FINE ROOT TRAITS OF TROPICAL MONTANE TREES IN ECUADOR - EFFECTS OF ELEVATION, VARIATION BETWEEN TREE FUNCTIONAL TYPES, AND ABOVE-BELOWGROUND LINKAGE

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Abstract

Tropical montane forests in the Andes are one of the most species-rich ecosystems of the world, and are therefore both valuable from a conservation perspective and interesting for testing ecological hypotheses. Particularly the belowground component of tropical ecosystems is so far understudied, which due to small-scale heterogeneity of soil properties in tropical montane forests allows addressing a multitude of open questions about associations between roots and their environment. Functional traits of fine roots are indicators of belowground resource economics strategies. However, the leading dimensions of root trait variation, their covariation with aboveground plant functional traits, and how they vary along environmental gradients are not fully understood. Furthermore, very little is known about their functional diversity and its dependency on abiotic factors.

This thesis comprises results from three descriptive field studies on root functional traits in tropical montane forests of the southern Ecuadorian Andes. In all of these studies, morphological and chemical traits of fine roots were measured on the level of individual trees, with the combined datasets encompassing more than 200 tree species. The first and second of these main chapters deal with the community-level root trait variation along a small-scale topographic gradient in lower montane forests, and a 2000 m elevational gradient respectively. The third one focuses on fewer tree species on three elevational levels, and examines the relationships between their microhabitat preferences, and their aboveground and belowground functional trait syndromes.

Functional traits of fine roots were coordinated with each other, forming two separate axes of root trait variation. The first axis involved root tissue density and nutrient concentrations and reflects a growth–survival trade-off, with low tissue densities and high nutrient concentrations indicating an acquisitive strategy, and high tissue densities and low nutrient concentrations indicating a conservative strategy. The second axis reflects a gradient of root diameter that might, according to recent theories, be related to the degree of reliance on mycorrhiza. While the acquisition–conservation axis was highly coordinated with leaf and wood traits reflecting the same trade-off for aboveground plant organs, indicating selective pressures towards a

consistent whole-plant economics strategy, the diameter-related axis was independent from aboveground functional traits.

Most root functional traits varied both along the smaller-scale topographic and the larger-scale elevational gradient. Tree fine roots tended to display increasingly conservative trait syndromes and higher root diameters towards upper slope positions and higher elevations. Furthermore, root functional traits associated with the acquisition–conservation axis were dependent on both large-scale nitrogen and phosphorus availability, with root trait syndromes at sites with higher nutrient availability being more acquisitive. Diameter-related root traits, however, were independent from large-scale nutrient availability. The trends described above explained only relatively small fractions of total trait variation because many species with different root trait syndromes coexisted within plots. Decreasing functional diversity along both the topographic and elevational gradient indicated the coexistence of species with diverse belowground strategies under more beneficial environmental conditions, and the convergence towards more conservative fine root strategies under the less beneficial conditions of upper slopes and higher elevations.

These patterns of coexistence were further explained by measuring soil nutrient availability on the spatial scale of tree individuals instead of plots. Within communities, tree species with conservative trait syndromes tended to grow at local microhabitats that were less rich in nitrogen. Thus, the high small-scale edaphic heterogeneity lead to the coexistence of species with diverse strategies within the conservation–acquisition trade-off in close proximity. A similar trend could neither be found for soil phosphorus, nor for diameter-related root traits. Intraspecific trait variation played only a minor role.

All root functional traits displayed high degrees of phylogenetic signal. While previous results, stating that early-diverged angiosperms from the magnoliid clade tend to have thick fine roots, could be confirmed, the data in this work reveal that the later-diverged angiosperm tree families Meliaceae and Clusiaceae are similarly thick-rooted in spite of their high phylogenetic distance to the magnoliid clade.

In conclusion, this work provides comprehensive evidence that root functional traits and root functional diversity in tropical montane forests vary along gradients of soil fertility, as environmental filtering promotes trait convergence towards conservative resource use strategies under nutrient-poor conditions. Hereby, the root trait–environment associations were surprisingly most pronounced at the smallest spatial scale, indicating the relevance of small-scale heterogeneity for community assembly processes in tropical forests.

Chapter 1

Introduction

1.1 Tropical montane forests in the Andes

The tropical Andes are the most biodiverse region on earth (Myers *et al.*, 2000; Mittermeier *et al.*, 2011; Rahbek *et al.*, 2019a; Rahbek *et al.*, 2019b). Harboring an estimated 30,000 plant and more than 4,000 vertebrate species, they were classified as a biodiversity hotspot with conservation priority (Myers *et al.*, 2000; Mittermeier *et al.*, 2011). Notably, high percentages of the species occurring in the tropical Andes are endemic to the region and have small geographical ranges (Rahbek *et al.*, 2019b). For plants, the estimated endemism rate is 50 % (Mittermeier *et al.*, 2011). One reason for the high species diversity in the tropical Andes lies in the Andean orogeny itself, which constituted an important driver of plant diversification in the region (Luebert & Weigend, 2014; Pérez-Escobar *et al.*, 2022). A further reason why the tropical Andes harbor such extraordinary plant diversity is the wide range of climatic conditions found in close proximity; for example, an extremely high percentage of the combinations of mean annual temperature and mean annual precipitation occurring throughout global biomes are also represented in the Northern Andes (Rahbek *et al.*, 2019b).

Within the Andes, tropical montane forests (TMF) are the ecosystem with the highest plant diversity (Pérez-Escobar *et al.*, 2022). TMF occur globally in all tropical mountain ranges with a (semi-)humid climate, but have their largest distribution areas in the Andes (Richter, 2008). They cover the elevational range between tropical lowland rain forests and the timberline, but their elevational limits are variable (Salinas *et al.*, 2021). Often, 500 m or 1000 m a.s.l. are described as the altitudes where tropical lowland rain forests transition to TMF in the Andes (Richter, 2008; Mathez-Stiefel *et al.*, 2017). TMF differ considerably from lowland rain forests in terms of floristic composition, vegetation structure and functioning (Richter, 2008; Salinas *et al.*, 2021).

Apart from their extraordinary biodiversity, TMF in the Andes provide a number of ecosystem services such as functioning as a carbon sink (Spracklen & Righelato, 2014; de la Cruz-Amo *et al.*, 2020; Duque *et al.*, 2021) and regulating regional water supply and climate (Bruijnzeel *et al.*, 2011; Bendix *et al.*, 2013). These properties render them an especially valuable ecosystem, and highlight the need to protect them from the various anthropogenic threats they are exposed to (Mathez-Stiefel *et al.*, 2017). The most severe threats impacting TMF in the Andes are related to land use change and climate change (Peters *et al.*, 2013; Soh *et al.*, 2019). TMF in the Andes are under enormous anthropogenic pressure, as forest is cleared for pastures at alarming rates (Curatola Fernández *et al.*, 2015; Tapia-Armijos *et al.*, 2015, 2017). Global warming has already been shown to cause upward range shifts of species (Morueta-Holme *et al.*, 2015) and thermophilization of plant communities (Duque *et al.*, 2015; Fadrique *et al.*, 2018), and will likely affect plant-animal interactions in ways difficult to foresee (Schleuning *et al.*, 2020). In combination, these factors are likely to cause, and have already caused, severe biodiversity loss (Garavito *et al.*, 2015; Báez *et al.*, 2016).

In order to predict the response of TMF to future anthropogenic change and formulate conservation agendas, their ecology needs to be understood better (Mathez-Stiefel *et al.*, 2017). Species-rich mountain ecosystems like TMF are both a challenge and an opportunity for ecological research. On the one hand, the high diversity and the complex geomorphology of the landscape pose countless challenges for disentangling the complex processes and interactions that shape the TMF ecosystem. On the other hand, pronounced environmental gradients and extreme climatic contrasts in close spatial proximity, in combination with the enormous species richness, allow to answer fundamental questions of ecology, evolution, and ecosystem science within a relatively small study area (Tito *et al.*, 2020).

Interactions between elevation and topography, two abiotic gradients on different spatial scales, shape the composition of the vegetation of TMF (Homeier *et al.*, 2010; Apaza-Quevedo *et al.*, 2015; Bañares-de-Dios *et al.*, 2020). With increasing elevation, nitrogen instead of phosphorus limitation becomes increasingly relevant in limiting plant growth, as decreasing temperatures cause slower decomposition rates and thick organic layers accumulate (Tanner *et al.*, 1998). Most tree species in the research area are adapted to narrow elevational ranges, which leads to a rapid turnover of tree species along the elevational gradient (Homeier *et al.*, 2010; Bañares-de-Dios *et al.*, 2020; Malizia *et al.*, 2020). Furthermore, in TMF, biodiversity, vegetation structure, carbon dynamics, and most ecosystem functions and processes, strongly depend on altitude (Leuschner *et al.*, 2013; Apaza-Quevedo *et al.*, 2015; Báez *et al.*, 2015; Malizia *et al.*, 2020; Homeier & Leuschner, 2021; Homeier *et al.*, 2021). On a smaller scale, similar trends occur along the topographic gradient from valley bottoms to ridge forests (Homeier *et al.*, 2010; Lippok *et al.*, 2014; Apaza-Quevedo *et al.*, 2015; Werner & Homeier, 2015). Small-scale soil heterogeneity caused by topography is often named as a key factor in maintaining the high plant diversity in TMF (Homeier *et al.*, 2010; Jones *et al.*, 2011). For these reasons, the interplay of elevation and topography is a crucial research target for disentangling the heterogeneity of ecosystem properties and processes in TMF.

1.2 Functional traits

In megadiverse ecosystems like tropical montane forests, the use of plant functional traits has been proven to be a promising approach for understanding and modeling the complex biotic and abiotic interactions shaping the diverse communities (Báez & Homeier, 2018; Schleuning *et al.*, 2020; Bendix *et al.*, 2021; Dantas de Paula *et al.*, 2021). According to Violle *et al.* (2007), a functional trait is defined as "any [. . .] feature measurable at the individual level [. . .] without reference to [. . .] any other level of organization [. . .] which impacts fitness indirectly via its effect on growth, reproduction and survival". Functional traits are often classified into soft and hard functional traits, with hard functional traits usually being more directly causally related to the performance traits growth, reproduction and survival, but in many cases more difficult to measure. Soft traits are functional traits that are more straightforward to measure, but only indirectly linked to performance traits through their relationships with hard traits (De Bello *et al.*, 2021). Therefore, a common approach, which is also adopted in this work, is to assess easy to measure soft traits as surrogates for mechanistically more proximal hard traits. A further way to classify functional traits are the mutually non-exclusive concepts of response and effect traits. Response traits are functional traits that change their value in response to environmental factors, while effect traits are functional traits that determine the effects of organisms on ecosystem functioning (Lavorel & Garnier, 2002).

The possible applications of plant functional traits are manifold. By analyzing the correlation structure among sets of functional traits, it is possible to identify axes of trait covariation, which permit inference about spectra of plant strategies and the underlying trade-offs and selective pressures (Westoby *et al.*, 2002; Reich *et al.*, 2003; Wright *et al.*, 2004; Reich, 2014; Díaz *et al.*, 2016; Visser *et al.*, 2016). These strategies can be used to explain and predict species distribution patterns and responses to environmental gradients (Díaz *et al.*, 1998; Lavorel & Garnier, 2002; Diaz *et al.*, 2004; Westoby & Wright, 2006; Swenson & Weiser, 2010). When scaled up to community or ecosystem functional parameters (Violle *et al.*, 2007), functional traits can be used to understand and model community assembly processes (McGill *et al.*, 2006; Swenson, 2013; Enquist *et al.*, 2015), ecosystem functioning and ecosystem services (Lavorel & Garnier, 2002; Lavorel, 2013; Funk *et al.*, 2017), and ecosystem responses to environmental change (Suding *et al.*, 2008; Funk *et al.*, 2017).

Because functional traits are usually relatively consistent within species, they can be used both as a way to generalize information from one individual to other individuals of the same species without additional measurements, and as a tool to understand plant function without knowing species identity (Shipley *et al.*, 2016). This renders trait-based approaches advantageous in species-rich ecosystems.

In addition to the (abundance-weighted) mean functional trait values of a community, the degree of variation around these means can also be highly informative about community assembly and ecosystem functioning. This variation is a component of biodiversity that is usually termed functional diversity (FD), or “the diversity of species traits in ecosystems” (Schleuter *et al.*, 2010), and can be expressed by a multitude of indices (Mason *et al.*, 2005; Leps *et al.*, 2006; Mouchet *et al.*, 2010; Schleuter *et al.*, 2010). Throughout this work, I quantify FD based on functional dispersion, i.e. the mean distance of the species from the centroid in the multidimensional trait space (Laliberté & Legendre, 2010). Information about FD can further an improved understanding of community assembly processes (Pakeman, 2011; Swenson *et al.*, 2011; Purschke *et al.*, 2013) and trophic interactions (Albrecht *et al.*, 2018). It is often hypothesized to have an influence on ecosystem processes, services, and resilience to disturbance (Díaz & Cabido, 2001; Díaz *et al.*, 2007; Cadotte *et al.*, 2011; Mason & de Bello, 2013).

Even though FD of plant communities has been shown to vary along elevational and nutrient availability gradients in several instances (e.g., Mason *et al.*, 2012; Schellenberger Costa *et al.*, 2017; López-Angulo *et al.*, 2018; Ding *et al.*, 2019), evidence of such relationships, and mechanistic understanding of the processes driving them, is still sparse. Theoretically, it is to be expected that FD is lower under conditions of more intense physiological stress (e.g. colder or drier climates) and higher nutrient limitation because the range of functional strategies that can thrive under such conditions is narrower (Mason *et al.*, 2012; Spasojevic *et al.*, 2014). As this has never been tested for belowground functional traits, one central question posed in this work is whether similar trends can be confirmed for functional traits of fine roots along gradients of nutrient availability.

1.3 Fine root traits as indicators of belowground strategies

In comparison to the traits of other plant organs, functional traits of roots are still understudied (Iversen *et al.*, 2017; Defrenne *et al.*, 2021). However, the recent years have seen a rise in trait-based root ecology, exemplified by the high number of seminal articles on the topic published in 2021 alone (Carmona *et al.*, 2021; Cusack *et al.*, 2021; Freschet *et al.*, 2021a; Freschet *et al.*, 2021b; Laughlin *et al.*, 2021; Weigelt *et al.*, 2021). Roots are multifunctional organs that are essential both from the perspectives of the individual plant and the whole ecosystem. Their contributions to plant functioning include nutrient and water uptake and transport, anchorage, exudation, symbiosis with fungi and bacteria, storage of metabolites and water, and asexual reproduction (Bardgett *et al.*, 2014; Freschet *et al.*, 2021a; Freschet *et al.*, 2021b). On the ecosystem level, roots are major components in the carbon, nitrogen and phosphorus cycles, are crucial to soil formation and stabilization, and exert a major influence on communities of soil organisms (Bardgett *et al.*, 2014; Rillig *et al.*, 2015; Mommer *et al.*, 2016; Rossi *et al.*, 2020; Freschet *et al.*, 2021b). The immense role of roots for the carbon cycle is illustrated by the fact that fine root production alone contributes an estimated 22-33 % to terrestrial net primary productivity (Jackson *et al.*, 1997; McCormack *et al.*, 2015). Functional traits of fine roots are linked to these processes and therefore highly relevant for understanding and predicting them on ecosystem level (Warren *et al.*, 2015; Weemstra *et al.*, 2016; Laliberté, 2017; McCormack *et al.*, 2017; Defrenne *et al.*, 2021; Freschet *et al.*, 2021b).

While all root functional traits measured throughout this work can be understood both as response and as effect traits, the main focus lies on their role as response traits. They are all soft traits that have been shown to be linked to hard traits and hence indirectly to plant fitness, as the following examples will illustrate. Average root diameter, specific root length (SRL), root tissue density (RTD), and root nitrogen concentration form a set of important root traits that were measured throughout all main chapters of this thesis. Root diameter relates to mycorrhizal colonization, root life spans, and foraging strategy. Species with thicker fine roots tend to be more strongly colonized by mycorrhizal fungi (Eissenstat *et al.*, 2015; Liu *et al.*, 2015) and have longer root life spans (Adams *et al.*, 2013; McCormack *et al.*, 2013), whereas thinner fine roots are more plastic and can proliferate nutrient-rich patches more rapidly (Eissenstat *et al.*, 2015; Liu *et al.*, 2015; Chen *et al.*, 2016; Liu *et al.*, 2019). SRL is defined as root length per root mass and thus describes the soil volume explored per invested biomass. It is linked to the functions of nitrogen, phosphorus and water uptake (Ostonen *et al.*, 2007; Freschet *et al.*, 2021b). RTD, or the root mass per root volume, is positively related to long life spans, mechanical resistance, low palatability, and high resistance to pathogens (Freschet *et al.*, 2021b). Because nitrogen is bound in many plant compounds that are involved in metabolic processes in fine roots related to N uptake, root nitrogen concentration is often viewed as a proxy for N uptake rates (Freschet *et al.*, 2021b). Simultaneously, higher nitrogen concentrations in roots increase the nutritional value of roots to herbivores (Freschet *et al.*, 2021b). Faster-growing species tend to have higher SRL and root N concentrations, and lower RTD (Comas *et al.*, 2002; Comas & Eissenstat, 2004; Kramer-Walter *et al.*, 2016; Assefa *et al.*, 2018). Furthermore, this combination of root traits is often associated with high nutrient uptake rates, high root respiration rates, and short root life spans (Comas *et al.*, 2002; McCormack *et al.*, 2013; Roumet *et al.*, 2016; Lugli *et al.*, 2019; Paradiso *et al.*, 2019).

