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Above- and belowground strategies of tropical montane tree species are coordinated and driven by small-scale nitrogen availability

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Abstract

1. The question whether the strategies of above- and belowground plant organs are coordinated as predicted by the plant economics spectrum theory is still under debate. We aim to determine the leading dimensions of tree trait variation for above- and belowground functional traits, and test whether they represent spectra of adaptation along a soil fertility gradient in tropical Andean forests.

2. We measured leaf, stem and fine root functional traits, and individual-level soil nutrient availability for 433 trees from 52 species at three elevations between 1000 and 3000 m a.s.l.

3. We found close coordination between above– and belowground functional traits related to the trade-off between resource acquisition and conservation, whereas root diameter and specific root length formed an independent axis of covarying traits. The position of a tree species along the acquisition–conservation axis of the trait space was closely associated with local soil nitrogen, but not phosphorus, availability.

4. Our results imply that above- and belowground plant functional traits determine at which edaphic microhabitats coexisting tree species can grow, which is potentially crucial for understanding community assembly in species-rich tropical montane forests.

KEYWORDS
Ecuador, fine roots, functional traits, intraspecific trait variability, microhabitats, plant economics spectrum, tropical montane forest, within-species centring

1 | INTRODUCTION

A central goal of trait-based ecology is to identify general axes of trait covariation and link them with environmental gradients as a tool for understanding plant strategies and ecosystem processes as well as improving predictions (Bardgett et al., 2014; Bruelheide et al., 2018; Díaz et al., 2016; Laughlin, 2014; Suding et al., 2008; Westoby & Wright, 2006). The plant economics spectrum (PES) is a comprehensive framework that describes how the functional traits of plant roots, stems and leaves are subject to the same trade-off between fast, acquisitive and slow, conservative strategies (Reich, 2014). According to the PES, traits from roots, stems, and leaves should all be coordinated along this one axis of variation due to biophysical constraints that impair fitness, in case the plant would not pursue a consistent strategy for all its organs (Reich, 2014). However, empirical evidence has often pointed towards a multi-dimensional root trait spectrum that is at least partly decoupled from the aboveground PES (Kong et al., 2014; Kramer-Walter et al., 2016; Liese et al., 2017; Valverde-Barrantes et al., 2015). Bergmann et al. (2020) advanced this debate by proposing the theory of a two-dimensional fine root economics spectrum, where one axis represents the classical acquisition-conservation trade-off, while a second, orthogonal axis termed "the collaboration gradient" is formed by root diameter (and other closely associated morphological and anatomical traits) and the degree of reliance on mycorrhiza. Two recent contributions propose multi-dimensional whole-plant trait spectra, with partly conflicting outcomes: A review by Weigelt et al. (2021) concluded that there is a shared axis of trait coordination for leaf and root traits related to the acquisition-conservation trade-off with an orthogonal root collaboration gradient and separate axes for plant height and rooting depth. In contrast, Carmona et al. (2021) presented evidence from a global database that plant size, the leaf economics spectrum (LES), the root acquisition-conservation gradient and the root collaboration gradient all form independent dimensions of their own.

The different strategies of plant species that are reflected by their functional traits structure plant communities along environmental gradients through processes of environmental filtering and limiting similarity (Bruelheide et al., 2018; Díaz et al., 1998; Tilman, 1988). Resource availability, including soil fertility, is thought to be the key driver of the evolution of divergent strategies along the acquisition-conservation axis, with conservative strategies being an adaptation to nutrient scarcity and acquisitive strategies to nutrient abundance (Reich, 2014). In line with theoretical expectations, the leaf traits of tropical rainforest tree species vary with soil fertility (Asner & Martin, 2016; Báez, Cayuela, et al., 2022; Ding et al., 2019; Martin et al., 2020; Vleminckx et al., 2021). However, association patterns seem to be more complex for root traits (Lugli et al., 2019; Vleminckx et al., 2021), with their strength and direction being highly dependent on the environmental context (Cusack et al., 2021).

Trait variation along environmental gradients can be observed on different aggregation levels, that is within species, between species, and between communities. Because the underlying processes driving trait variation differ between those levels, the strength and direction of trait-environment associations can also differ (Clark et al., 2011; Petter et al., 2016). Intraspecific trait variation in particular has received increased attention in the past decade (Bolnick et al., 2011; Tautenhahn et al., 2019; Westerband et al., 2021). Occurrence of a pattern on one scale of aggregation does not imply that the same pattern holds on other scales of aggregation; rather, differing or even reversed relationships of traits with environmental factors on the intra- versus the interspecific level can obscure overall patterns (Anderegg et al., 2018; Dong et al., 2020; Laughlin et al., 2017).

As different community assembly processes operate on different spatial scales, trait-environment associations often depend on the spatial scale (Chalmandrier et al., 2017; Mokany & Roxburgh, 2010; Saar et al., 2017). Microhabitats within forest patches can harbour species with slightly different niches and thereby may contribute to high species numbers and affect the spatial structure of the community (Stark et al., 2017; Ulrich et al., 2017; Umaña et al., 2021). Such an effect is particularly relevant for tropical montane forests in rugged terrain (Inman-Narahari et al., 2014; Pierick et al., 2021; Werner & Homeier, 2015), where small-scale soil heterogeneity is assumed to contribute to the outstanding species diversity (Homeier et al., 2010; Jones et al., 2011). To address this, this study investigates inter- and intraspecific trait-environment associations in tropical montane forests on the microhabitat scale.

We measured soil nutrient availability in direct vicinity of more than 400 trees of 52 tree species distributed in nine 1-ha plots of tropical Andean forest at three elevations, and investigated its association with the trees' above- and belowground functional traits.

This study builds on the work of Homeier et al. (2021), who studied the variation of leaf functional traits of 52 tree species from three elevations in highly diverse tropical montane forests in the Andes. Here, we use the same leaf trait dataset and complement it with individual-level wood and fine root trait data in conjunction with highly resolved data on nutrient availability to answer the following questions:

1. Which are the leading dimensions of trait variation, and are functional traits of fine roots, stems and leaves coordinated with each other? To answer this question, we investigate whether the observed trait coordination in the studied Ecuadorian tropical forests agrees with the whole-plant spectra proposed by Reich (2014) (one-dimensional coordination of traits from all organs), Weigelt et al. (2021) (integrated leaf and root acquisition-conservation gradient with decoupled root collaboration gradient) or Carmona et al. (2021) (separate acquisition-conservation gradients of leaves and roots, plus a decoupled root collaboration gradient).

