installation (e.g. Hendricks et al., 2006; Vogt et al., 1998). Despite the shortcomings of the method, however, we have found good agreement between the ingrowth core and screen rhizotron techniques, collected in a subset of these sites (Huaraca Huasco et al., unpublished analysis).

5 | CONCLUSIONS

We quantified fine root dynamics and investigating the relationships between fine root dynamics, soil nutrient content, and climatic variables in montane and lowland tropical rainforest ecosystems in three continents. One remarkable feature of our results is that soil physics and chemistry are the strongest drivers of root dynamics, whereas climate variables hardly feature as explanatory variables.

We found a strong positive linear relationship between fine root productivity and soil sand content. This positive relationship was even stronger when we considered fine root allocation as a fraction of total NPP, demonstrating that understanding of total NPP adds explanatory power to understanding fine root productivity. Fine root residence time was a function of multiple factors: soil sand content, soil pH, and maximum water deficit, with longest residence times in acidic, sandy, and water-stressed soils in lowland forests. In montane forests, fine root productivity was a strong positive linear function of mean annual temperature, fine root residence time was a strong positive function of soil nitrogen content, and fractional allocation of total NPP to fine roots increased with decreasing soil P availability. In contrast to the lowlands, environmental conditions were a better predictor of fine root productivity than of fractional allocation to fine roots root, suggesting that fine root productivity may be a dominant driver of NPP allocation in tropical mountain regions.

Our understanding of global fine root dynamics needs refining. A logical next step to understand the effect of drought events across the tropics would be to expand this analysis to seasonal variation of root dynamics. There are important gaps in our understanding of the belowground ecosystem functioning of tropical forests, and how they will respond to rapidly changing climate.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available here: https://doi.org/10.5061/dryad.k98sf7m5q.

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SUPPORTING INFORMATION

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