1.4 The role of root traits within the plant economics spectrum

Based on the above listed observations, the theory of the root economics spectrum (RES) was developed, and is vividly discussed by root ecologists ever since (Kong *et al.*, 2014; Kramer-Walter *et al.*, 2016; Roumet *et al.*, 2016; Weemstra *et al.*, 2016). In analogy to the leaf economics spectrum (LES, Wright *et al.* (2004)), the RES postulates that, due to a growth–survival trade-off, root functional traits form a one-dimensional axis of trait covariation between acquisitive and conservative trait syndromes (Kong *et al.*, 2014; Kramer-Walter *et al.*, 2016; Roumet *et al.*, 2016; Weemstra *et al.*, 2016).

Plants with an acquisitive root strategy invest into faster growth and resource uptake rates, at the cost of shorter life spans, more vulnerable tissue, and higher palatability. Typical syndromes of soft root traits associated with this strategy are high SRL, low

RTD, and high root nitrogen concentrations, while the opposite is characteristic for conservative root strategies (Kong *et al.*, 2014; Kramer-Walter *et al.*, 2016; Roumet *et al.*, 2016; Weemstra *et al.*, 2016).

While this attempt to simplify the dimensionality of root functional traits is appealing, the reality is more complex. A vast majority of studies about the RES concluded that more than one dimension is needed to adequately describe root functional trait variation, though the identified trait dimensions are inconsistent between these studies (e.g., Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2015a; Kramer-Walter *et al.*, 2016; Liese *et al.*, 2017; Wang *et al.*, 2018; Liu *et al.*, 2019; McCormack & Iversen, 2019). A number of explanations have been proposed for these contrasting results, e.g., a high degree of phylogenetic conservation in some root traits, mycorrhiza offsetting selective pressures on fine roots, and the multifunctional nature of roots (Weemstra *et al.*, 2016). An explanatory approach by Bergmann *et al.* (2020) is gaining acceptance, which proposes a second axis of trait variation, the collaboration gradient, that forms an orthogonal axis to the acquisition–conservation gradient. The collaboration gradient encompasses traits related to root diameter and mycorrhizal colonization, and is assumed to reflect the trade-off between relying heavily on mycorrhiza for nutrient supply ("outsourcing strategy"), which requires thick roots, or having thin, highly branched roots, that allow more efficient direct nutrient uptake, but are less strongly colonized by mycorrhizal fungi ("Do-it-yourself strategy") (Bergmann *et al.*, 2020).

In a further extension of this framework, the plant economics spectrum (PES) theory states that resource economics strategies of roots, leaves, and stems are coordinated along a one-dimensional axis representing the acquisition-conservation trade-off, because acquisitive or conservative strategies in one of the plant organs alone are not beneficial if the rest of the plant does not pursue a consistent strategy (Freschet *et al.*, 2010; Reich, 2014). Whether functional traits of stems and leaves are correlated with root functional traits in a consistent fashion remains debated; there are studies in full support (Freschet *et al.*, 2010; Pérez-Ramos *et al.*, 2012; de la Riva *et al.*, 2018), partial support (Holdaway *et al.*, 2011; Kramer-Walter *et al.*, 2016; Liese *et al.*, 2017), and contradicting (Valverde-Barrantes *et al.*, 2015a; Delpiano *et al.*, 2020; Vleminckx *et al.*, 2021) the hypothesis of aboveground–belowground trait association. Reflecting this unresolved debate, two recent articles, Carmona *et al.* (2021) and Weigelt *et al.* (2021), suggested contradicting variations of an updated whole-plant trait spectrum. The key difference between these publications is that Carmona *et al.* (2021) assume that root trait variation is independent from trait variation of other plant organs, whereas Weigelt *et al.* (2021) propose a shared axis of covariation for leaf and root traits related to resource acquisition. Therefore, another central research question treated in this thesis is whether root traits are coordinated with each other and with aboveground traits in a manner that is consistent with the predictions of either of the theories described above.

1.5 Fine root trait responses to environmental gradients

Fine root trait associations with environmental gradients have been demonstrated from the local to the global scale, for a plenitude of biomes, and on several levels of aggregation (though mostly on the interspecific and community level). Globally, functional traits of fine roots vary along large-scale climatic gradients, as demonstrated, e.g., by higher root diameters in warmer climates (Freschet & Roumet, 2017; Valverde-Barrantes *et al.*, 2017; Ma *et al.*, 2018; Laughlin *et al.*, 2021). On regional and local scales, root traits often vary along gradients of soil fertility (Pérez-Ramos *et al.*, 2012; Kramer-Walter *et al.*, 2016; de la Riva *et al.*, 2018; Shen *et al.*, 2019; Ding *et al.*, 2020). According to the theory of the PES, acquisitive strategies are an adaptation to environments with high nutrient availability, where high degrees of competition render it advantageous to out-compete neighbors through fast growth. Conservative strategies, on the other hand, are seen as an adaptation to nutrient scarcity, where it is essential for plants to protect their once invested resources (Reich, 2014). This could be confirmed for a number of different ecosystems and spatial scales (Pérez-Ramos *et al.*, 2012; Kramer-Walter *et al.*, 2016; de la Riva *et al.*, 2018; Shen *et al.*, 2019; Ding *et al.*, 2020). Others reported a lack of root trait association with soil fertility (Delpiano *et al.*, 2020; Hogan *et al.*, 2021; Vleminckx *et al.*, 2021), or reversed directions of such associations (Holdaway *et al.*, 2011), demonstrating that this pattern is not universally present, and the conditions under which it emerges need to be understood better. Evidence on root trait-environment relationships in tropical forests is still sparse, and contradictory (Cusack *et al.*, 2021). Especially for tropical montane forests, the question whether belowground strategies vary along environmental gradients remains largely unanswered. Therefore, the central objective of this work is to investigate associations of root functional traits with gradients of soil fertility in tropical montane forests.

1.6 Aims, scope and structure of this thesis

The present doctoral thesis is embedded in the RESPECT project ("Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPonse and feedback effECTs"), which combines trait-based approaches with land surface models and dynamic vegetation models with the aim to predict ecosystem responses to global change in species-rich tropical montane forests in southern Ecuador (Bendix *et al.*, 2021).

This work is structured around the results from three observational studies on root functional traits of tree species in Andean tropical montane forests (see below). After a general introduction in Chapter 1 and a description of the study area and the methodological approaches in Chapter 2, the results of the aforementioned studies are presented in the three following chapters.

Chapter 3 deals with the variation of root functional traits and functional diversity along the topographic gradient in lower montane forests at 2000 m a.s.l. With a similar research question and design, Chapter 4 treats the variation of root functional traits and functional diversity along the elevational gradient from 1000 m to 3000 m a.s.l. These two chapters aim at describing general patterns of trait-environment association at the interspecific and community level. In Chapter 5, the focus is shifted to 52 tree species of interests at three elevational levels. Using soil nutrient availability data on the level of the tree individual, this chapter addresses to which degree the functional trait syndromes of the focal species match their microhabitat preferences. Chapter 5 furthermore tackles the questions if root traits are associated with aboveground functional traits, and whether there is intraspecific trait variation along small-scale gradients of soil nutrient availability. Throughout Chapters 3-5, the following research questions guided our work:

- Which are the leading dimensions of root trait variation? *Chapter 3 and 5*
- Are above- and belowground trait syndromes coordinated with each other? *Chapter 5*
- How do root functional traits vary along topography, elevation, and nitrogen and phosphorus availability? On which spatial scale and level of aggregation do trait-environment associations occur? *Chapter 3, 4 and 5*
- How does root functional diversity vary along topography, elevation, and nitrogen and phosphorus availability? *Chapter 3 and 4*
- To which degree are root functional traits phylogenetically conserved? What are typical root traits syndromes of important tree families in Andean tropical

montane forests? *Chapter 3 and 4*

Finally, the general implications of the body of work is synthesized in Chapter 6.

1.7 Publications featured in this thesis

- Chapter 3: **Pierick K, Leuschner C, Homeier J. 2020.** Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. *New Phytologist* **230**: 129-138. Part of special issue "Filling gaps in our understanding of belowground plant traits across the world".
- Chapter 4: **Pierick K, Link RM, Leuschner C, Homeier J.** Elevational trends of tree fine root traits in species-rich tropical Andean forests. *Oikos:* In review. Submitted for special issue "Root traits and functioning: from individual plants to ecosystems".
- Chapter 5: **Pierick K, Leuschner C, Link RM, Báez S, Velescu A, Wilcke W, Homeier J.** Above- and belowground strategies of tropical montane tree species are coordinated and driven by small-scale nitrogen availability. In preparation. Submission to *New Phytologist* planned.

Chapter 2

Methodology

This chapter will provide a general overview over the methodological approaches applied in Chapters 3-5. After a description of the study area, it will focus on the sampling designs applied, and on aspects of measuring root traits that are still controversial, and therefore worth discussing more thoroughly than in the Chapters 3-5. For all further details regarding the research methods, please consult the respective methods sections of these chapters.

2.1 Study area

The study area in the present research project is located in the Andes of southern Ecuador, in the provinces Loja and Zamora-Chinchipe, in proximity to the province capitals Loja and Zamora (Fig. 2.1). It is situated on the eastern slopes of the Cordillera Real, the eastern of the two main mountain ranges in the Ecuadorian Andes. In contrast to northern Ecuador, where the Andean mountain ranges include many volcanic peaks exceeding 5000 m a.s.l., the Andes in southern Ecuador and northern Peru, also called the depression of Huancabamba, do not exceed 4000 m a.s.l. (Beck *et al.*, 2008; Richter *et al.*, 2013). The study area is furthermore located in the region of the "Nudo de Loja" (knot of Loja), a geographical anomaly where the otherwise largely parallel mountain ranges of the Andes, characteristic for the relief of northern Ecuador, are replaced by a more complex layout of mountain ranges, leading to a rugged topography of the Andes in the region (Beck & Richter, 2008). The landscape is dominated by deep ravines and steep slopes with angles mostly ranging from 25° to 40° (Beck & Richter, 2008). Landslides are therefore frequent and an important factor of disturbance. Data for the Chapters 3-5 of this thesis were gathered at five sites at altitudes from 1000 m a.s.l. to 3000 m a.s.l. (Fig. 2.2). The

Figure 2.1: Topographic map of Ecuador showing the location of the study area.

lowermost two sites (Bombuscaro, 1000 m and Mirador, 1500 m a.s.l.) are located in the valley of the Río Bombuscaro at the eastern edge of Podocarpus National Park. The sites at 2000 m and 2500 m a.s.l., San Francisco and Curva Misteriosa, are located in the Río San Francisco valley. Curva Misteriosa is located just outside the Podocarpus National Park, whereas the San Francisco site is located within the protected area Reserva San Francisco. The uppermost site, Cajanuma at 3000 m a.s.l., is situated south of Loja, at the western edge of the Podocarpus National Park. At all sites, a tropical humid climate with slight seasonality is prevalent. Easterlies bring clouds from the Amazon basin throughout most of the year, and convection leads to high amounts of rainfall at the eastern slopes of the Andes (Beck *et al.*, 2008; Beck & Richter, 2008; Richter *et al.*, 2013). Precipitation peaks from June to August and is lowest from September to December. Still, all months are humid and on average receive more than 100 mm of precipitation (Emck, 2007; Beck *et al.*, 2008; Bendix *et al.*, 2008). A further characteristic of the climate in the study area is high fog and cloud frequencies, especially at higher elevations (Beck & Richter, 2008; Rollenbeck *et al.*, 2011; Richter *et al.*, 2013). Due to the complex topography,

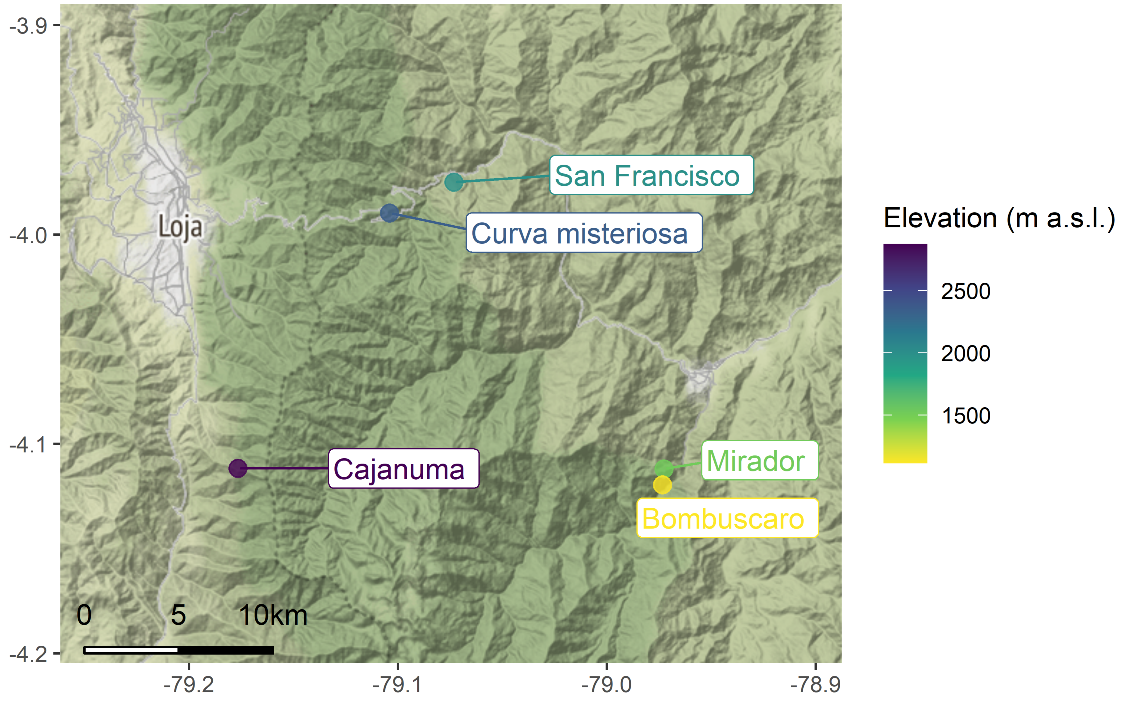

Figure 2.2: Topographic map of the study area with the locations and elevations of the five study sites.

climatic variation in the study area is large, with drastic climatic differences on small scales. Mean annual temperatures decrease with elevation from 20 °C at 1000 m to 9.5 °C at 3000 m a.s.l., while mean annual precipitation increases from 2000 mm to 4500 mm along the elevational gradient.

The bedrock consists of granodioritic rocks at the two sites in the Río Bombuscaro valley, and metamorphic schists and sandstones at the other sites (Wolf *et al.*, 2011). The soils are comparably young and developed in postglacial landslide material or periglacial cover beds (Wilcke *et al.*, 2011). According to Wolf *et al.* (2011), the prevailing soil types are Cambisols, Histosols, and Planosols, depending on their elevation and topographic positions. Soils at higher elevations and at ridge tops accumulate thick organic horizons, are more acidic, more waterlogged and have lower nutrient availability than soils at lower elevations and at lower slope positions (Wilcke *et al.*, 2008a, 2011; Wilcke *et al.*, 2008b; Wolf *et al.*, 2011). The differences along the elevational gradient are mostly driven by the decrease in temperature, slowing down decomposition and therefore the turnover of organic matter. Furthermore, the immense precipitation rates lead to permanently waterlogged soils at the highest site (Wilcke *et al.*, 2008a; Wilcke *et al.*, 2008b). The edaphic variability along topographic gradients is primarily driven by down-slope water fluxes that wash out nutrients at the ridge tops (Wilcke *et al.*, 2011). Due to the rugged topography of the landscape, the soils are therefore highly heterogeneous on a small spatial scale (Wilcke *et al.*, 2008a, 2011; Werner & Homeier, 2015).