2. Are leaf, stem and root traits associated with soil N and P availability on the intra- and interspecific level? We expect tree species with more acquisitive functional traits to grow in local habitats with higher nutrient availability, and vice versa. Furthermore, we expect to detect corresponding patterns on the intraspecific level as a result of phenotypic plasticity in response to local environmental conditions.

2 | METHODS

2.1 | Study area

The study was conducted in tropical montane forests on the eastern slope of the Andes in southern Ecuador (Figure S1). Sampling was conducted at three different elevations (1000, 2000 and 3000 m a.s.l.) subsequently referred to as 'sites' (for their coordinates, see Table S1). The sites at 1000 and 3000 m are located in the Podocarpus National Park, while the 2000 m site is in the adjacent San Francisco Reserve. The study sites represent a pronounced climatic gradient, with mean annual temperatures decreasing from 20°C to 9.5°C, and annual precipitation increasing from 2000 to 4500 mm from the lowest to the highest site. Typically, precipitation shows a moderate seasonality with a wetter season from June to August and a drier season from September to December. Nevertheless, the climate is humid throughout the year, with all months on average receiving >100 mm precipitation (Bendix et al., 2008; Emck, 2007).

The study sites are characterized by relatively nutrient-poor soils on granodiorite, mica-schists and quartzite (1000 m), phyllites and meta-sandstones (2000 m) or semipelites and black phyllites (3000 m). There is a pronounced decrease in soil N availability with increasing elevation and also from lower to upper slope positions in the rugged terrain, which is reflected by decreasing forest biomass and productivity along these gradients (Homeier & Leuschner, 2021; Wilcke et al., 2008; Wolf et al., 2011).

The studied forest types are classified as evergreen premontane forest (1000 m), evergreen lower montane forest (2000 m), and evergreen upper montane forest (3000 m). Floristic composition changes rapidly with elevation, as most tree species in the study area are only found in narrow elevational belts (Homeier et al., 2008). With increasing elevation, tree height decreases and tree root-shoot ratio increases (Leuschner et al., 2007).

Research permits for conducting fieldwork were granted by the Ministerio del Ambiente del Ecuador (Ecuadorian Environmental Department) under the permit numbers 033-2019-IC-FLO-FAU-DP AZCH-UPN-VS/MA and 016-2019-IC-VS-UPN-DPAL-MAE.

2.2 | Study design

Sampling was conducted on three permanent 1 ha-plots at each site. We selected 52 tree species (20 species each at 1000 and 2000 m; 12 species at 3000 m, Table S2) that fulfilled the criteria of (a) being common enough to find enough replicates in the plots, and (b) covering the full spectrum of tree functional types found in the ecosystem, ranging from pioneer to late-successional species, as well as both understory and canopy trees. The latter aspect was supported by taking into account trait data from previous studies (specific leaf area, SLA and wood specific gravity, WSG, Báez & Homeier, 2018; Báez, Cayuela, et al., 2022). Except for one gymnosperm (*Podocarpus oleifolius* D.Don at 2000 m), all species were dicotyledonous angiosperm trees. Most selected species had a restricted elevational distribution, occurring only at one of the three elevations. Only two species

were present at two elevations: *Heliocarpus americanus* L. at 1000 m and 2000 m, and *Clethra revoluta* (Ruiz & Pav.) Spreng. at 2000 m and 3000 m, but the former was only sampled at 2000 m and the latter only at 3000 m. Per species, we randomly selected 8–10 replicate individuals from the total number of individuals per species found in the plots. In some cases, practical obstacles encountered in the field (such as, no accessible fine roots) made it impossible to collect leaf, root and wood samples from all initially selected trees. In these cases, additional samples from replacement trees of the same species were taken whenever possible. Table S2 gives an overview of the sample size per tree species. In total, 433 trees were sampled, with 4–10 replicates per species for each of the plant organs.

2.3 | Trait measurements

An overview of all measured functional traits, their abbreviations and units is provided in Table 1. The leaf trait data used in this work were collected in February to March 2019 and are already published in Homeier et al. (2021), and a more detailed description of the methods employed in measuring them is given there. In short, from each tree, two to three branches were collected in the crown top, and leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf N (N_{leaf}) and leaf P (P_{leaf}) concentrations were measured on 20 leaves per tree. Leaf thickness ($Thick_{leaf}$) and leaf toughness ($Tough_{leaf}$) were determined on three further leaves. We quantified wood specific gravity (WSG, g cm^{-3}) for each studied tree by collecting a wood core (5 cm length, 5.15 mm diameter) with an increment corer (Haglöf, Langsele, Sweden) at a stem height of 1.30 m in October to December 2019. WSG was then obtained by dividing core dry mass by core fresh volume.

Fine roots were sampled between October 2018 and January 2019. From each tree, we collected one intact, distal fine root strand (diameter <2 mm) by tracing coarse roots from the stem base in distal direction until reaching fine root systems. The root samples were taken either from the organic layer or, in case of thin organic layers, mineral topsoil

TABLE 1 Traits, trait abbreviations and units.

Trait	Abbreviation	Unit
Average root diameter	d_{root}	mm
Specific root length	SRL	m g^{-1}
Root tissue density	RTD	g cm^{-3}
Root nitrogen concentration	N_{root}	mg g^{-1}
Root phosphorus concentration	P_{root}	mg g^{-1}
Leaf dry matter content	LDMC	mg g^{-1}
Leaf toughness	$Tough_{leaf}$	kN m^{-1}
Leaf thickness	$Thick_{leaf}$	mm
Leaf area	LA	cm^2
Specific leaf area	SLA	cm^2 g^{-1}
Leaf nitrogen concentration	N_{leaf}	mg g^{-1}
Leaf phosphorus concentration	P_{leaf}	mg g^{-1}
Wood specific gravity	WSG	g cm^{-3}

(0–10 cm depth). After collection in the field, the samples were stored in a fridge at 8°C for no more than 2 days. Next, the roots were washed carefully in tap water, dead and damaged-looking root parts were removed, and absorptive fine roots were separated from transportive fine roots based on morphological criteria (periderm colour and surface texture, root diameter, root elasticity and presence of root hairs, as in McCormack et al. (2015) and Pierick et al., 2023). Depending on the species, the absorptive fine roots included material up to the 2nd to 4th root order. All following steps were conducted on absorptive fine roots only. The roots were placed in an acrylic glass tray filled with demineralized water and scanned with a flatbed scanner (Scanjet G4050, Hewlett Packard, Houston, TX, United States) as 600 dpi greyscale images. We then used the software WinRhizo 2013 Basic (Régent Instruments Inc., Quebec, Canada) to estimate average root diameter, total root length, and total root volume from the scanned images. After scanning, the root samples were oven-dried for at least 48 h at 60°C and weighed on an analytical balance. With these data, we calculated the morphological traits specific root length (SRL) and root tissue density (RTD). Finally, the root samples were ground with a vibrating disc mill and the nitrogen (N) concentration was measured with a CN elemental analyser (Vario EL III, Hanau, Germany), and the P concentration by ICP-OES analysis (Thermo Scientific iCAP 7000 ICP-OES, Thermo Fisher Scientific, Germany) after HNO_3 digestion of the ground material.

2.4 | Soil chemical analyses

We measured the chemical properties of the mineral topsoil in close vicinity (distance <1 m from stem) of each of the 433 trees sampled. Samples were taken from the 0–10 cm depth layer of the mineral soil, dried at 40°C. Total C and N concentrations were measured by elemental analysis (Euro EA, Hekatech, Wegberg, Germany) via thermal combustion in milled aliquots.

Because of the acidic soil (pH <6), all C was assumed to be soil organic carbon. Soil C/N ratios were calculated as an indication of the rates of soil organic matter turnover and associated nutrient supply via mineralization. High soil C/N ratios indicate slow turnover of organic matter, resulting in low N availability to plants. The plant-available P concentration was determined in the <2 mm soil fraction by extraction with 0.5 M $NaHCO_3$ (Olsen et al., 1954) and PO_4-P concentration measurement with continuous flow analysis and high-resolution colorimetry (San++, Skalar, Breda, The Netherlands).

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Individual tree (then averaged per species)	52 species along continuous gradient
Individual tree	Individual tree	4–10 per species

2.6 | Data analysis

2.6.1 | Aboveground–belowground trait relationships

All data analyses were conducted in R (R Core Team, 2020 Version 4.1.0). We calculated three principal component analyses (PCA) with the species-level trait means, one including all 13 measured above- and belowground functional traits (PCA_{all}), one including only leaf traits (PCA_{leaf}), and another one including only root traits (PCA_{root}). All traits were natural log-transformed and standardised before running the PCA. To test whether the main axes of root and leaf trait variation are coordinated, we fitted a linear regression with the species scores on the first principal component of PCA_{root} in dependency of their scores on the first principal component of PCA_{leaf}.

2.6.2 | Trait relationships with local soil nutrient availability

To test for associations between traits and soil nutrient availability in direct vicinity of the sampled trees, we used mixed models with the technique of within-species centring (Isasa et al., 2023; van de Pol & Wright, 2009), which allows discriminating between within-species and between-species trends by splitting the effect of the original continuous predictor into an interspecific and an intraspecific component. For the interspecific component, the mean of the original predictor variable for the observations of a given species is used as a predictor; for the intraspecific component, the values of the original predictor are centered within each species. For detailed model equations see Methods S1. We fitted one model for each combination of the 13 functional traits and the two predictors soil C/N ratio (as a measure of N availability) and P availability, leading to a total of 26 models. We chose this approach instead of fitting models with both predictors included because we were interested in the magnitude and direction of trait associations with N and P availability rather than in the marginal effects of each predictor after controlling for the other. All traits were natural log-transformed and standardised, except for WSG, which was not log-transformed. The log transformations were done to address heteroscedasticity and right-skewed trait distributions, while the centring and scaling was done to be able to compare parameter estimates among models. We also centred and scaled both predictors, and additionally log-transformed the soil P data to correct for right-skewness. The models were fitted in a hierarchical Bayesian framework using R package brms version 2.15.0 (Bürkner, 2017). For details about the model fitting, prior choice, prior predictive checks and convergence diagnostics, see Methods S1.

Furthermore, we tested whether the species' position in the trait space depended on their preferences for local nutrient availability by fitting linear models of the species' scores on the first and second axes of PCA_{all}, PCA_{leaf} and PCA_{root} in dependency of the mean N and P availabilities measured directly adjacent to the tree individuals of that species.

3 | RESULTS

3.1 | Principal component analyses

In the PCA performed with above- and belowground traits (PCA$_{all}$, Figure 1), leaf thickness, leaf toughness, WSG, LDMC and RTD were highly positively associated with the first axis (44.1% of variance explained), while all leaf and root nutrient concentrations, leaf area and SLA were negatively associated with it. Root diameter was positively and SRL negatively associated with the second axis (20.7% of variance explained). The species from the three elevations did not separate into distinct clusters but were distributed along a continuum. However, there was a visible tendency for species from the 1000 m site to occupy the negative range of PC1, whereas species from the 2000 m and 3000 m sites tended to have positive scores on PC1. Certain species deviated strongly from this pattern, notably *Heliocarpus americanus* L. from 2000 m and *Siparuna muricata* Ruiz & Pav. from 3000 m with much more negative scores on PC1 than all other taxa at these sites.

In the leaf trait PCA (PCA$_{leaf}$, Figure 2a), the first axis explained 61.5% and the second axis 14.9% of variation. Leaf area, SLA, and foliar N and P concentrations were positively, and leaf toughness, leaf thickness and LDMC, negatively associated with the first axis. Like in PCA$_{all}$, there was only a weak differentiation between the species from the three sites, with species from 2000 and 3000 m having lower, and species from 1000 m, higher values on PC1.

In the PCA with root traits (PCA$_{root}$, Figure 2b), the first axis explained 54.6% of variation and was positively associated with RTD and negatively with root N and P. The second axis explained 34.0% of variation and was positively associated with SRL and negatively with root diameter, with the species being not visibly clustered by site.