The vegetation at the study sites consists of evergreen montane rain forests that are subject to a characteristic altitudinal zonation (Homeier *et al.*, 2008). From 800-1300 m a.s.l., premontane forest that reaches a canopy height of up to 40 m prevails. Characteristic tree families in this zone are Fabaceae, Moraceae, Myristicaceae, Rubiaceae, and Sapotaceae. At 1300-2100 m a.s.l., they are replaced with lower montane forest, harboring mostly Euphorbiaceae, Lauraceae, Melastomataceae, and Rubiaceae. Upper montane forest occurs from 2100-2700 m a.s.l., with the characteristic plant families including Aquifoliaceae, Clusiaceae, Cunoniaceae, and Melastomataceae. The canopy height, decreasing along elevation, reaches only 8-10 m in this zone (Homeier *et al.*, 2008; Homeier *et al.*, 2021). At higher altitudes (2700-3000 m a.s.l.), smaller-statured elfin forests are the last forest zone before the timberline is reached and Páramo vegetation prevails (Homeier *et al.*, 2008). Tree species turnover between these zones is almost complete (Homeier *et al.*, 2021). With 2700-3100 m a.s.l., the timberline in the Huancabamba depression is found at relatively low altitudes compared to other parts of the tropical Andes (Beck & Richter, 2008; Homeier *et al.*, 2008). A further remarkable feature of these high elevation forests is their species richness and the absence of the genus *Polylepis* that usually dominates timberline vegetation in the tropical Andes (Beck & Richter, 2008; Homeier *et al.*, 2008).

As described in more detail in Section 1.1, tropical montane forests on the eastern slopes of the Andes are highly diverse and have high endemism rates in several organism groups, including vascular plants. This is also true for tree communities in the study area; more than 1000 tree species have been tallied there so far (Chapter 4). Within the studied altitudinal range, tree species richness does not depend on elevation (Homeier & Leuschner, 2021). Floristically, the study area belongs to the Northern Andes floristic region (Pérez-Escobar *et al.*, 2022), but is also influenced by the Central Andes region, and harbors both species from Amazonian lowland forests that reach their upper distribution limit and typical montane species, which is a major contributing factor to the high species richness (Homeier *et al.*, 2010). Small-scale environmental heterogeneity caused by topography creates a variety of microhabitats with differing floristic composition which further contributes to the high tree species diversity (Homeier *et al.*, 2010).

Figure 2.3: Vegetation in the study area: a) Bombuscaro (1000 m), b-e) San Francisco (2000 m), f-g) Cajanuma (3000 m a.s.l.).

2.2 Sampling approaches

When measuring traits of plant communities in highly diverse tropical forests, several problems related to sampling arise. Ideally, the aim would be to gather reliable (i.e., satisfactorily replicated) information on all species in a community. This is often not possible in tropical forests for the following reasons: Firstly, it is often not feasible to sample all the species due to their sheer diversity, and limited temporal and financial resources in the research project. Secondly, most species occur in low densities, and therefore it is difficult to find enough individuals to replicate them satisfactorily. Finally, often not all species in tropical forests can be identified to the species level, and a considerable proportion might not even be described yet. In our study area, thanks to a long history of ecological research, most of the tree species are described, and most of the trees in the permanent plots are identified to the species level. Still, as measuring root traits is especially time-consuming, our limited resources caused a trade-off between sampling many species, and replicating species well. Therefore, we decided to adopt two different kinds of designs, one to capture the trait variation between communities along environmental gradients (Random Trees), and one where we attempted to obtain reliable information on selected species (Replicated Species, Table 2.1). These two approaches are suited to answer different questions and complement each other to acquire a whole picture.

The Random Trees design was used in Chapters 3 and 4, where we address questions about the functional composition of communities along a small-scale topographic gradient (Chapter 3) and along a larger-scale elevational gradient (Chapter 4). As our available resources did not allow us to measure the root traits of all species in the community, we randomly selected a fixed number of trees per community, which lead to common species being replicated better than rare species. The performance of several incomplete sampling methods in comparison with a complete sampling of tree communities in species-rich neotropical forests has been assessed by Baraloto *et al.* (2010b) and Paine *et al.* (2015). While Baraloto *et al.* (2010b) concluded that the ideal cost-benefit ratio is achieved when every species in the community is at least sampled once, random sampling approaches like our Random Trees approach still scored well. In the assessment by Paine *et al.* (2015), they even turned out to be the most accurate of the compared approaches.

In Chapter 5, we were interested in the strategies of specific focal species and therefore applied the Replicated Species approach. For this design, we selected 52 tree species of interest from three elevational levels based on their abundance (they had to be abundant enough to find a sufficient number of replicate individuals within our plots) and previous knowledge about their functional role in the community (e.g., both pioneer and late-successional, canopy and understory species were represented at all sites). Each of these species was replicated with 6-11 individuals. This more intensive replication (as compared to the Random Trees approach, where many species were only replicated once) allowed us to draw reliable conclusions about the functional strategies of our focal species, and assess their intraspecific trait variation.

Table 2.1: Details about the methodology applied in Chapters 3-5.

	Main questions			Observational level			
Chapter	Trait-environment relationships	Trait-trait relationships	Elevational levels (m a.s.l.)	Traits	Predictors	Sampling approach	Root classification method
3	Trait variation along topographic gradient		2000	tree individual	plot	Random Trees	diameter-based
4	Trait variation along elevational gradient		1000, 1500, 2000, 2500, 3000	tree individual	plot	Random Trees	functional
5	Intra- and interspecific trait variation along N and P availability	Interspecific relationships between above- and belowground traits	1000, 2000, 3000	tree individual	tree individual	Replicated Species	functional

2.3 Sampling fine roots

Fine roots, traditionally defined as the most distal parts of root systems with diameters $\leq 2\,\mathrm{mm}$, are an essential organ of plants, being the part of the root system where the absorption of water and nutrients happens (Chapter 1). Although properties of fine roots have been a target of investigation for many decades, the optimal methods to measure them are still discussed (Freschet *et al.*, 2021a). These difficulties can be condensed into two main intrinsic problems of studying roots: In contrast to other plant organs like leaves, they are not morphologically and functionally distinct. On the contrary, there is a continuous transition from roots with a primarily absorptive function to roots with a primarily transportive function. In addition, the inevitable fact of roots existing (mostly) underground makes it less straightforward to access them, with a plenitude of possible methods existing (Freschet *et al.*, 2021a). In the following, I describe which methods I applied for collecting and classifying root samples.

2.3.1 The tracing method

The present work aimed to measure functional traits of roots on the level of individual trees to answer questions related to phylogenetic signal (Chapter 3 and 4), functional diversity (Chapter 3 and 4) and intraspecific trait variation (Chapter 5). The upper layer of the soils in the study area is pervaded by a dense, entangled mesh of fine roots from the many tree species of the community. Even though fine roots of the tree species in the communities display a high level of between-species morphological variability and can have species-specific distinctive features (Figure 2.4), the tree communities are too species-rich to identify fine roots to the species level based on their morphology. Therefore, the commonly used method of sampling fine roots from soil cores (Freschet *et al.*, 2021a) could not be applied in our case, as it does not give information about to which tree the sampled roots belong, except if DNA barcoding is used (Luo *et al.*, 2021). Instead, we applied a so-called tracing method in all sampling campaigns, where coarse roots emerging from the stem of a target tree are carefully traced through the soil using bare hands and simple gardening equipment until strands of distal fine roots are encountered and removed from the soil (Chen *et al.*, 2013; Kong *et al.*, 2014). This way, only root segments definitely attached to the target tree are harvested. The tracing method is challenging and time-consuming, which is why extracting roots using the soil core method is usually applied if research questions on the community level are addressed (Freschet *et al.*, 2021a). However, it

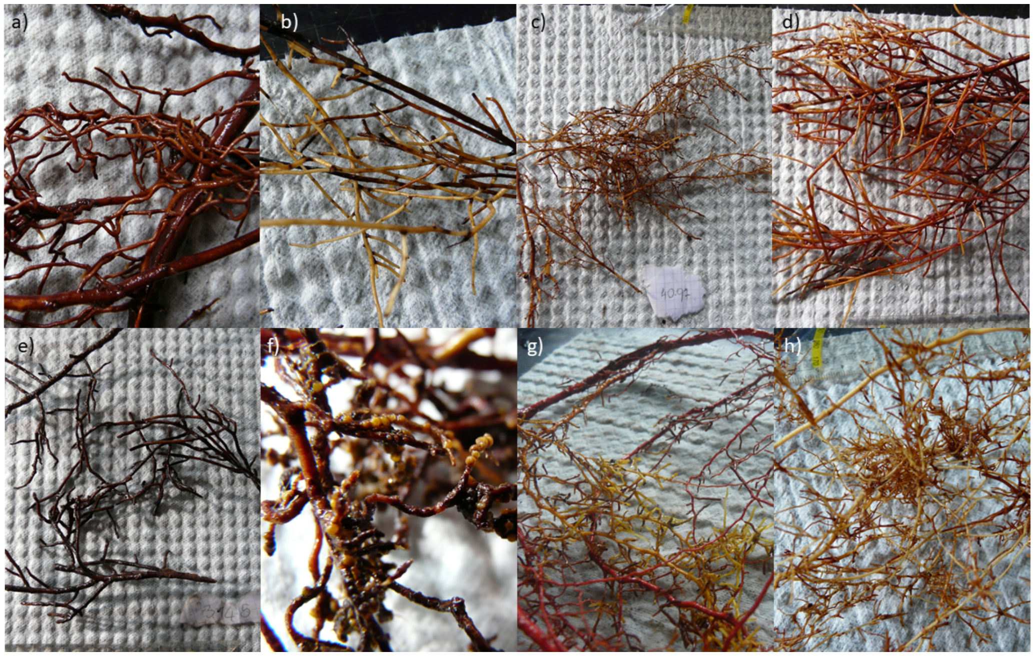

Figure 2.4: Exemplary images of distal root segments from several tree species in the study area. a) *Clusia* sp., Clusiaceae, b) *Endlicheria* sp., Lauraceae, c) *Meriania franciscana*, Lauraceae, d) *Guarea kunthiana*, Meliaceae, e) *Otoba parvifolia*, Myristicaceae, f) *Podocarpus oleifolius*, Podocarpaceae, with nodules that host arbuscular mycorrhizal fungi, g) *Clarisia racemosa*, Moraceae, h) *Critoniopsis floribunba*, Asteraceae.

is the only way described so far to measure *in situ* root traits of adult trees in species-rich forests on the individual tree level. The measurement of functional traits on the roots of hundreds of trees of previously unexplored tropical montane tree species is a unique feature of this work and contributes to its novelty and relevance.

2.3.2 Functional root classification

Traditionally, roots have been sorted into fine roots and coarse roots based on their diameter, usually with a cut-off point at a diameter of 2 mm, with the aim to include predominantly the parts of the root system that are involved in nutrient and water acquisition (reviewed in McCormack *et al.*, 2015; Freschet & Roumet, 2017; Freschet *et al.*, 2021a). This approach was applied in Chapter 3 (Table 2.1). In the last decade, however, several shortcomings of the diameter-based root classification method have been pointed out. The root fraction $\leq$ 2 mm often comprises several functionally different root orders (Pregitzer *et al.*, 2002; Guo *et al.*, 2008; Jia *et al.*, 2011; Rewald *et al.*, 2011; Rewald *et al.*, 2014). Furthermore, the diameter of a root segment depends on its ontogeny and changes throughout several successive developmental processes (Freschet *et al.*, 2021a). As species differ in their root diameter distribution, a general diameter threshold can lead to the inclusion of functionally very different fractions of the root systems into the fine root pool, especially for woody species (McCormack *et al.*, 2015; Freschet & Roumet, 2017; Laliberté, 2017). This last point became especially evident to us when we first sampled roots of *Otoba parviflora*, an extremely thick-rooted Myristicacean tree species found in our plots at 1000 m a.s.l. Had we applied the 2 mm cutoff method on this species, *Otoba parviflora* would have had to be classified as a species without fine roots. Similarly, in many species from the Lauraceae and Meliaceae, only very small proportions of the distal root strands would have fallen below the 2 mm threshold, in contrast to thin-rooted families like Moraceae, where the pool of roots thinner than 2 mm included root strands of up to half a meter.

An order-based classification method is often applied to accurately separate distal root strands into functionally comparable segments (e.g., Guo *et al.*, 2008; Kong *et al.*, 2014). This method is usually considered to be the gold standard in terms of accurately mirroring root function (McCormack *et al.*, 2015; Freschet *et al.*, 2021a), even though Freschet & Roumet (2017) pointed out that it also has its pitfalls, e.g. that the functionality of certain root orders is still not consistent within and between species, and that it is especially sensitive to the developmental stage of the root strand and to the presence of specialized roots like pioneer or tap roots. Most of all, it is the most time-consuming classification method and was not applicable with our available resources. A further impairment to the application of an order-based classification method was in our case that some of the species we sampled, for example many Rubiaceae, had distal root systems so thin, highly branched and with short internodal segments, that we would have had to dig out an enormous amount of root material to acquire enough first-, second- or third-order roots for proper trait measurements.

Therefore, we decided to adopt a functional root classification method as described in McCormack *et al.* (2015), for the roots sampled for Chapter 4 and 5 (Table 2.1). McCormack *et al.* (2015) and Shao *et al.* (2019) suggested to divide the traditional fine root fraction into absorptive and transport roots according to the root segments' predominant function. Absorptive and transport roots are distinguished anatomically by the presence of secondary xylem and a suberized cork layer (Zadworny *et al.*, 2016). The transition from a mostly absorptive to a mostly transport function can be continuous instead of occurring discretely at a well-defined point (Freschet *et al.*, 2021a). Which root orders fall into the absorptive root pool is species-specific, and has been reported to vary between the most distal two to five root orders of woody species (Kong *et al.*, 2016; Zadworny *et al.*, 2016; Trocha *et al.*, 2017; Wang *et al.*, 2019). Ideally, species-specific thresholds should be determined by prior anatomical analyses (McCormack *et al.*, 2015). This was not feasible in our project due to the high number of analyzed species. Instead, we classified the roots based on morphological criteria (root color and surface texture, root diameter, root elasticity and presence of root hairs). Especially root color and elasticity changed discretely and in a coordinated way somewhere between the second and fourth order for almost all species, which is why we assume that these changes represented the transition from absorptive to transportive segments of the root system.

2.4 Measuring root functional traits

The root traits we measured, and their relevance to root functioning, are introduced in Section 1.3. They can be grouped into morphological traits (root diameter, specific root length (SRL), absorptive fine root fraction (AFRF), root branching intensity (RBI), root tissue density (RTD)) and chemical traits (N and P concentration). Morphological traits are in most cases ratios of two characteristics of the root sample, like total length, total volume, number of root tips, and dry weight. Except for dry weight, these variables can be measured by placing the cleansed root samples in transparent, water-filled trays and scanning them, and subsequently analyzing the scanned images with the software WinRhizo. This image recognition program can distinguish root segments from the background, and estimate their properties like average diameter, total volume, total length, number of tips, and many more (see Tab. 2.2 for details on the calculation of these traits). The chemical traits, N and P concentration, were measured with a CN elemental analysis and inductively coupled plasma mass spectometry (ICP-MS) respectively. Not all traits were measured in all chapters, because measurements of RBI would have been biased by the functional classification method, as it results in many small root segments in some species, and the image recognition algorithm cannot distinguish true root tips from cutoff points. AFRF can per definition only be measured in combination with a functional classification method. For more details on the trait measuring protocols and further aspects of the applied methodology, please consult the respective methods sections of Chapters 3-5.

Table 2.2: Root functional traits measured in Chapters 3-5.

Full name	Abbr.	Unit	Description	Chapters
Average root diameter	d_{root}	mm	Average root diameter	3, 4, 5
Specific root length	SRL	m g^{-1}	Root length per dry mass	3, 4, 5
Absorptive fine root fraction	AFRF	g g^{-1}	Absorptive root dry mass per fine root ($\leq$ 2mm) dry mass	4
Root branching intensity	RBI	tips cm^{-1}	Root tips per length	3
Root tissue density	RTD	g cm^{-3}	Dry mass per root volume	3, 4, 5
Root nitrogen concentration	N_{root}	mg g^{-1}	N content per dry weight	3, 4, 5
Root phosphorus concentration	P_{root}	mg g^{-1}	P content per dry weight	4, 5

Chapter 3

Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest

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3.1 Abstract

- We investigated the variation in tree fine root traits and their functional diversity along a local topographic gradient in a Neotropical montane forest to test if fine root trait variation along the gradient is consistent with the predictions of the root economics spectrum on a shift from acquisitive to conservative traits with decreasing resource supply.
- We measured five fine root functional traits in 179 randomly selected tree individuals of 100 species and analysed the variation of single traits (using Bayesian phylogenetic multilevel models) and of functional trait diversity with small-scale topography.
- Fine roots exhibited more conservative traits (thicker diameters, lower specific

root length and nitrogen concentration) at upper slope compared with lower slope positions, but the largest proportion of variation (40–80 %) was explained by species identity and phylogeny. Fine root functional diversity decreased towards the upper slopes.