We interpret the first principal component (PC1) of PCA$_{leaf}$ as an expression of the LES and the first principal component of PCA$_{root}$ as an expression of the root economics spectrum. For consistency, we multiplied the species scores on PC1 of PCA$_{root}$ by −1, so that low values stand uniformly for more conservative, and high values for more acquisitive resource use strategies in the leaf and the root economics spectra. There was a weak but significant positive relationship between axes representing the leaf and root economics spectrum ($p = 0.006$, $R^2 = 0.14$, Figure 2c).
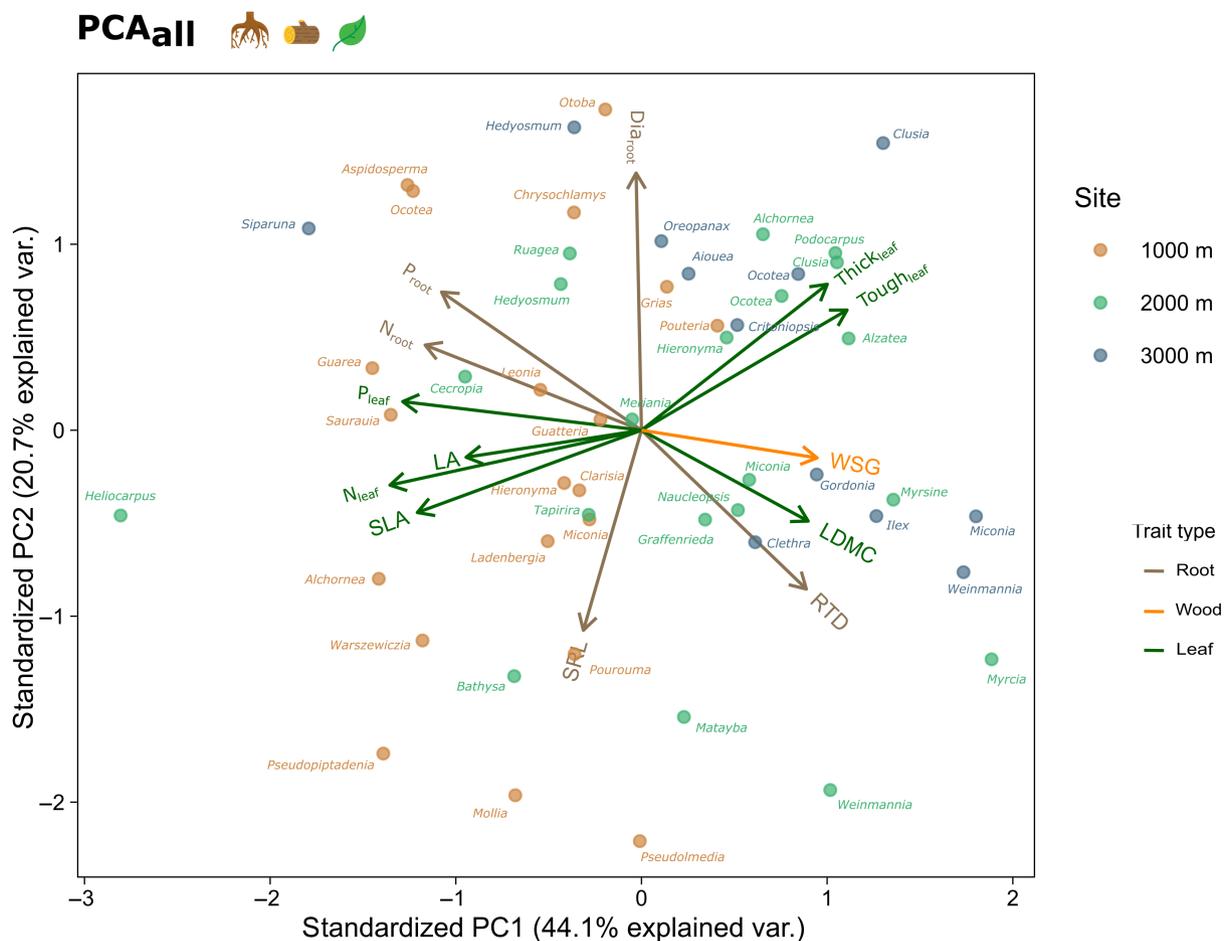
FIGURE 1 Principal component analysis of mean root, stem and leaf functional traits of 52 tree species from three elevational levels. For abbreviations of functional traits, see Table 1.
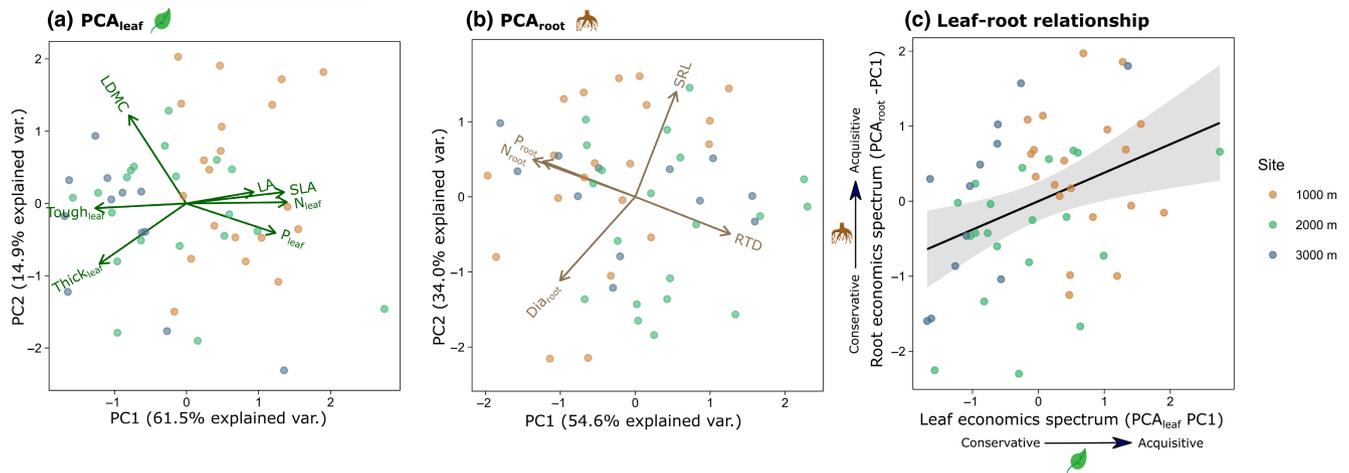
FIGURE 2 Coordination of above- and belowground functional trait dimensions. (a) Principal component analysis of leaf functional traits (PCA_{leaf}). (b) Principal component analysis of root functional traits (PCA_{root}). (c) Relationship between the respective first principal components (PC) from PCA_{leaf} and PCA_{root}. PCA_{root}PC1 was multiplied with −1 for consistency. The regression line shows the predictions from a linear regression with 95% confidence intervals ($p = 0.006$, $R^2 = 0.14$). For abbreviations of functional traits, please consult Table 1.