- Our results suggest that local topography and the related soil fertility and moisture gradients cause considerable small-scale variation in fine root traits and functional diversity along tropical mountain slopes, with conservative root traits and greater trait convergence being associated with less favorable soil conditions due to environmental filtering. We provide evidence of a high degree of phylogenetic conservation in fine root traits.

Keywords: Bayesian multilevel models, Ecuador, functional dispersion, phylogenetic regression, root economics spectrum, root functional traits, tropical montane forest

3.2 Introduction

The variation of fine root functional traits along environmental gradients is currently a widely discussed topic in plant functional ecology (e.g. Addo-Danso *et al.*, 2020; Delpiano *et al.*, 2020; Ding *et al.*, 2020). By contrast with aboveground plant organs, which have been studied extensively (Westoby *et al.*, 2002; Wright *et al.*, 2004; Chave *et al.*, 2009; Díaz *et al.*, 2016), less is known about the leading dimensions of root functional traits and their association with abiotic factors (Laliberté, 2017). Only during recent years, our understanding of fine root functionality has deepened. Fine roots fulfill several functions that are crucial for the growth and survival of plants, notably water and nutrient uptake, carbohydrate storage, anchorage and various interactions with the rhizosphere (Mommer *et al.*, 2016; Weemstra *et al.*, 2016). With fine root production representing an estimated 22 % (McCormack *et al.*, 2015) to 33 % (Jackson *et al.*, 1997) of terrestrial net primary productivity, fine root traits influence carbon and nutrient cycling in the soil directly through organic matter input as well as indirectly via their influence on soil microbial communities (Bardgett *et al.*, 2014). Hence, a better understanding of fine root functional traits and their variation along environmental gradients is critical for improving our capacity to predict ecosystem functioning in changing environments (Iversen, 2010; Bardgett *et al.*, 2014). Knowledge gaps with respect to plant functional properties are especially large in species-rich tropical forests (Freschet & Roumet, 2017).

Trait syndromes of fine roots are often discussed in the light of the root economics spectrum (RES, Kong *et al.*, 2014). In analogy to the widely accepted leaf economics spectrum (Wright *et al.*, 2004), the RES predicts a growth-survival trade-off for fine roots, in which root form and function are optimized either for quick growth and high resource acquisition rates, or for long life spans and lower resource uptake (Freschet *et al.*, 2010; Reich, 2014; Roumet *et al.*, 2016; Weemstra *et al.*, 2016; Laliberté, 2017). In this framework, thin, strongly branched fine roots with low tissue density, high specific root length (SRL), and high nitrogen concentration are considered acquisitive, because they allow efficient soil exploration and resource uptake at relatively low carbon investment. Conversely, thicker diameters, higher tissue densities, lower degrees of branching, and lower SRL and nitrogen concentrations indicate resource conservation (Reich, 2014; Weemstra *et al.*, 2016). This concept is supported by comprehensive evidence linking morphological and chemical root traits to whole-plant growth rates (Comas & Eissenstat, 2004; McCormack *et al.*, 2013; Kramer-Walter *et al.*, 2016), root lifespan (Withington *et al.*, 2006; Adams *et al.*, 2013; McCormack *et al.*, 2013; Sierra Cornejo *et al.*, 2020), root respiration (Tjoelker *et al.*, 2005; Makita *et al.*, 2009; Paradiso *et al.*, 2019), and nutrient uptake rates (Comas *et al.*, 2002; Lugli *et al.*, 2019). However, while some studies reported a mostly one-dimensional RES (e.g. Freschet *et al.*, 2010; Pérez-Ramos *et al.*, 2012; Roumet *et al.*, 2016; de la Riva *et al.*, 2018), most evidence on the dimensionality and coordination of root traits points towards more complex, multidimensional relationships among root traits with the axes of variation being inconsistent between studies (e.g. Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2015a; Kramer-Walter *et al.*, 2016; Wang *et al.*, 2018; Liu *et al.*, 2019; McCormack & Iversen, 2019). Common explanations for the complexity of fine root trait relationships are the multiplicity of functions that roots have to fulfill and the collaboration with mycorrhizal fungi that can offset the selective pressure on certain root functional traits (Weemstra *et al.*, 2016).

Another important factor determining fine root trait syndromes of tree species is their evolutionary history. It is widely agreed that many fine root traits are highly phylogenetically conserved (e.g. Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2015a; Liese *et al.*, 2017; Liu *et al.*, 2019), with gymnosperms and early-diverged angiosperms having more conservative traits than later diverged angiosperms due to a historical shift in mycorrhizal collaboration (Chen *et al.*, 2013; Comas *et al.*, 2014; Yahara *et al.*, 2019).

Even though being most likely not one-dimensional, the RES is linked to gradients of resource availability. Many studies have found fine root properties to vary along environmental gradients, and specifically fertility gradients, in a coherent manner, with abundant resources promoting rather acquisitive strategies, and resource scarce-ness promoting conservative strategies (Reich, 2014). It is assumed that acquisitive strategies are more successful when resources are abundant, because trees need to be highly efficient in their resource acquisition to grow fast and be able to withstand high degrees of competition (de la Riva *et al.*, 2018; Addo-Danso *et al.*, 2020; Fort & Freschet, 2020). Resource scarcity, conversely, is believed to exclude fast-growing plants and require species to conserve invested resources (de la Riva *et al.*, 2018; Delpiano *et al.*, 2020). Fine root properties were found to vary along environmental gradients as predicted by the RES framework for different life forms and ecosystems and at different spatial scales (Holdaway *et al.*, 2011; Kramer-Walter *et al.*, 2016; de la Riva *et al.*, 2018; Ding *et al.*, 2020; Fort & Freschet, 2020). While the majority of studies on root trait variation along soil fertility and climate gradients compared different ecosystem types or even different biomes, soil chemical variation also occurs on small spatial scales within ecosystems, for example along small-scale topographic gradients at the same elevation.

On the rugged terrain of tropical montane forests, fertility and water availability are strongly linked to topography, which creates a mosaic of heterogeneous microclimatic, hydrologic and edaphic conditions on the local scale (Takyu *et al.*, 2003; Weintraub *et al.*, 2015). This has a significant impact on patterns of vegetation structure, productivity, species composition and diversity (Homeier *et al.*, 2010; Lippok *et al.*, 2014; Liu *et al.*, 2014; Werner & Homeier, 2015; Jucker *et al.*, 2018; Muscarella *et al.*, 2019). Induced by downhill fluxes of water and organic matter, soils at the lower slopes are less acidic, richer in nitrogen and plant-available phosphorus and with a higher base saturation than at upper slopes (Wolf *et al.*, 2011; Werner & Homeier, 2015). Studies investigating the functional composition of tropical tree communities along topographical gradients have found that, in gorges and at lower slope positions, trees tend to have more acquisitive life history strategies than on ridges and upper slopes (Liu *et al.*, 2014; Apaza-Quevedo *et al.*, 2015; Jucker *et al.*, 2018; Blanchard *et al.*, 2019; Muscarella *et al.*, 2019), but all cited studies only investigated aboveground functional traits. de la Riva *et al.* (2018) found a decrease of root dry matter content of woody plants towards wetter and more fertile conditions along a local topographic gradient in a Mediterranean mountain range.

The diversity of functional traits in a plant community (represented by the species' differences in single functional traits or the combination of traits) may influence ecosystem functioning, notably productivity, through complementarity effects and facilitation, and it can increase community resilience after disturbance, when the species differ in their recovery rates (Díaz & Cabido, 2001; Díaz *et al.*, 2007; Pakeman, 2011; Purschke *et al.*, 2013). The functional diversity of leaf and shoot traits has been shown to vary along broad climatic and land use gradients (de Bello *et al.*, 2006). Several studies have found an effect of environmental filtering on aboveground functional diversity in trees (e.g. Mason *et al.*, 2012; Asefa *et al.*, 2017; Ding *et al.*, 2019). In general, the range of co-occurring trait values, and thus functional diversity within a habitat is expected to be smaller under more stressful environmental conditions as a result of functional convergence and, in resource-limited habitats, environmental filtering should lead to the preferential selection of species with more conservative resource-use strategies (e.g. Asner *et al.*, 2014; Šímová *et al.*, 2015). However, when root traits are addressed, functional trait diversity has been less a study focus than the composition of functional traits in a community. While root traits have sometimes been included in indices of functional diversity in the context of attempts to explain ecosystem functions (Butterfield & Suding, 2013; Valverde-Barrantes *et al.*, 2015b; Fotis *et al.*, 2018), to our knowledge this study was the first to investigate root functional diversity using five important traits from the RES.

In this study, we explored how the fine root functional traits root diameter (d_{root}), SRL, root tissue density (RTD), root branching index (RBI), and root nitrogen concentration (N_{root}) varied in trees along topographical gradients in species-rich tropical forests in rugged terrain, as is characteristic for the Andes and other tropical humid mountains. We further investigated whether belowground functional diversity changed with topography, and to what degree variation in fine root traits is explained by environment, phylogeny and phylogenetically independent species effects. With a comprehensive root trait data set covering 100 tree species, we aim to contribute to a better understanding of variation of fine root traits along environmental gradients and the nature and significance of a RES. By studying a highly diverse Neotropical montane forest, our findings should also help to better understand tree community assembly in tropical forests. We hypothesized that:

1. Tree root trait syndromes shift from a more acquisitive strategy at the more fertile lower slope to a more conservative strategy at the upper slope, which is reflected in an increase in root diameter and RTD, and a decrease in SRL, RBI and root N concentration.
2. Large parts of the variation that cannot be explained by environmental differences are attributable to phylogenetic relatedness between species.
3. Belowground functional diversity is lower at upper slope positions where the less fertile soils constitute a stronger environmental filter.

3.3 Material and methods

3.3.1 Study area

The study was conducted in the montane forests of the Reserva San Francisco in southern Ecuador (Province Zamora-Chinchipe; Fig. A.1 a). The study area is located in the Rio San Francisco valley on the eastern slopes of the Andean mountain range Cordillera Real at around 2000 m a.s.l., bordering Podocarpus National Park. The climate is humid tropical montane with a mean annual temperature of 15 °C and a mean annual precipitation of 2200 mm (Bendix *et al.*, 2008). Seasonal thermic and hygric differences are weak with a drier, but still humid, period from October to December. The vegetation at the research sites is constituted by undisturbed old-growth stands of evergreen lower montane forest (Homeier *et al.*, 2008). The most common soil types are humic and dystric cambisols (Wolf *et al.*, 2011). The terrain is rugged with often steep slopes (20–50 ° inclination) and many small ravines, which create a heterogeneous topographic mosaic with pronounced small-scale differences in soil properties. Topography has a strong influence on forest structure and species composition. Valleys and lower slope positions have higher tree species richness and taller trees in comparison with ridges and upper slope positions (Homeier, 2008; Homeier *et al.*, 2010), and are more productive (Paulick *et al.*, 2017). Tree species turnover along the topographical gradient is high (< 10 % of tree species are shared between lower and upper slope positions) (Homeier *et al.*, 2010).

3.3.2 Study design

The root samples were collected from 18 permanent plots of 20 m × 20 m size covering a broad topographic range from lower to upper slope positions (Fig. A.2 b; Table A.1). The slope position of the plots was characterized through the topographic position index (TPI, Guisan *et al.*, 1999; Weiss, 2001), an algorithm derived from the relative position of a raster cell in a digital elevation model (DEM) in relation to the average elevation of the surrounding cells (Kübler *et al.*, 2016). We used a DEM with 10 m resolution based on triangulation from aerial photographs and calculated the TPI for a circular neighborhood within a radius of 200 m (Link, 2018). Negative values indicated lower slope positions, positive values upper slope positions, and values around zero characterized either mid-slope positions or plateaus. Considering that steep slopes prevailed throughout the study area and plateaus were virtually absent, it can be assumed that all TPI values around zero indicated mid-slope positions. The TPI ranges from about -1 to +1 and is centered around 0. Plot elevation varied only slightly between 1913 m and 2089 m a.s.l. and was independent of TPI.

In each plot, we randomly selected 10 trees with a diameter at breast height (dbh) of $\geq$ 10 cm. In cases in which the roots of the randomly selected trees could not be accessed, appropriate substitute trees were selected at random from the remaining trees in the plot. This selection method led to a data set comprised of 179 tree individuals (two had to be excluded afterwards due to low quality of root samples, while an additional sample was collected in one plot). The final sample contained individuals from 39 families, 68 genera and 100 species. Three trees were gymnosperms (two individuals of *Podocarpus oleifolius* and one of *Prumnopitys montana*), the remaining 176 individuals were angiosperms. The most common species in the data set was *Guarea kunthiana* (13 replicates), while the majority of species was only sampled once or twice. Our sample covered between 29 % and 100 % of the tree species present in each plot as adult trees (dbh $\geq$ 10 cm, average: 44 %, Table A.2). The full species list is given in the Table A.3.

3.3.3 Measurement of fine root traits

Fine root functional traits were measured from October to December 2016. One intact fine root strand of at least 10 cm length was sampled from each tree by tracing coarse roots from the stem until fine roots (diameter $\leq$ 2 mm) were reached. Even though the arbitrarily chosen diameter threshold of 2 mm has recently been criticized for not adequately capturing the most active absorptive finest root segments (McCormack *et al.*, 2015; Shao *et al.*, 2019), Freschet & Roumet (2017) pointed out that measurements on roots $\leq$ 2 mm produce only marginally different results to measurements on the first three root orders. An analysis based on root orders is much more labor intensive, and according to Freschet & Roumet (2017), the 2 mm category is appropriate when the focus is on nutrient acquisition strategies. As the study goal was to investigate topographic effects on fine root morphology in relation to nutrient acquisition in these hyperdiverse forests through the analysis of as many species as possible, we preferred to analyse a larger species number over greater analytic detail in a smaller sample.

The root systems were carefully removed from the soil, placed in plastic bags, transported to the nearby research station and stored at 4 °C until further processing, which was carried out within 3 days. In the following step, the roots were washed and dead material was discarded. Then the roots were placed in a water-filled Plexiglas$^{\text{TM}}$ tray avoiding overlap of root segments and subsequently scanned with a Hewlett

Packard Scanjet G4050 scanner in grey scale at 600 dpi. The images were analysed with the software WINRHIZO 2013 Basic (Regent Instruments Inc., Quebec, Canada) measuring root volume, total length, average diameter and number of root tips. The samples were then oven dried at 60 °C for at least 48 h and weighed afterwards. SRL (total fresh root length per dry mass), RTD (dry mass per fresh volume) and RBI (number of root tips per fresh length) were calculated from the aforementioned data. The samples were ground and their nitrogen concentration (N_{root}) was analysed using a C:N elemental analyzer (Vario EL III; Elementar, Hanau, Germany) at the Department of Plant Ecology, University of Göttingen, Germany.

3.3.4 Statistical analysis

Soil parameter variation with topography

Before the main analyses, we inspected the relationships between TPI and several soil parameters measured in our plots by Wolf *et al.* (2011) (Fig. A.2). Furthermore, we conducted a principal components analysis (PCA) with these parameters and inspected the correlation coefficients of the first two axes with TPI (Fig. A.3). The soil parameters and PCA axes were highly associated with TPI. As topographic position can be assumed to be the main cause of small-scale gradients in soil properties in the research area Wolf *et al.* (2011), we limited the analysis to TPI to avoid issues with multicollinearity (cf. Dormann *et al.*, 2013).

Phylogeny

The phylogenetic relationships of the involved tree species were extracted from the mega-tree of vascular plants ‘GBOTB.extended.tre’ using the R package `V.PhyloMaker` (Jin & Qian, 2019). The resulting phylogeny for our species can be found in Fig. A.4.

Phylogenetic multilevel models

We used the R package `brms` (Bürkner, 2017) to fit five Bayesian phylogenetic multilevel models (Bürkner, 2020), to describe each of the five investigated fine root traits as response to TPI. The responses were log transformed in order to handle skewness and heteroscedasticity. The random effects structure contained a phylogenetically correlated random species effect and an unstructured random species effect, which accounted for additional species differences not explained by phylogenetic relatedness. This model structure can be interpreted analogously to a classical PGLS model (cf. Bürkner, 2020). Furthermore, plot identity was incorporated as a random effect to account for possible random variation between plots that could not be explained by topography. The models were fit with `brms`'s default weakly informative priors for 10000 iterations. A detailed description of the method is given in Methods A.1. The contribution of different model components to the total variance in the data was decomposed based on the approach of Gelman *et al.* (2019), extended to a multilevel context analogous to Nakagawa & Schielzeth (2013).