3.2 | Soil N and P availability and trait association with nutrient availability

Soil C/N ratios measured beneath the individual trees ranged from 9.8 to 18.9 and reached lower values at 1000 m (10.4–13.1, mean 11.9) and 3000 m (13.8–16.7, mean 14.8) than at 2000 m (9.8–18.9, mean 16.1), revealing no clear elevational trend. Olsen-extractable soil P concentrations at all three sites showed highly right-skewed distributions as are typical of element concentrations in soil, with lower values at 1000 and 2000 m (means around 3 mg kg^{-1}, maxima of 11.5 and 5.9 mg kg^{-1}, respectively) than at 3000 m (mean 19.1, maximum 28.4, Figure S2). Soil C/N ratios and soil P concentrations were not significantly correlated ($\rho = -0.15$). Due to the site differences in soil nutrient availability outlined above, the observations clustered by site when plotting both variables against each other (Figure S3).

Most measured traits (all leaf traits, RTD and WSG) were credibly associated with soil C/N ratio on the interspecific, but not on the intraspecific level (Figure 3, Table S3). RTD, DMC, leaf toughness, leaf thickness, and WSG increased with increasing soil C/N ratios, whereas leaf area, SLA, and foliar N and P concentrations decreased with increasing soil C/N ratios. SRL was not associated with soil C/N ratios among species, but decreased with increasing C/N ratios at the intraspecific level. Root N and P concentrations decreased with increasing soil C/N ratios at the intra- and the interspecific levels, but slopes were steeper for the between-species relationship. Root diameter did not credibly change with soil C/N ratios neither on the intraspecific nor the interspecific level. While the C/N ratios as a measure of N availability had a very high explanative power in all of our models of the 13 traits (conditional R^2 values ranging from 66% for RTD to 95% for leaf area, Table S4), a large proportion of the variance in the traits was explained by random effects, most importantly by the random species intercepts, which by far contributed the largest fraction of explained

variance in most models. Consequently, the proportion of variance explained by overall within- and between-species trends alone (marginal R^2 value) was lower, with the highest variance explained in the models of root and foliar N concentrations (both 34%), and the lowest in the model for root diameter (1%).

In contrast to the influence of the soil C/N ratios, there were almost no relationships of traits with Olsen-extractable soil P concentrations on the inter- or intraspecific level (Figure 4, Table S5). The only exceptions were a positive interspecific relationship of leaf thickness, a negative interspecific relationship of leaf area, and a positive intraspecific relationship of SRL, with the available P concentration in the soil. As in the models with soil C/N ratio as explanatory variable, the standard deviations of the random intercepts for species were high in all models, while the random variability among plots and random species-specific differences in slopes were negligible (Table S5). The variance explained by the whole model was similar to the models with C/N ratio as explanatory variable, but the variance explained by the fixed effects was smaller for all traits except root diameter (marginal R^2 with C/N ratio: 0.01, marginal R^2 with P: 0.02, Table S4). The largest marginal R^2 values were found for leaf area and leaf thickness (both 11%).

3.3 | Association of the species' position in the trait space with local nutrient availability

We found a significant positive relationship between the species scores on the first axis of PCA_{all}, representing the PES (higher values interpretable as conservative and lower values as acquisitive), and the average soil C/N ratio measured beneath individual trees ($p < 0.001$, $R^2 = 0.53$, Figure 5). In this plot, the species separated clearly by site. The species growing at high soil C/N ratios and scoring high on PC1 of PCA_{all} were mostly from the 2000 m site, while
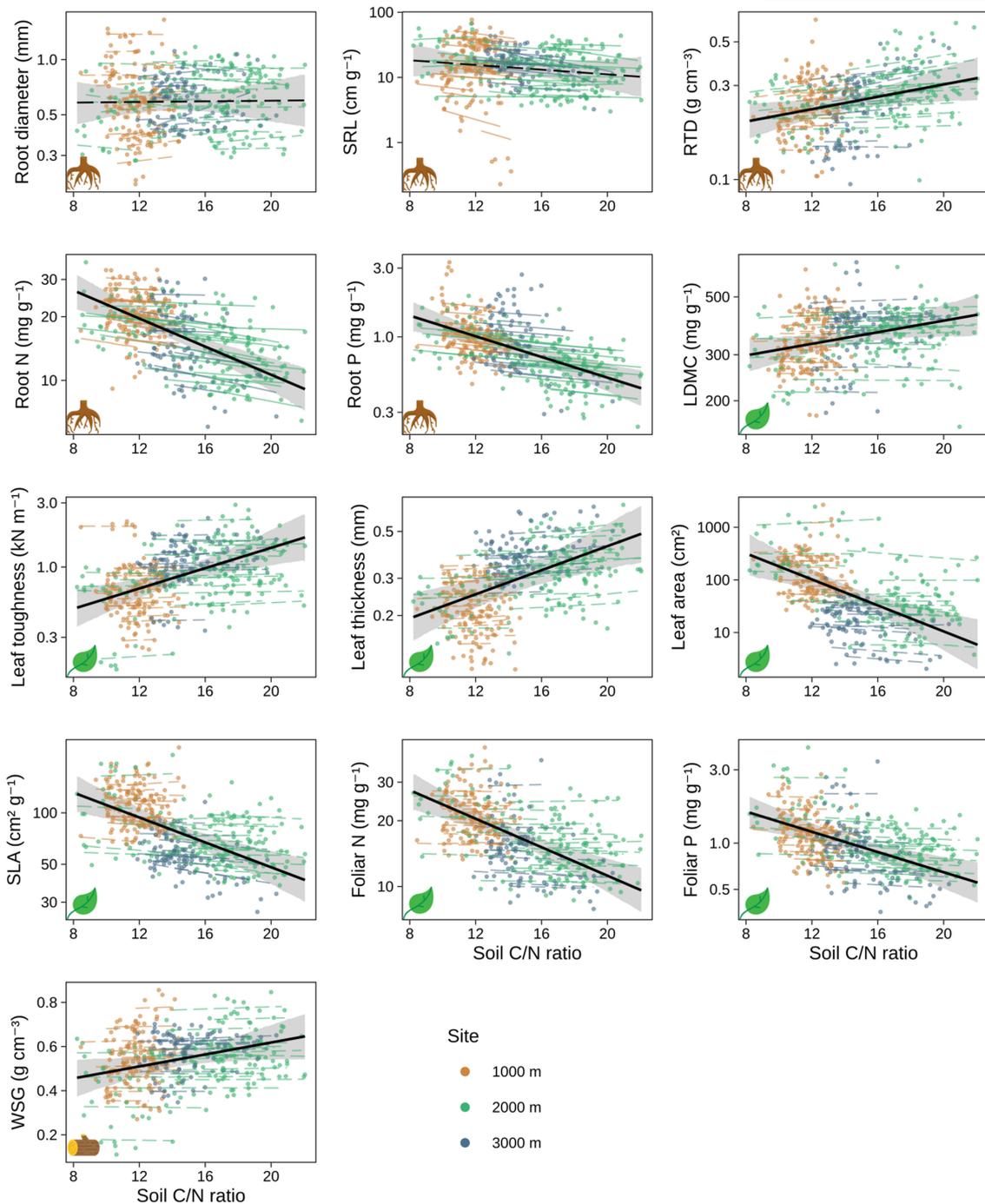
FIGURE 3 Relationships between the soil C/N ratios beneath the tree individuals and functional traits. Shown are the data in combination with predictions from mixed models with within-species centring. Each point represents one individual tree. The thin, coloured lines show intraspecific model predictions for the 52 tree species; the black lines show the overall interspecific trend with 95% confidence intervals. Dashed lines indicate slope parameters that did not credibly differ from 0; solid lines indicate slope parameters that were credibly different from 0. Please note that except for WSG, all y axes are displayed on a log scale. For abbreviations of functional traits see Table 1.