Phylogenetic PCA

A phylogenetic PCA on species level was performed with the five log-transformed root traits using the R package `phytools` (Revell, 2012). The input variables were centered and scaled.

Functional diversity

We chose functional dispersion (FDis) as a measure of functional diversity because it is unaffected by species richness, can be applied for any number of traits, and is robust against outliers (Laliberté & Legendre, 2010). FDis is the mean distance of the species from the centroid in the multidimensional trait space. We calculated fine root FDis of the five combined fine root traits d_{root}, SRL, RTD, RBI and N_{root} for the tree sample from each plot using the `dbFD` function in the R package `FD` (Laliberté *et al.*, 2014). In order to test for a significant effect of TPI on FDis, we fitted a linear regression. We further asked whether trends in FDis are explained by variation in phylogenetic diversity along the gradient. This was done by calculating Faith's phylogenetic diversity (PD, Faith, 1992) for the trees of our sample using the R package `picante` (Kembel *et al.*, 2010). We tested whether PD depended on TPI, and FDis on PD, using linear regressions in R.

3.4 Results

3.4.1 Soil chemistry along topography

A PCA of 10 soil chemical variables and organic layer depth revealed two largely independent factor complexes, the concentration of exchangeable basic cations (Ca, K, Mg) and phosphorus, and the availability of nitrogen (Fig. A.3 a). Both factor groups were positively associated with TPI, indicating that nutrient concentrations decreased from lower to upper slope positions. The topsoil pH decreased, while organic layer thickness increased from the lower to upper slopes (Fig. A.2, A.3 b).

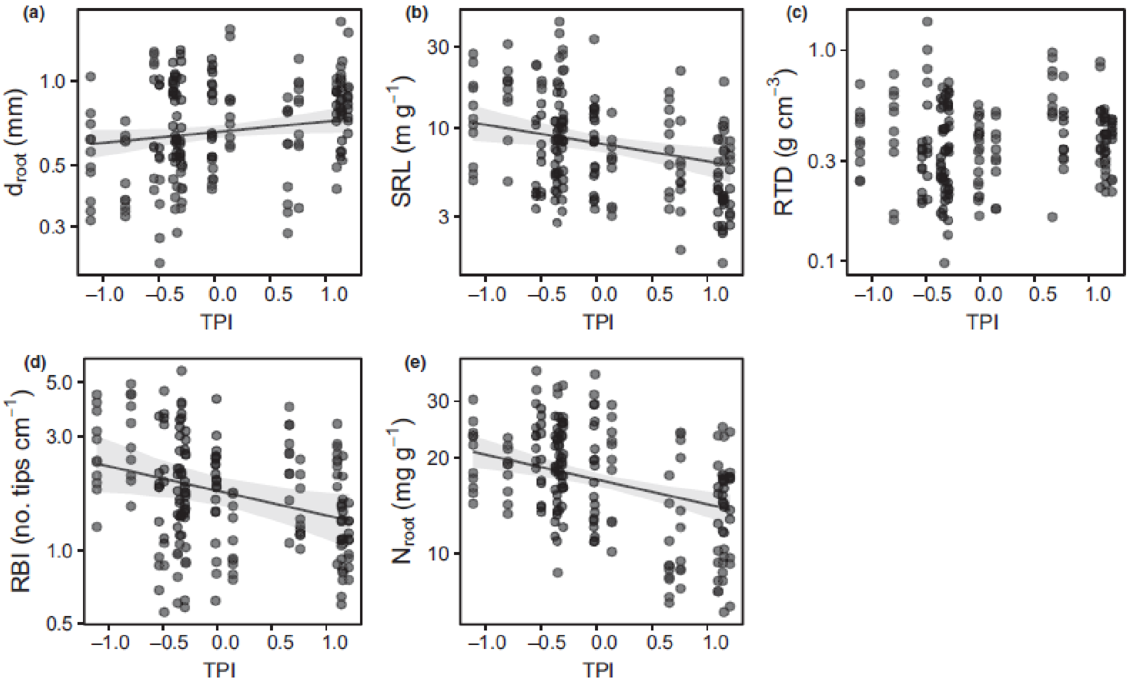

Figure 3.1: Fine root traits in dependency of the topographic position index (TPI). Shown are the raw data on individual tree level (n = 179) and marginal predictions (posterior mean with 95 % highest density intervals) from the Bayesian phylogenetic multilevel models if the effect of TPI was credibly different from zero. Root traits: (a) root diameter (d_{root}), (b) specific root length (SRL), (c) root tissue density (RTD), (d) root branching intensity (RBI), and (e) root nitrogen concentration (N_{root}).

3.4.2 Variation of fine root traits with topography

We found a credible positive effect of TPI on root diameter and credible negative effects on SRL, RBI, and N_{root}, while TPI did not influence RTD. According to the model results, fine roots were thinner, more branched, contained more nitrogen and invested less biomass per absorbing area at lower slope positions (Fig. 3.1, 3.2; Table A.4). However, only small proportions of the variance (11.0 % and 12.4 % for RBI and N_{root}, respectively, and less than 10 % for d_{root} and SRL) were explained by the effect of topography. By contrast, species effects, that is phylogenetically correlated and independent species effects combined, explained much greater amounts

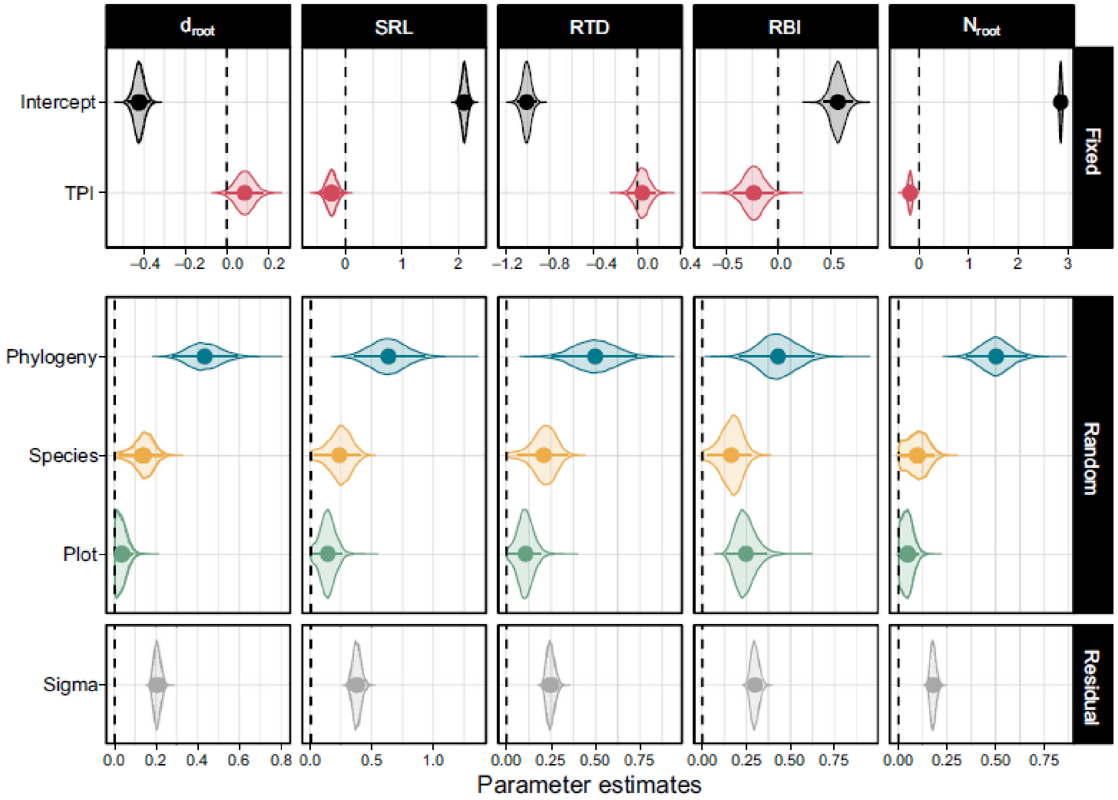

Figure 3.2: Posterior distributions of model parameters in the Bayesian phylogenetic mixed models for the five log-transformed root traits. The fixed part includes the general intercept and the slope parameter for the predictor topographic position index (TPI). In the random part, standard deviations of the random effects are shown. ‘Phylogeny’ stands for the phylogenetically correlated species effect and ‘species’ for the independent species effect. Sigma quantifies the residual variation that could neither be explained by the fixed nor the random part of the model. The posterior distributions of the parameters are displayed as effect sizes (standard deviations on log scale) to allow for comparisons between models. Points and lines: posterior mean ± 95 % highest density intervals. d_{root}, root diameter; SRL, specific root length; RTD, root tissue density; RBI, root branching intensity; N_{root}, root nitrogen concentration.

of variation of all fine root traits (ranging from 40.2 % for RBI and SRL to 79.9 % for N_{root}). In all models, the influence of phylogenetically correlated species effects was much greater than that of the independent species effects. Plot effects explained only small proportions of variance except for RBI (17.3 %). The conditional R^2 (the total amount of variance explained by fixed and random effects combined) ranged from 67.5 % (SRL) to 79.9 % (N_{root}) (Fig. 3.3). The combined random intercepts

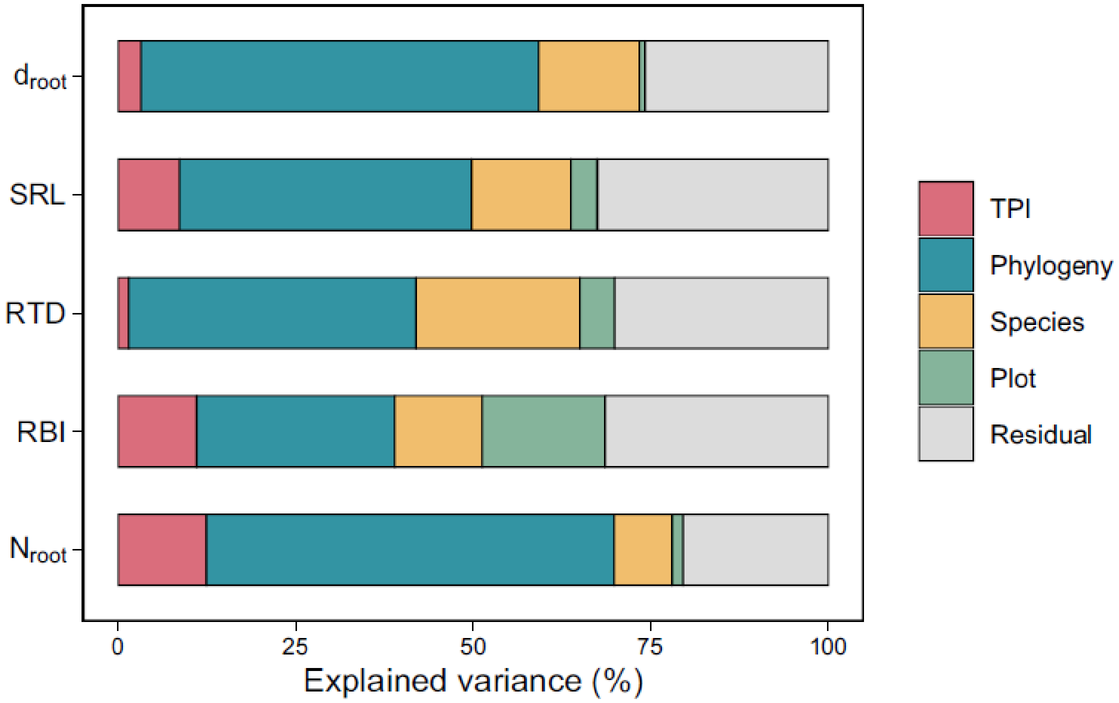

Figure 3.3: Variance decompositions of Bayesian phylogenetic multilevel models. Shown are the fractions of total variance explained by the components of the mixed models. Included traits: root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), root branching intensity (RBI), and root nitrogen concentration (N_{root}). TPI, topographic position index.

for phylogenetically dependent and independent species effects as fitted by the five models are displayed for all studied species in Fig. A.5.

3.4.3 Phylogenetic PCA

The phylogenetic PCA for the five fine root traits showed no clear one-dimensional spectrum. RBI and d_{root} were mostly associated with the first axis (which accounted for 45 % of variation), whereas RTD, SRL and N_{root} loaded similarly high on the first and second axis. The second axis explained 34 % of variation. Plant species occurring on upper slope positions were associated with higher RTD and d_{root}, and lower SRL and N_{root} (Fig. 3.4).

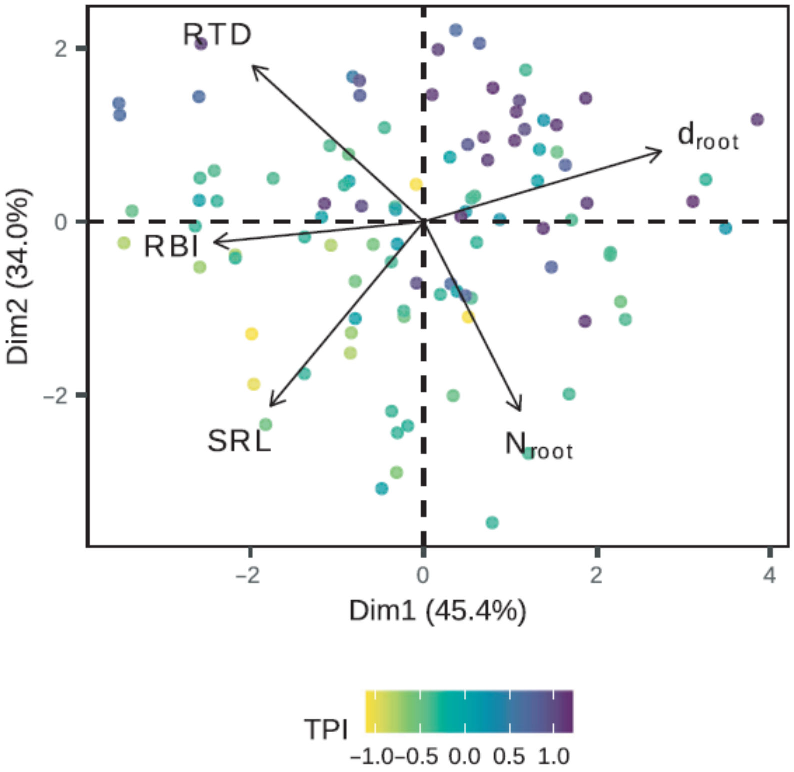

Figure 3.4: Phylogenetic principal components analysis of 100 tree species, colored by their average topographic position index (TPI) value. Included fine root traits: root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), root branching intensity (RBI), and root nitrogen concentration (N_{root}).

3.4.4 Functional dispersion

The functional dispersion of fine root traits decreased significantly by about 30 % from plots at the lower slope to plots in upper slope positions ($p = 0.001$, $R^2 = 0.45$) (Fig. 3.5). The relationships between neither PD and TPI ($p = 0.81$, $R^2 = 0.003$) nor between PD and FDis ($p = 0.13$, $R^2 = 0.14$) were significant. As the observed positive relation between PD and FDis is caused by a single outlying plot (Fig. A.6, it should be interpreted with care.

3.5 Discussion

3.5.1 The impact of phylogeny

In all of our models, species differences in accordance with phylogenetic relatedness explained by far the most variance in fine root traits, exceeding not only the variance

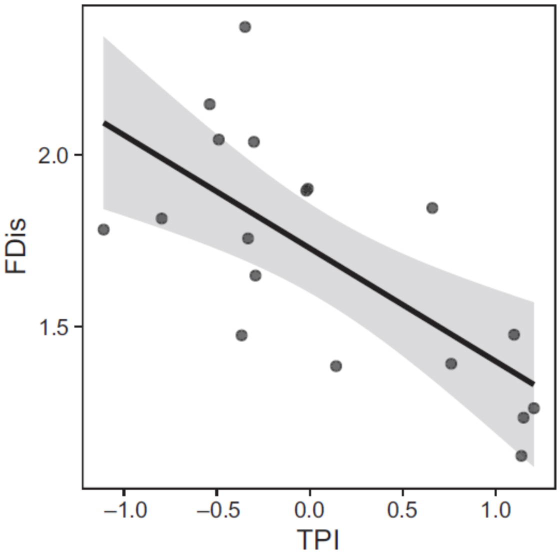

Figure 3.5: Functional dispersion (FDis) along the topographic position index (TPI). FDis was calculated with five fine root traits for 18 plots. Shown are the data with predictions from a linear model and confidence interval.

explained by topography but also by phylogenetically independent species effects. Thus, the differences in root traits found between species corresponded predominantly to the species' phylogenetic relatedness indicating strong phylogenetic conservation. There is overwhelming evidence that fine root traits, especially those linked to root diameter, are highly phylogenetically conserved (Kong *et al.*, 2014; Liese *et al.*, 2017; Valverde-Barrantes *et al.*, 2017), which is supported by our results. In particular, early-diverged angiosperms from the Magnoliid clade have larger fine root diameters than later diverged monocots and eudicots (Chen *et al.*, 2013; Valverde-Barrantes *et al.*, 2015b; Ma *et al.*, 2018; Liu *et al.*, 2019). In accordance with this finding, the Lauraceae (Magnoliid clade) had the thickest fine roots in our data set. Even though our species sample covers only part of the regional tree flora and thus may have missed certain tree genera with specific root traits, it is likely that the random sampling selected the bulk of the more abundant species and thus those taxa with highest importance for ecosystem functioning.