the species related to low C/N ratios and with low scores were predominantly from the 1000 m site; the species from 3000 m took an intermediate position in this plot. Exceptions are some species from 2000 m (*Cecropia angustifolia* Trécul, *Bathysa mollis* (Rusby) C.M. Taylor & Maldonado, and *Merania franciscana* C. Ulloa & Homeier) situated in a range otherwise filled by species from 1000 m. In

addition, *Heliocarpus americanus* L. and *Siparuna muricata* Ruiz & Pav. from 2000 m and 3000 m represented striking outliers, with scores on PC1 of PCA$_{all}$ being unusually low for their average soil C/N ratio compared to the overall pattern. We did not find significant relationships of PC2 of PCA$_{all}$ with soil C/N ratios, or of any of the axes with Olsen-extractable soil P concentrations (Figure S4).
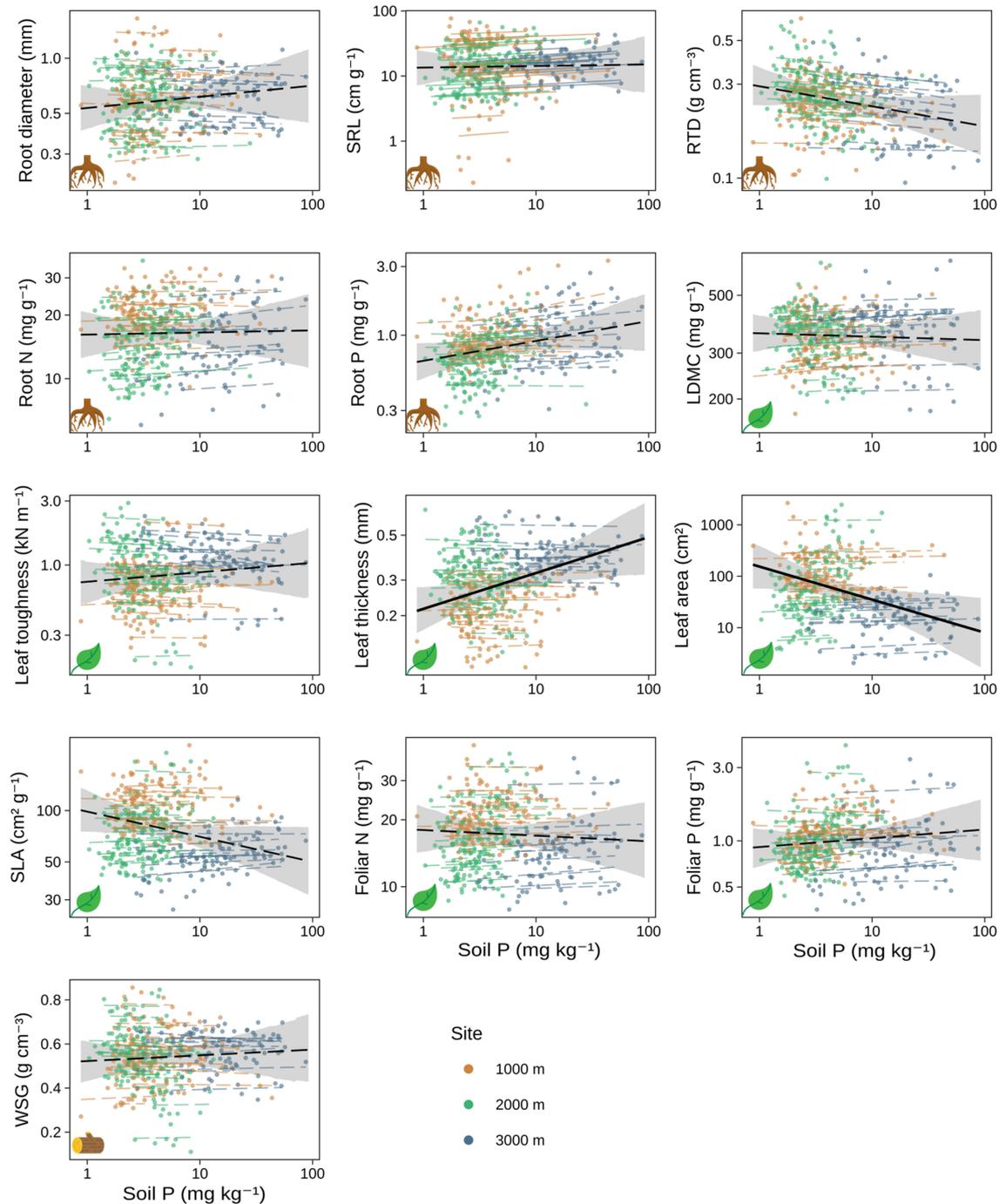
FIGURE 4 Relationships between the Olsen-extractable soil P concentrations beneath the tree individuals and functional traits. Shown are the data in combination with predictions from mixed models with within-species centring. Each point represents one individual tree. The thin, coloured lines show intraspecific model predictions for the 52 tree species; the black lines show the overall interspecific trend with 95% confidence intervals. Dashed lines indicate slope parameters that did not credibly differ from 0; solid lines indicate slope parameters that were credibly different from 0. Please note that except for WSG, all *y* axes are displayed on a log scale. For abbreviations of functional traits, please consult Table 1.

4 | DISCUSSION

4.1 | Resource-use traits of all plant organs are coordinated

Our results provide clear evidence that leaf morphology and nutrient concentrations, wood specific gravity (WSG), fine root nutrient concentrations, and RTD of 52 tree species in tropical montane forests were coordinated. Thin, large and soft leaves, high leaf and fine root nutrient concentrations, and low tissue densities are indicative of an acquisitive, fast resource use strategy, while a conservative strategy is characterized by opposite properties (Reich, 2014; Weemstra et al., 2016; Wright et al., 2004). The trade-off between resource acquisition and conservation results from the constraint

FIGURE 5 Relationship between the soil C/N ratios beneath the tree individuals and the species positions in the plant economics space (PCA$_{all}$PC1). The line shows predictions from a linear regression with 95% confidence intervals ($p < 0.001$, $R^2 = 0.53$).

that investment in long tissue life-span and protection against herbivory and mechanical damage comes at the cost of slow growth, low resource acquisition rates, and therefore generally slow return of invested resources (Reich, 2014). On the other hand, investment in fast growth, high resource acquisition rates and, as a consequence, fast resource return comes at the cost of more vulnerable tissues and shorter tissue life-spans (Reich, 2014; Weemstra et al., 2016; Wright et al., 2004).

According to the PES theory, leaves, stem and roots are subject to the same resource acquisition-conservation trade-off, and traits related to resource economics of all plant organs are correlated with each other (Reich, 2014). While there is broad support for a general local- or regional-scale linkage between functional traits of aboveground and belowground plant organs for a great number of growth forms in different ecosystems (e.g. de la Riva et al., 2018; Freschet et al., 2010; Hu et al., 2019; Marañón et al., 2020; Pérez-Ramos et al., 2012; Shen et al., 2019), other studies reported a lack of association between aboveground and belowground traits of woody plants (e.g. Burton et al., 2020; Valverde-Barrantes et al., 2015; Vleminckx et al., 2021). This contradiction is also reflected in recent studies of broader scope, that is a review and a global database study: While Weigelt et al. (2021) concluded that leaf and root traits related to the resource economics trade-off form an integrated axis from slow to fast resource return, Carmona et al. (2021) found that leaf, root and stem traits were decoupled from each other, forming separate dimensions of trait covariation. Our results are further evidence for the existence of a PES as proposed by Reich (2014) and Weigelt et al. (2021). On the other hand, the relationship between PCA axes representing the leaf and root economics spectrum (Figure 2c) explained only 14% of variation in the data, which indicates that the

coupling of above- and belowground traits is no strict imperative but that species still have considerable degrees of freedom in their evolution of above- and belowground resource acquisition strategies.

4.2 | The root collaboration axis

We observed that root diameter and SRL formed their own axis of trait variation, which was orthogonal to the resource economics axis. Similarly, Kramer-Walter et al. (2016), Liese et al. (2017), and others found that, while root nutrient concentrations and RTD were coordinated with traits of the LES, they were decoupled from traits related to root diameter. Bergmann et al. (2020) proposed a theoretical framework in which functional traits related to fine root diameter form their own axis in the root trait space, the so-called collaboration gradient. According to these authors, this gradient is driven by a trade-off between investing either into cost-effective proliferation of the soil by fine roots with high SRL, or alternatively into high mycorrhizal colonization of fine roots with higher diameters, thereby "outsourcing" part of the costs of soil proliferation and nutrient acquisition to the fungal partners. This theory is supported by the finding that thick fine roots are more intensively colonized by mycorrhizal fungi than thinner, more short-lived fine roots (Comas et al., 2014; Eissenstat et al., 2015; Liu et al., 2015; McCormack & Iversen, 2019). In accordance, there is wide agreement that diameter-related root traits are to a larger degree phylogenetically conserved, whereas other fine root morphological traits and nutrient concentrations are more plastic and often more closely related with soil fertility (Kong et al., 2014; Liu et al., 2019; Wang et al., 2018). Both the global data base analysis by Carmona

et al. (2021) and the review by Weigelt et al. (2021) found evidence supporting the existence of the collaboration gradient. While the underlying mechanisms need validation against empirical data that cover not only root morphology but also mycorrhizal colonization and fine root functioning (Freschet et al., 2021), our results are a further piece of evidence for multi-dimensional concepts of the fine root trait space.

4.3 | Small-scale N availability drives the PES

All of the traits assigned to the resource economics spectrum in our study were credibly associated with the local soil C/N ratio on the interspecific level, while there was no evidence for an interspecific association of root diameter and SRL with soil C/N ratios. The direction of the trait associations with N availability confirmed the expectation of species with conservative traits being confined to locations with wide C/N ratios (i.e. low N availability), whereas species with acquisitive traits were found in local habitats with narrow C/N ratios (i.e. high N availability). These results for single traits are supported by the relationship between the species' average soil C/N ratios and their score on a PCA axis that represents the resource economics spectrum (PC1 of PCA$_{all}$).