3.5.2 Fine root trait variation along the topographical gradient

As expected from earlier fine root studies along environmental gradients, we found plot averages of fine root diameter to increase, and SRL, RBI and N_{root} to decrease, from the lower slope to the upper slope. One cause of this variation could be within-species phenotypic plasticity in root traits in these forests. Yet, our data set does not allow firm conclusions on the role of intraspecific variation. However, the small altitudinal distribution ranges and thus narrow niches of most tree species in this region (Homeier, 2008; Werner & Homeier, 2015) suggested that tree species turnover along the mountain slope is the main factor that drives root trait variation along the topographic gradient, rather than phenotypic plasticity. Even though several microclimatic, edaphic and hydrologic factors are known to vary along topographical gradients (Takyu *et al.*, 2003), our PCA of soil variables suggested that variation in the availability of all five plant macronutrients (N, P, Ca, K, Mg) is a major factor differentiating between lower slope and upper slope positions. The results of a fertilization experiment in the montane forests of the study region revealed a general co-limitation of tree growth by nitrogen and phosphorus (Homeier *et al.*, 2012; Cárate-Tandalla *et al.*, 2018). Furthermore, nitrogen availability has been shown to decrease greatly towards the upper slope (Wolf *et al.*, 2011). Down-slope transport of nutrients with percolating water is thought to be the principal cause of the soil fertility gradient from lower to upper slopes, which is enhanced by decreasing foliar litter quality from valleys to ridges (Werner & Homeier, 2015). Data on the change in tree species composition, stand structure, productivity, herbivory rate and decomposition support these conclusions (Homeier *et al.*, 2010; Werner & Homeier, 2015; Paulick *et al.*, 2017).

Clearly, soil moisture is another factor that changes from more favorable to less favorable from lower slope to upper slope positions, even in this perhumid montane environment with more than 2000 mm of rain annually. In irregularly occurring extended periods of low rainfall, ridge soils may temporarily expose the roots to water shortage, which could influence fine root morphology. This is less likely to happen in the moister valley soils, where downhill surface and subsurface water flow adds to the moisture received from rainfall. Many studies have shown that tree fine roots typically are thicker, less branched and have lower SRL at drier than moister sites (Brunner *et al.*, 2015). This makes it difficult to separate underlying soil fertility and soil moisture effects along the slope. Moreover, soil drought often induces nutrient shortage (Kreuzwieser & Gessler, 2010). Long-term hydrological sampling along the topographic gradient would be needed to answer this question.

Our results implied that soil conditions acted as an environmental filter, sorting species based on their root traits from more acquisitive at the lower slope to more conservative at the upper slope. Consistent with both the theoretical framework introduced by Reich (2014) and several empirical studies across different ecosystems and spatial scales (Craine & Lee, 2003; Freschet *et al.*, 2010; Pérez-Ramos *et al.*, 2012; de la Riva *et al.*, 2018), our results hereby confirm that trees with conservative fine root traits seem to be more successful, where resources are scarce. Nevertheless, the results from the trait PCA do not indicate a one-dimensional RES, as found in other studies (Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2015b; Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016). Root diameter, branching and SRL can be interpreted as one dimension and RTD and N_{root} as a second dimension, which both seem to be related to the topographic gradient.

3.5.3 Fine root functional diversity along the topographical gradient

A key result of our study is that not only functional trait values, but also fine root functional diversity (measured as functional dispersion) decreased from lower slope to upper slope positions. Whereas some studies on aboveground functional traits along topographical gradients in tropical forests found no topography effect on functional diversity (Apaza-Quevedo *et al.*, 2015; Muscarella *et al.*, 2019), Liu *et al.* (2014) observed, in agreement with this study, a higher functional diversity at the lower slopes in a tropical rain forest. Also matching is the finding of Mason *et al.* (2012) who reported a positive relationship between nutrient availability and leaf functional diversity in a temperate rain forest. The possible mechanism behind these patterns is probably the restrictive environmental filtering by the lower nutrient supply at the upper slope, which leads to functional convergence (cf. Ding *et al.*, 2019). Here, a conservative resource economics strategy is the only possibility for the trees, whereas more fertile conditions allow for a broader range of strategies (Mason *et al.*, 2012). At the lower slope positions of the study area, not only the average availability of all five macronutrients is higher, but also the spatial heterogeneity of nutrient supply is larger (Homeier *et al.*, 2010). This enables a higher functional differentiation among tree species under stronger competition for light (Mason *et al.*, 2012; Liu *et al.*, 2014; Werner & Homeier, 2015). As the functional dispersion index is independent from species richness (Laliberté & Legendre, 2010), the observed trend toward higher functional differentiation at the lower slopes cannot be a result of the higher tree species richness here. As phylogenetic diversity in our tree sample was only weakly associated with functional diversity, PD is an unlikely cause of the decrease in functional diversity in upslope direction. Therefore, it can be assumed that the same underlying edaphic gradient directly drives both the functional trait variation and diversity of tree fine roots in this tropical montane forest.

In conclusion, marked changes in tree fine root traits and their functional diversity were detected in these tropical montane forests on a local scale of a few hundred meters that could be related to the pronounced small-scale soil heterogeneity. Fine root traits varied from acquisitive at the more fertile lower slope to conservative at the more impoverished upper slope, with a pattern of decreasing root functional diversity from the lower to the upper slope that is likely to be due to environmental filtering processes. Detailed soil chemical and physical investigations along topographic gradients are needed to identify the main abiotic drivers (different soil nutrient species, water) of the root functional differentiation along the slope. In any case, a larger fraction of the root trait variation was explained by species effects related to phylogeny than by topography or plot, which shows that phylogeny is key to understanding the diversity of co-existing root trait syndromes. Our results suggested that tree species in tropical montane forests assemble along topographical gradients in accordance with their belowground resource economics strategies and the associated root trait combinations.

3.6 Acknowledgements

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3.7 Author contributions

KP and JH designed the study, KP performed field work and analysed the data, KP, CL and JH interpreted the results and wrote the manuscript.

Chapter 4

Elevational trends of tree fine root traits in species-rich tropical Andean forests

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4.1 Abstract

With increasing elevation, trees in tropical montane forests have to invest larger fractions of their resources into their fine roots in order to compensate for increasingly unfavorable soil conditions. It is unclear how elevation and related edaphic changes influence the variability in tree fine root traits and belowground functional diversity.

We measured six fine root traits related to resource acquisition on absorptive fine roots of 288 trees from 145 species along an elevational gradient from 1000 m to 3000 m a.s.l. in tropical montane forests of the Ecuadorian Andes. We analyzed trait relationships with elevation and soil nutrient availability, and tested whether root functional diversity varied along these gradients.

Fine roots at higher elevations and at more nutrient-poor sites were thicker, had higher tissue densities, and lower specific root length and nutrient concentrations than at lower elevations. These trends were diluted by the co-existence of tree species with a broad range of different root traits within communities particularly towards lower elevations, where root functional diversity was significantly higher.

We conclude that nutrient limitation and waterlogged, acidic conditions at higher elevations are strong environmental filters that lead to trait convergence towards a conservative resource use strategy, whereas different trait syndromes are equally successful at lower elevations.

Keywords: Elevational gradient, fine roots, functional diversity, functional traits, tropical montane forest, Ecuador

4.2 Introduction

Tropical montane forests in the Andes are among the most species-rich ecosystems in the world (Myers *et al.*, 2000; Pérez-Escobar *et al.*, 2022). Harboring an enormous plant species diversity and highly variable topographic, climatic and edaphic conditions on a small area, they are ideal study systems to investigate the varying strategies of plant species along environmental gradients. Tree root systems play extraordinary roles for ecosystem functioning in tropical montane forests, notably as important sinks for carbon and nutrients and due to their crucial role for soil formation and stabilization (Hertel & Leuschner, 2011). The relationships between soil conditions and root properties differ considerably between tropical lowland forests and tropical montane forests (Huasco *et al.*, 2021). With increasing elevation, the root/shoot biomass ratio greatly increases, which is usually attributed to a reduction in nutrient availability and the frequent occurrence of waterlogged, oxygen-deficient and acidic soils at higher elevations (Graefe *et al.*, 2008; Soethe *et al.*, 2008; Moser *et al.*, 2011). High fine root biomasses and fine root productivity found in high elevations indicate that the trees allocate substantial amounts of their resources to their root systems in order to thrive in the upper tropical montane forests (Röderstein *et al.*, 2005; Leuschner *et al.*, 2007; Soethe *et al.*, 2007). While the processes driving community-level fine root dynamics and aboveground/belowground carbon allocation patterns in trees are already quite thoroughly understood in these ecosystems, we still lack insight into the resource use strategies and functional trade-offs that shape fine root properties of different tree species and their variation along environmental gradients. We expect that trees at higher elevations do not only generally have to allocate more of their resources into the root systems, but also have root adaptations to more effectively acquire nutrients under adverse soil conditions.

The integration of root traits into theoretical frameworks of resource use trade-offs and their associated functional trait syndromes has been a major achievement of belowground ecology in the past years (Reich, 2014; Weemstra *et al.*, 2016; Freschet *et al.*, 2021b; Vleminckx *et al.*, 2021). Despite large variation across plant species, ecosystem types and different scales of observation, many root ecologists agree today that one main axis of variation in fine root functional traits reflects a trade-off between resource acquisition and resource conservation, the so-called root economics spectrum (Kong *et al.*, 2014; Roumet *et al.*, 2016; Weemstra *et al.*, 2016; Bergmann *et al.*, 2020; Weigelt *et al.*, 2021). Compared to conservative fine roots, acquisitive fine roots are thinner, have a higher specific root length (SRL), lower root tissue density (RTD), and higher nutrient concentrations. Acquisitive fine roots are moreover associated with shorter life spans, higher metabolic and resource acquisition rates, lower concentrations of secondary compounds and typically occur in resource-rich environments (Weemstra *et al.*, 2016). While these patterns have not always been found in tropical forests (Sierra Cornejo *et al.*, 2020; Vleminckx *et al.*, 2021), tree fine roots at mid-elevations in tropical montane forests in the research area varied accordingly along local topography-driven edaphic gradients (Pierick *et al.*, 2021). We expect fine root traits to vary along elevational gradients more strongly than along small-scale topographic gradients, with the nutrient-deprived, waterlogged and acidic soil conditions at higher elevations filtering for tree species with more conservative fine root strategies. Our expectation to find more conservative fine root strategies at higher elevations is further enhanced by the results of Homeier *et al.* (2021) on elevational change in leaf traits in neotropical montane forests, demonstrating that tree species at higher elevations have more conservative leaf traits than at lower elevations. As leaf and root traits are often linked to each other (Shen *et al.*, 2019; Hogan *et al.*, 2020), a shift from acquisitive to conservative fine roots with increasing elevation, analogous to leaves, appears likely.

While plant functional traits are often studied along environmental gradients as community means, the range of trait variation within communities is far less investigated. Especially in species-rich communities tropical montane forests, it can be expected that species with very different trait syndromes co-exist in close proximity. Furthermore, soil conditions are highly heterogeneous on a small scale in the rugged terrain of tropical montane forests (Wolf *et al.*, 2011; Werner & Homeier, 2015), which may further promote the co-occurrence of tree species with different belowground strategies. Therefore, we focus not only on community-level trait means, but also analyze functional traits of fine roots on the level of individual trees. We perform this for a large number of tropical montane forest tree species, which has not been done so far. Through this approach, we want to illustrate the range of coexisting root trait syndromes that would be obscured when only using community-aggregated data, and to compare trait variation along environmental gradients on two different scales of aggregation. Additionally, we measured functional diversity, which expresses the variability of various traits in the multi-dimensional trait space, a feature that is generally assumed to influence ecosystem functioning and resilience in a positive way (Díaz & Cabido, 2001; Díaz *et al.*, 2007). While the variation of functional diversity along environmental gradients is far less studied than the variation of trait means, there is some evidence that the functional diversity of trees tends to increase with resource availability (Mason *et al.*, 2012; Ding *et al.*, 2019). However, most related studies consider only aboveground traits, whereas the functional diversity of fine root traits has barely been explored. In our study area, we already found that functional diversity of tree fine roots increased with nutrient availability on a small scale at lower montane elevations (Pierick *et al.*, 2021). We expect that a similar trend also exists along the large-scale elevational gradient.

With this study, we explore how fine root functional traits of trees and their functional diversity change with elevation and soil fertility in order to improve our understanding of the intricate ecological processes in highly species-rich Andean forests. The following hypotheses were tested:

1. Fine root traits at higher elevations and lower nutrient availability pursue a more conservative resource use strategy with a higher root tissue density, absorptive fine root fraction and root diameters, and lower specific root length and nutrient concentrations.
2. Different tree species within the same community can follow a broad range of belowground strategies, resulting in high within-site trait diversity.
3. The functional diversity of root traits decreases with elevation and increases with nutrient availability.

4.3 Methods

4.3.1 Study area

The study was conducted in the southern Ecuadorian Andes, on the east-facing slopes of the Cordillera Real mountain range. Investigations took place in an elevation transect ranging from 1000 m to 3000 m a.s.l. either within or close to Podocarpus National Park in the Ecuadorian provinces Loja and Zamora Chinchipe. A map of plot locations as well as a list of plot coordinates and elevations is provided in the supplementary material (Fig. B.1 and Table B.1, respectively). The area is part of the Tropical Andes biodiversity hotspot (Myers *et al.*, 2000). The climate of the study area is tropical humid with highest precipitation from June to August and a less humid period between September and December. Typically, all months receive > 100 mm precipitation. Over the observed altitudinal range, the climate changes drastically. Mean annual temperature decreases from 20 °C at 1000 m to 9.5 °C at 3000 m, while annual precipitation increases from around 2000 mm at 1000 m to 4500 mm at 3000 m (Emck, 2007; Bendix *et al.*, 2008). The study area is characterized by relatively nutrient-poor soils on metamorphic schists and sandstones (2000 and 3000 m) or granodioritic rocks (1000 m) (Wolf *et al.*, 2011). In general, soils are slightly more fertile at lower elevations and also on lower slope positions than at higher elevations and on upper slopes (Wilcke *et al.*, 2008a; Wolf *et al.*, 2011). The decreasing nutrient availability is reflected by decreasing forest biomass and productivity with increasing elevation (Homeier & Leuschner, 2021). Floristic composition, species richness and structural forest characteristics are subject to pronounced elevational change (Homeier *et al.*, 2008): The premontane rain forest at the lowermost study site reaches 40 m in height with common tree families being Fabaceae, Moraceae, Myristicaceae, Rubiaceae, and Sapotaceae. It is replaced at 1300–2100 m by smaller-statured lower montane rain forest with Euphorbiaceae, Lauraceae, Melastomataceae, and Rubiaceae as characteristic tree families, and above 2100 m by upper montane rain forest with a canopy height rarely exceeding 8–10 m. Common tree families of the latter forest type are Aquifoliaceae, Clusiaceae, Cunoniaceae, and Melastomataceae.