It is well documented for many biomes that average functional traits of communities typically shift from more conservative to more acquisitive with increasing N availability (e.g. de la Riva et al., 2018; Ding et al., 2020; Kramer-Walter et al., 2016; Pérez-Ramos et al., 2012). The most likely explanation why conservative strategies are more successful when N is scarce, and acquisitive strategies are more advantageous at higher N availability, is that resource conservation is required to survive under infertile conditions, whereas increased aboveground competition under fertile conditions renders it advantageous to grow faster than competitors and thus pursue an acquisitive strategy (Reich, 2014). While, as the examples above demonstrate, the phenomenon is well described for the community level and larger spatial scales, we observed it for co-existing species within communities. We conclude that tree species, even if they co-exist within the same elevational belt, have preferences for different levels of local soil fertility, and are adapted to these microhabitats by differing trait combinations that are explained by the PES. Additionally, it is possible that mechanisms mediated by litter quality feed back on edaphic heterogeneity (Hobbie, 2015; Laughlin et al., 2015).

The local heterogeneity in soil conditions demonstrated by our data is most likely a result of small-scale topographic heterogeneity, which has been shown to cause considerable variation in nitrogen availability (Wolf et al., 2011) and therefore is profoundly influencing vegetation composition and ecosystem functioning in the study area on scales of a few to a few hundred meters (Báez, Fadrique, et al., 2022; Homeier et al., 2010; Pierick et al., 2021; Werner & Homeier, 2015; Wilcke et al., 2010). These studies at medium spatial scale show that trees at the less fertile upper slope have lower basal area increment rates than those at the more fertile lower slope

(Homeier et al., 2010), a lower foliage and litter quality (Werner & Homeier, 2015), and more conservative leaf, wood and fine root traits (Báez, Fadrique, et al., 2022; Pierick et al., 2021). Our study conducted at even finer spatial resolution of soil chemical predictor variables (<1 m to about 5 m) highlights how crucial small-scale environmental variation is for community assembly in topographically complex mountain landscapes.

We found almost no credible trait associations with available P concentrations in soil, neither for single traits, nor for the PCA axes summarizing them. While P is a limiting resource that drives functional trait distributions in most tropical lowland forests (Cusack et al., 2021; Lugli et al., 2019; Yaffar et al., 2021), N limitation plays a more prominent role in tropical mountain ecosystems due to lower mineralization rates at colder temperatures (Leuschner et al., 2007). Our results suggest that N is playing a more important role than P in structuring the functional composition of tree communities in these tropical montane forests.

Intraspecific trait variation along gradients of nutrient availability did not play a significant role for the majority of traits in our species sample. The only credible intraspecific trait-environment patterns observed were negative associations of SRL, root N concentrations and root P concentrations with soil C/N ratios, and a positive association of SRL with Olsen-P concentrations. Strikingly, these are all root traits. Roots can be highly plastic both in terms of tissue element concentrations and morphology (Hodge, 2004). Our results agree with findings showing that intraspecific trait variation is larger in fine roots than in leaves (Delpiano et al., 2020), and that fine root nutrient concentrations are more responsive to the environment than most other traits (Liu et al., 2019). The outcome of only minor intraspecific trait variation could result from the absence of overall within-species trait variability along our environmental predictors, or from species-specific differences in the direction and strength of the relationship (Kumordzi et al., 2019; Weemstra et al., 2020). Judging from the small standard deviation of species-specific random slopes, the former of the two explanations seems to be the case. While our results seem to contradict evidence from other tropical forests where significant intraspecific leaf and root trait variation along environmental gradients has been found (Hogan et al., 2020; Schmitt et al., 2020), it is possible that we would have seen clearer intraspecific trait-environment associations if more distant populations of a species had been included and the spatial scale and the edaphic variation covered for each species in the study had been larger.

4.4 | Adaptation to edaphic microhabitats promotes coexistence

We found evidence for highly variable soil conditions within 1-ha plots, and a broad overlap of N and P availability among the three elevations. Besides, tree species from different sites were not on average functionally distinct but occupied largely overlapping areas in the trait space. Conversely, species coexisting in close proximity

within the same 1 ha-plot exhibited highly diverse functional strategies. Further, as discussed before, the functional strategies of the tree species were strongly associated with the mean N availability measured beneath the sampled individuals of the species. Taken together, this information implies that the coexistence of a high number of tree species in the studied forests is partly enabled by small-scale soil heterogeneity in conjunction with specific adaptation of the species to the different microhabitats, as was proposed by Homeier et al. (2010) and Jones et al. (2011).

5 | CONCLUSIONS

Our investigation of wood, leaf and fine root traits in species-rich tropical montane forests shows that the functional traits of the 52 studied tree species can be arranged in an integrated multi-dimensional space, which is structured by the acquisition-conservation trade-off axis, and a decoupled root collaboration dimension, supporting concepts proposed by Reich (2014), Bergmann et al. (2020) and Weigelt et al. (2021). While the tree species' strategies tended to shift from acquisitive to more conservative from lower to higher elevation, heterogeneous N availability within the 1 ha-plots overlaid elevational differences and was the most powerful predictor of the species' functional strategy. These findings highlight the advantages of measuring highly resolved environmental predictors as opposed to plot- or community-level means, and provide a plausible explanation for the outstanding tree species richness of tropical montane tree communities. The strong relationship between a species' microhabitat preference and its position in the trait space may represent a valuable functional link to be included in future trait-based vegetation modelling approaches.

STATEMENT ON INCLUSION

This study is the result of a fruitful collaboration between Ecuadorian and German authors.

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SUPPORTING INFORMATION

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

Figure S1. Map of the study area.

Figure S2. Soil C/N ratios and plant available P at the three elevational levels.

Figure S3. Relationship between soil C/N ratios and plant available P.

Figure S4. Relationship between PCA axis scores and nutrient availability.

Table S1. List of permanent plots, their coordinates, and elevations.

Table S2. List of tree species.

Table S3. Inference and diagnostics from models with soil C/N ratio.

Table S4. Marginal and conditional R^2 values of models.

Table S5. Inference and diagnostics from models with soil P.

Methods S1. Within-species centring models.