4.3.2 Experimental design

We collected fine root samples in pre-existing permanent plots at elevations of about 1000 m, 1500 m, 2000 m, 2500 m and 3000 m a.s.l., where the tree species already had been identified. These five elevational levels are hereafter termed ‘sites’. We selected mid-slope plots, as the strong influence of topographic position on fine root traits in this rugged terrain has already been demonstrated in an earlier study for the study area (Pierick *et al.*, 2021). At 1000 m, 2000 m and 3000 m, we collected samples in six plots of 400 m^2 per elevation level (the mid-slope plots established by Wolf *et al.* (2011)). At 1500 m, we used three, and at 2500 m a.s.l. two 1000 m^2 plots (a subset of plots used by Tiede *et al.* (2017)). The exact shapes, elevations and locations of the plots are given in Table B.1. So far, more than 1000 tree species have been registered in the study area; this makes a complete sampling of all species almost impossible. Therefore, our approach was to randomly select 60 trees per site from the population of all adult tree individuals (diameter at breast height $\geq$ 10 cm) with the samples distributed equally over the plots of the site. This led to a dataset where not all species were sampled, and common species were replicated more often than rare species. In comparison with other incomplete trait sampling strategies, the accuracy of randomized approaches in species-rich tropical forests has been evaluated positively (Baraloto *et al.*, 2010a; Paine *et al.*, 2015), in a similar manner as sampling strategies, where common species are more thoroughly sampled than rare species (Carmona *et al.*, 2015). Of the 300 originally selected trees, 12 had to be discarded due to insufficient fine root sample quality (e.g. too little or damaged material or likely misidentification of species). The final data set comprised samples belonging to 288 individuals, 145 species and 47 families (see species list in Table B.2). The most common species were *Clusia elliptica* with 11 observations and *Alchornea lojaensis*, *Graffenrieda* aff. *uribei*, *Otoba parvifolia* and *Tapirira* cf. *guianensis* with seven observations each. Eighty species were only present with one individual. The most common plant families were Melastomataceae (43 observations), Lauraceae (30), Clusiaceae (25) and Moraceae (25). The number of species sampled per site ranged from 23 species at 2500 m to 38 species at 2000 m a.s.l., without an elevational trend. Only five species were sampled at more than one site.

4.3.3 Soil chemical and physical analyses

Data on chemical and physical topsoil properties were available for the plots at 1000, 2000 and 3000 m from the study of Wolf *et al.* (2011). For the plots at 1500 and 2500 m, we measured soil organic layer depth and followed the methods described in Wolf *et al.* (2011) to analyze the chemical properties of the upper 10 cm of mineral soil. Briefly, the availability of the plant macronutrients N and P and soil acidity were analysed in the soil of all study plots. P availability was estimated as resin-exchangeable P, which may give an estimate of plant-available P (P_{av}). Soil C:N ratio (CN_{soil}) was determined for characterizing the decomposability of soil organic matter, providing an estimate of mineral N supply. In addition, effective cation exchange capacity was determined by salt exchange (0.2 N $BaCl_2$ solution), applying a standard protocol for the chemical analysis of forest soils (for analytical details see Wolf *et al.* (2011)). Base saturation at the cation exchangers was calculated as the percentage of exchangeable base cations (Na, K, Ca and, Mg) in the total of exchangeable cations. Furthermore, pH (H_2O) was measured (Wolf *et al.*, 2011). The general increase in organic-layer depth with elevation, accompanied by an increase in CN_{soil} and a reduction in pH, is an expression of reduced organic matter decomposition rates with decreasing temperature and a lowered nutrient supply through mineralization.

4.3.4 Root trait measurements

Roots were sampled from the uppermost 20 cm of soil (incl. organic layer) by tracing coarse roots of a target tree from the trunk until strands of fine roots (diameter $\leq$ 2 mm) were reached. Per tree, at least one complete and undamaged fine root strand $>$ 15 cm length, or more material if possible, was harvested. The roots were then washed, dead and damaged material was removed, and the samples separated into absorptive and transportive fine roots on the basis of morphology. Such a functional approach has been suggested by McCormack *et al.* (2015) and Shao *et al.* (2019), based on the notion that both order-based and diameter-based fine root definitions can be arbitrary (Freschet *et al.*, 2017). The classification of fine roots of woody plants into primarily absorptive and transportive roots bases on the analysis of the anatomy of fine roots in cross sections, as done by e.g. Kong *et al.* (2016), Trocha *et al.* (2017) and Wang *et al.* (2019), with most authors agreeing that the most distal two to four root orders maintain a mainly absorptive function. Since we analyzed a large number of species, we were not able to investigate root cross-sections in all sampled species, and therefore relied on morphological criteria (periderm color and surface texture, root diameter, root elasticity, and presence of root hairs) for classifying roots into absorptive and transportive fine roots. For almost all species, we found a clear and very discrete change in color, elasticity and surface texture between lower-order and higher-order root segments and assumed that these morphological differences reflect a shift in root function. This discrete change in morphology was visible between the second and fifth root order in all species. All distal root segments that we classified as absorptive were separated from the material classified as transportive. We oven-dried the transportive root material for at least 48 h at 60 °C and subsequently used the dry weights to calculate absorptive fine root fraction (AFRF), the dry weight fraction of absorptive fine roots of the whole fine root sample with diameter $\leq$ 2 mm. By introducing this new trait, we aimed at estimating the error introduced when only the classical 2 mm-cutoff method would be employed for root sampling. We expect it to be positively correlated with the average diameter of the absorptive fine roots, and therefore to be interpretable in a similar way. All other functional traits (average root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), and root N and P concentrations (N_{root}, P_{root})) were only measured on absorptive fine roots.

Table 4.1: Trait names, abbreviations, and units. All root traits besides AFRF were measured on the absorptive fine roots.

Trait	Abbreviation	Unit
Average root diameter	d_{root}	mm
Specific root length	SRL	m g^{-1}
Root tissue density	RTD	g cm^{-3}
Absorptive fine root fraction	AFRF	g g^{-1}
Root nitrogen concentration	N_{root}	mg g^{-1}
Root phosphorus concentration	P_{root}	mg g^{-1}

We arranged the root samples in a plexiglass tray filled with demineralized water and used a Hewlett Packard Scanjet G4050 scanner to obtain grey-scale images with a resolution of 600 dpi. The resulting images were then analyzed with the software WinRhizo 2013 Basic (Régent Instruments Inc., Quebec, Canada), obtaining average root diameter, total root length and total root volume. Afterwards, we oven-dried the root samples for at least 48 h at 60 °C and weighed them on an analytical balance. With these data, we calculated specific root length (root length/dry weight) and root tissue density (dry weight/root volume). For chemical analyses, the dried samples were ground with a vibrating disc mill. The ground samples were used to measure the N content with a CN elemental analyzer (Vario EL III, Hanau, Germany), and the P content by ICP analysis (Thermo Scientific iCAP 7000 ICP-OES, Thermo Fisher Scientific, Germany) after HNO3 digestion of the ground material. A full list of the measured traits and their units is given in Table 4.1.

4.3.5 Data analyses

We calculated a principal component analysis (PCA) with all standardized soil variables in order to select a set of meaningful predictor variables that are as independent of each other as possible and represent main axes of variation in soil parameters. Based on the result (see Fig. B.2), we selected CN_{soil} (which is positively correlated with depth of organic layer, soil C concentration and soil N concentration) and P_{av} (which is positively correlated with base saturation, pH, and cation exchange capacity) as predictors together with elevation above sea level (which is a proxy for temperature). We then tested for linear relationships of each CN_{soil} and P_{av} with elevation using linear models. In order to test if the root functional traits d_{root}, SRL, RTD, AFRF, N_{root} and P_{root} varied with elevation and soil parameters, and to quantify their within-site variability, we combined two approaches, i.e. community-weighted means (CWM) and linear mixed models (LMM) (Hypothesis 1 and 2). We calculated community-weighted means for each plot with the subset of species sampled, comparing both CWM values weighted by the number of individuals and the total basal area of each species, using the trait means of the tree species sampled within the plots. We then fitted linear models of the CWM for each trait in dependency of elevation, CN_{soil} and P_{av}. In a second approach, we fitted one linear mixed model for each of the traits using the R package `glmmTMB` version 1.0.2.1 (Brooks *et al.*, 2017). We fitted the models with tree individuals as the observational unit. As random effects, we included random intercepts for species, site, and plot nested in site. As all functional traits were left-skewed and strictly positive, they were log-transformed prior to analysis for both types of models to avoid heteroscedasticity issues and ensure normality of residuals. To test hypothesis 3, we chose functional dispersion (FDis) as a measure for functional diversity, as it is unaffected by species richness (Laliberté & Legendre, 2010). FDis of the six studied fine root traits of the sampled species was calculated for each plot using the R package `FD` version 1.0.12 (Laliberté *et al.*, 2014). Subsequently, the relationship of FDis with elevation, soil C:N ratio and plant available phosphorus was tested using a linear model. We visualized trait values of families and large phylogenetic clades within the context of their evolutionary history. To do so, we extracted the phylogeny of the species contained in our sample from the megatree GBOTB.extended using the R package `V.PhyloMaker` version 0.1.0 (Jin & Qian, 2019). To complement our analyses, we also calculated Pagel's λ, a measure of the strength of the phylogenetic signal, using the R package `phytools` version 0.7.70 (Revell, 2012). All analyses were conducted with R version 4.0.2 (R Core Team, 2020) in the `tidyverse` programming framework (version 1.3.1, Wickham *et al.* (2019)).

4.4 Results

4.4.1 Elevational changes in soil properties

Our soil chemical data did not show significant increases in topsoil C:N ratio and decreases in plant-available P contents, as were expected from earlier studies in the transect (Fig. 4.1), which was mainly a result of comparatively high soil N and P_{av} contents in the plots at 2000 m a.s.l.

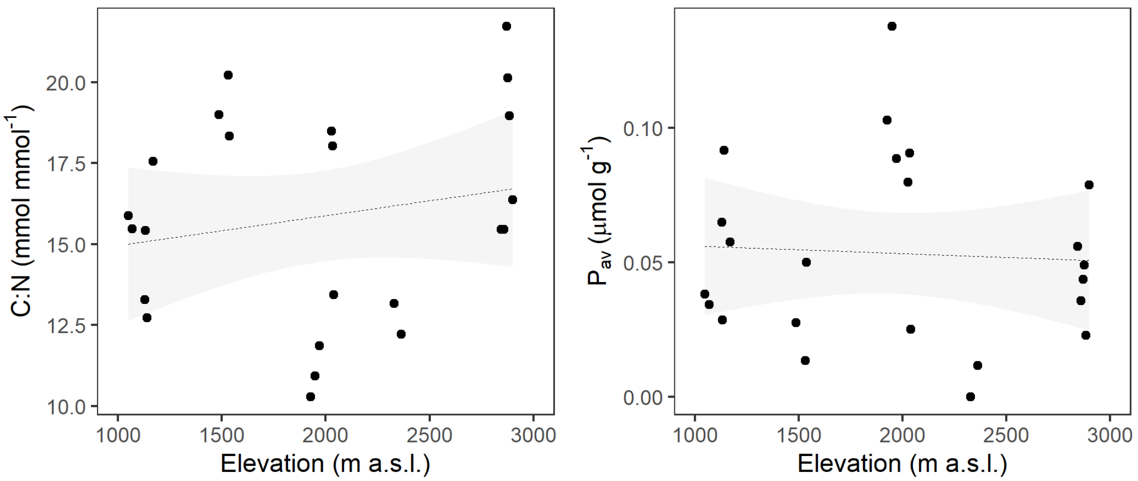

Figure 4.1: Soil C:N ratio and plant available P in dependency of elevation above sea level for 23 plots overlayed with linear regression lines with their 95 % confidence intervals (CN_{soil}: $p = 0.370$, $R^2 = 0.04$; P_{av}: $p = 0.8$, $R^2 = 0.0003$).

4.4.2 Trait relationships with elevation and soil properties

Our data revealed that there were slight elevational trends in some fine root traits, though the trait variability within sites exceeded the trait differences between sites by far for all traits (Fig. B.3). Different methods to aggregate the individual-level data on the plot level led to similar results (Fig. B.4). The inference from our linear models on the level of community-weighted means and the linear mixed models on individual tree level yielded very similar results in terms of significance, slope and directions of trait-environment relationships (Fig. 4.2, Tables B.3 and B.3). Our models indicated that all traits, except for RTD, depended significantly on elevation (but the relationship of d_{root} was significant only on the CWM level). d_{root} and AFRF increased with elevation, whereas SRL, N_{root} and P_{root} decreased (Fig. 4.2). While CN_{soil} and P_{av} had no significant effect on d_{root} and SRL, and affected AFRF positively only on the individual level, RTD increased significantly with CN_{soil} and decreased significantly with P_{av} (only at the individual level). Both chemical traits, N_{root} and P_{root}, decreased with CN_{soil} and increased with P_{av}. The linear models on the level of CWM explained between 25.3 % (d_{root}) and 78 % (N_{root}) of the variance in the different traits (Table B.3). The linear mixed models on the individual level generally explained a large part of the observed variation, ranging from 52 % explained variance in case of RTD to 71 % explained variance for N_{root} concentration (Table B.4). However, in all cases, most explained variance was attributable to species identity, while environment (both in form of the linear predictors and the random effects for site and plot) was much less important. The variance explained by the fixed effects ranges from 3.1 % for d_{root} to 39.6 % for P_{root} ((Table B.4).

4.4.3 Functional dispersion

Functional dispersion of the six fine root traits analyzed decreased significantly with elevation ($p < 0.001$), whereas soil C:N ratio and plant-available P did not have a significant effect on functional dispersion ($R^2 = 0.411$, Fig. 4.3).

4.4.4 Phylogenetic signals in root traits

Of the major plant clades Rosidae, Asteridae, Magnoliidae, and Gymnosperma, the latter deviated from the rest in terms of most root traits. Since our dataset only comprises two gymnosperm species (both from the Podocarpaceae family), this result should not be overly interpreted (Fig. 4.4, Fig. B.5). Magnoliidae generally had thicker fine roots with lower SRL than Rosidae and Asteridae, which was mostly driven by thick-rooted species within the Myristicaceae and Lauraceae families. Nevertheless, Clusiaceae, Euphorbiaceae, and Meliaceae from the Rosidae clade had also comparatively thick roots. In many cases, related plant families tended to be similar in their root traits (Fig. 4.4), even if they occurred at rather different elevations. This was exemplified by the closely related Myrtaceae and Melastomataceae, in which all species had thin and nutrient-poor roots, even though they occurred along the entire elevational range (Fig. 4.4). However, Cunoniaceae, Clusiaceae and Aquifoliaceae are examples of families that were sampled exclusively at high elevations, and had strikingly high root tissue densities and low nutrient concentrations, compared to related families (Fig. 4.4). We found marked phylogenetic signals for all traits except AFRF (SI10), which yielded a Pagel's λ of 0.31, whereas all other traits showed λ values between 0.57 (P_{root}) and 0.76 (N_{root}).

4.5 Discussion

4.5.1 Root trait variation with elevation and soil fertility

Supporting our first hypothesis, we found that tree absorptive fine roots at higher elevations were thicker, had lower SRL, higher AFRF and lower concentrations of N and P than fine roots at lower elevations. Further, absorptive fine roots at more

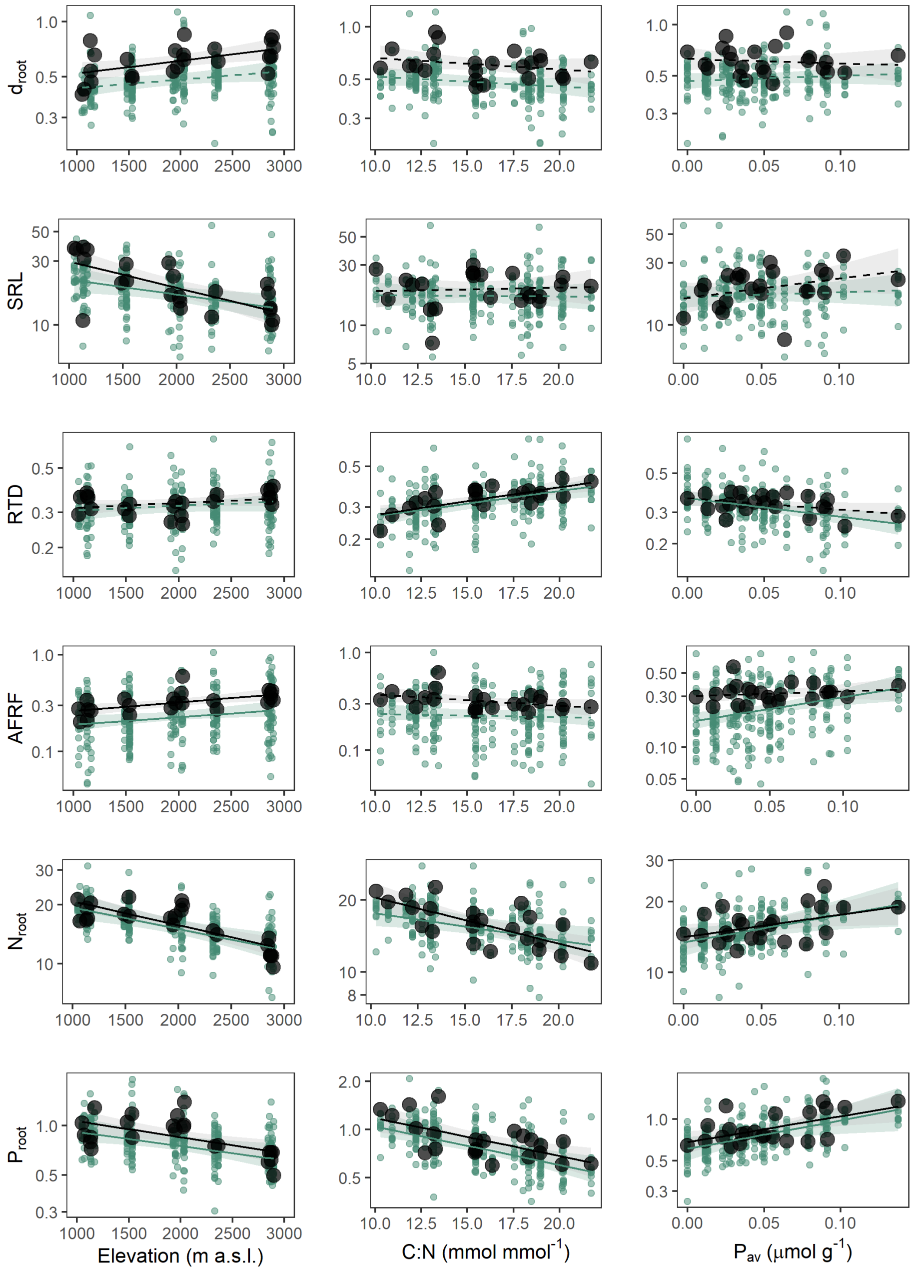

Figure 4.2: Partial residual plots of models predicting fine root traits in response to elevation, soil C:N ratio and plant available P. Points: partial residuals; lines: partial predictions; ribbons: 95 % confidence intervals. Solid lines indicate significant relationships ($p \leq 0.05$), dashed lines indicate insignificant relationships. Results from linear models calculated on the level of community weighted means are shown in black. Results from linear mixed models calculated on the level of individual trees, with random effects accounting for plot, site, and species, are shown in green. Trait acronyms and units can be found in Tab. 1.

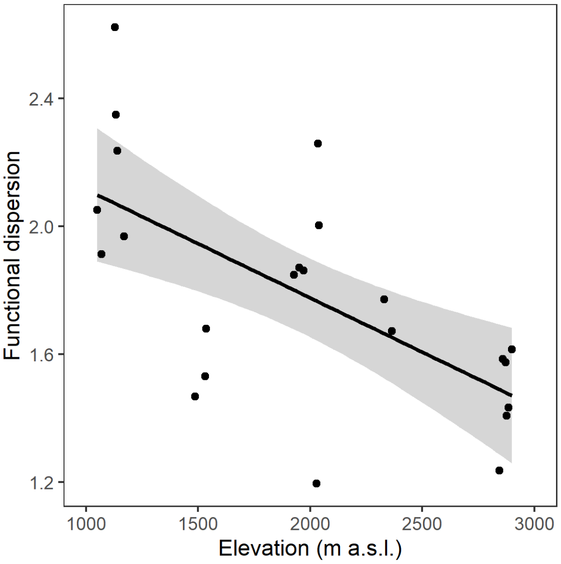

Figure 4.3: Functional dispersion of six fine root traits in 23 plots in dependency of elevation with the predictions and 95 % confidence intervals from a linear model ($p < 0.001$, $R^2 = 0.38$).

nutrient-limited sites showed elevated RTD and reduced N and P concentrations than on more fertile sites. So far, only few studies on root morphological and chemical traits of from tropical montane forests do exist, as the focus of tree fine root studies in these systems has mostly been on fine root biomass, productivity and turnover (Hertel *et al.*, 2003; Leuschner *et al.*, 2006, 2007; Girardin *et al.*, 2013). Decreasing root nutrient concentrations with elevation on the community level have similarly been reported by Soethe *et al.* (2007) and Graefe *et al.* (2010) in our study region, confirming our individual- and community-level results. Moreover, in a previous study at the individual level along a small-scale topographic gradient in our study area, we found that roots were thicker and less branched, and had lower SRL and N concentrations at the more nutrient-limited upper slopes than at the more fertile lower slopes Pierick *et al.* (2021). In the Paleotropics, Sierra Cornejo *et al.* (2020) found non-linear dependencies of root diameter, SRL and N concentration on elevation at the community level on Mt. Kilimanjaro, Tanzania. Ushio *et al.* (2015) reported an increase in specific root area and a decrease in fine root diameter with decreasing P availability in lower montane forests on Mt. Kinabalu, Malaysia. Our results differ from these two studies, in that the trait relationships with elevation are clearer and more linear than in Sierra Cornejo *et al.* (2020), but unlike Ushio *et al.* (2015), we did not find relationships of root diameter or SRL (which usually is closely linked to specific root area) with P availability. These differences are likely attributable to the

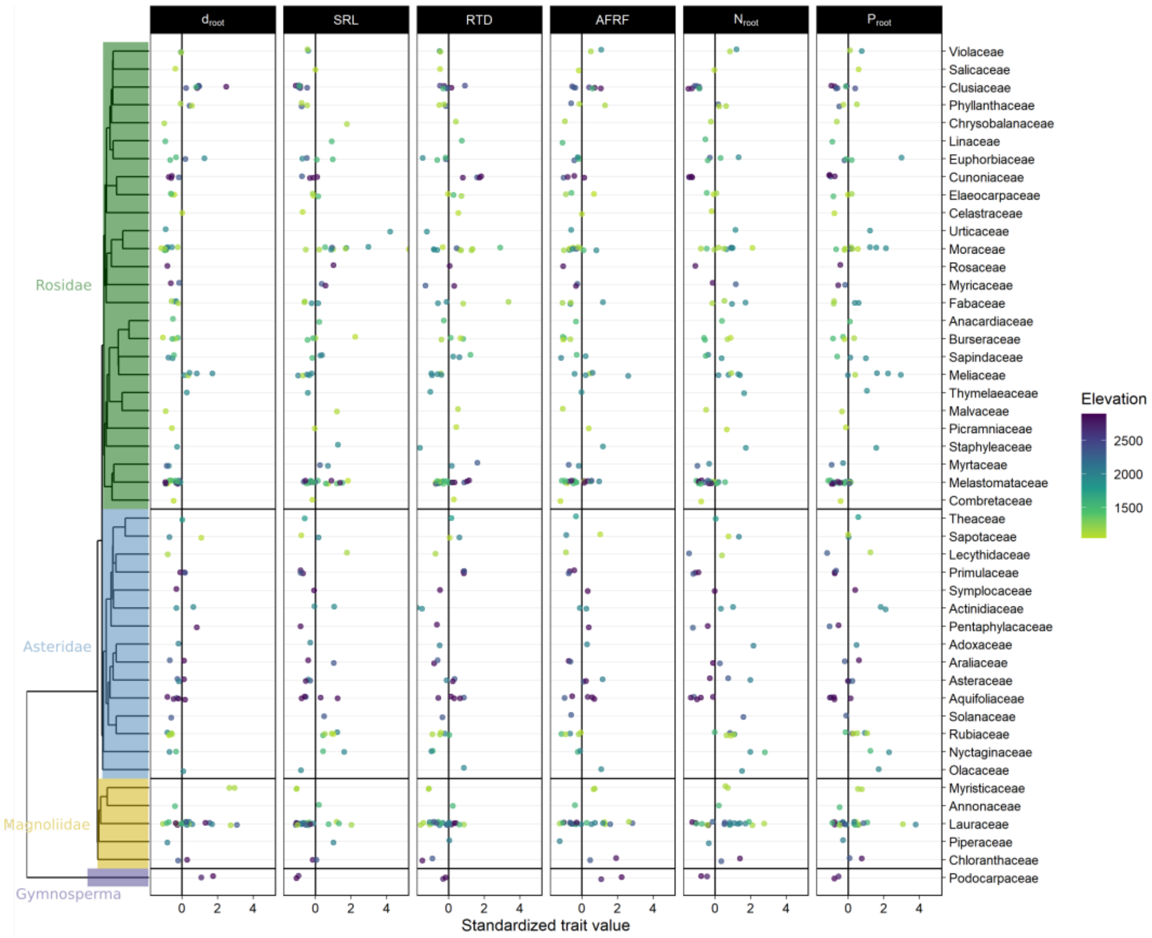

Figure 4.4: Standardized mean trait values of 288 tree species, sorted by plant family and phylogenetic clade. The traits shown are root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), absorptive fine root fraction (AFRF), root nitrogen concentration (N_{root}), and root phosphorus concentration (P_{root}). Each dot represents one tree species, with the color indicating the species' average elevation of occurrence.

fact that both the vegetation on Mt. Kilimanjaro and Mt. Kinabalu, and the study designs of Ushio *et al.* (2015) and Sierra Cornejo *et al.* (2020) differed principally from our study design. Notably, Sierra Cornejo *et al.* (2020) studied vegetation belts from savannas to Ericaceae-dominated dwarf shrub communities, whereas Ushio *et al.* (2015) conducted their investigation along a P limitation gradient caused by different geological substrates within the same elevation. Furthermore, we have to acknowledge a certain degree of uncertainty in the generalizability of our results, because our available resources only allowed for an incomplete sampling of the tree communities. This illustrates our fragmentary knowledge about root traits in tropical montane forests and demonstrates the need of more studies comparing root trait patterns between montane forests of the different tropical regions of the world.

Our results support the hypothesis that fine roots in more resource-limited environments tend to pursue a more conservative resource use strategy as compared to roots in more fertile sites, as predicted by the root economics spectrum framework (Kong *et al.*, 2014; Roumet *et al.*, 2016; Weemstra *et al.*, 2016). The root economics spectrum in its simplest form postulates that, in equivalence to the leaf economics spectrum (Wright *et al.*, 2004), also in roots there should be also in roots a trade-off between fast growth and rapid resource acquisition on the one hand, and long life spans and conservative resource use on the other hand (Kong *et al.*, 2014; Roumet *et al.*, 2016; Weemstra *et al.*, 2016). Conservative fine roots are expected to be thicker and less branched, to have higher tissue densities and lower nutrient concentrations, while acquisitive roots should exhibit the opposite properties (Weemstra *et al.*, 2016). Fine roots with conservative trait syndromes are expected to be more successful in harsh or resource-limited environments, while building acquisitive fine roots should be advantageous in ecosystems with abundant resources and high competition intensity (Kramer-Walter *et al.*, 2016). Some studies did not find evidence for such root trait-environment relationships (e.g. Vleminckx *et al.* (2021), in neotropical lowland forests), and many authors have stressed that understanding fine root traits exclusively in the light of this one-dimensional trade-off is a simplification (e.g. Valverde-Barrantes *et al.*, 2015a; Weemstra *et al.*, 2016; McCormack & Iversen, 2019; Bergmann *et al.*, 2020). However, there is a large amount of evidence of trends toward more conservative root traits under more resource-limited conditions (Pérez-Ramos *et al.*, 2012; de la Riva *et al.*, 2018; Shen *et al.*, 2019; Fort & Freschet, 2020; Hogan *et al.*, 2020). This includes a study from a small-scale topographic gradient in the same study area as studied here (Pierick *et al.*, 2021), confirming our results. In correspondence, leaf functional traits in our study area also exhibit a general shift from more acquisitive to more conservative traits with increasing elevation in our study area (Homeier & Leuschner, 2021).

In a recent study on root traits of 11 plant species along an elevational gradient in the French Alps, Weemstra *et al.* (2020) highlighted the important role of intraspecific trait variation along elevational gradients. We are convinced that, contrary to the temperate mountainous ecosystem studied by Weemstra *et al.* (2020), in tropical montane forests, intraspecific trait variation plays only a minor role compared to species turnover. In our highly diverse study region with more than 1000 tree species, most species occur only within narrow elevational belts and the species turnover between the elevational levels is consequently high (Homeier, 2008). This is visible also at the family level, since certain families only occurring at the highest elevations (Cunoniaceae, Aquifoliaceae, Clusiaceae) consistently had conservative traits, whereas the opposite was observed, for example, in case of the Rubiaceae, which were only sampled at the lower sites. Therefore, we argue that species turnover driven by environmental filtering is the underlying process that drives fine root trait variation along environmental gradients.

4.5.2 Nutrient availability as a possible driver of changes in root traits

Previous research in our study region has highlighted the elevation effect on many biotic and abiotic properties and processes in these tropical montane forests, notably the temperature effect on decomposition and mineralization rates, which leads to the accumulation of thick organic layers and decreased nutrient availability at higher elevations (Leuschner *et al.*, 2007; Soethe *et al.*, 2008). Both nitrogen and phosphorus availability have been found to decrease with elevation (Soethe *et al.*, 2008; Wilcke *et al.*, 2008a; Wolf *et al.*, 2011). Unexpectedly, the soil data used in this study do not reflect these results, but small-scale variation seems to overlay elevational trends. We assume that this pattern is attributable to the pronounced geological and edaphic heterogeneity at the scale of meters to hundreds of meters in the topographically rugged, mountainous study area. Even though we attempted to select only mid-slope plots, it appears that local topographic differences resulted in unexpectedly high nutrient availabilities at lower montane elevation at 2000 m a.s.l., masking a principal general trend toward lower N availability and wider C:N ratios in upslope direction (Soethe *et al.*, 2008; Wolf *et al.*, 2011). Fertilization experiments and foliar N:P ratios suggest that both macronutrients are co-limiting plant growth along the whole elevation gradient, but N supply becomes more critical than P supply towards higher elevations (Soethe *et al.*, 2008; Graefe *et al.*, 2010; Homeier *et al.*, 2013; Cárate-Tandalla *et al.*, 2018) (even though patterns of nutrient limitation differ among species, Cárate-Tandalla *et al.* (2018), Báez & Homeier (2018)). Additionally, high soil water contents cause frequent oxygen deficiency at higher elevations, and soils become increasingly acid (Moser *et al.*, 2011). While overall productivity and aboveground biomass both decrease with elevation as a consequence of lowered temperature, nutrient limitation and other adverse soil conditions (Leuschner *et al.*, 2007; Homeier & Leuschner, 2021), root biomass and fine root productivity and root-shoot ratio increase towards the upper montane forest in southern Ecuador (Röderstein *et al.*, 2005; Leuschner *et al.*, 2007; Moser *et al.*, 2011). The higher fine root biomass at higher elevations has been interpreted as a compensation of the trees to cope with low nutrient availability (Moser *et al.*, 2010; Moser *et al.*, 2011) and reduced root uptake activity in a temporarily oxygen-deficient soil (Soethe *et al.*, 2007), whereas the observed higher fine root turnover and production is interpreted as a compensation for increased root mortality under adverse soil conditions (Graefe *et al.*, 2008; Moser *et al.*, 2011). Combining these findings on elevational trends in root biomass and dynamics with the here reported trend of increasingly conservative fine root resource use strategies towards higher elevations, the general picture emerges that tree species at higher elevations have to allocate a larger proportion of their assimilates to establish and maintain sturdy and extensive root systems in order to guarantee sufficient nutrient supply under harsher edaphic and climatic conditions.

4.5.3 Co-existence of complementary root strategies

Already the inspection of the raw trait data along the elevation gradient clearly shows the large within-site variation of root traits. This variation is mirrored by the results of the linear mixed models, in which species random effects are explaining a far greater variation than fixed and plot random effects combined, which confirms our second hypothesis. Similar results have been reported by Valverde-Barrantes *et al.* (2013) for North American temperate tree species and Weemstra *et al.* (2020) for alpine species: in both cases, species identity was by far more important than environment for explaining variance in fine root traits. The observed variation in root traits within the study sites is primarily a consequence of the co-existence of a large number of tree species with different belowground strategies and thus different root traits in a small area. Several underlying mechanisms can be identified that drive the trait variation: 1) a particularly high diversity of root trait syndromes in tropical forests, 2) a high local soil heterogeneity, 3) the multidimensional nature of the root economics spectrum, and 4) a possible feedback of root trait diversity on species co-existence and tree species diversity. With respect to root trait diversity (1), previous studies have pointed out that the pool of root trait syndromes present in the tropics is in general considerably larger than in colder regions (Chen *et al.*, 2013; Ma *et al.*, 2018). Vleminckx *et al.* (2021) argued that a high phylogenetic diversity in the tropics both at lower and higher taxonomic levels may cause root trait overdispersion in tropical environments. In our species sample, several examples demonstrate how phylogenetically outstanding species are contributing markedly to widen the trait space within the study sites. For instance, at the lowermost site at 1000 m a.s.l., most species had relatively thin root diameters, except for a group of species with mean absorptive fine root diameters > 1 mm (Fig. B.3), which consisted of two Myristicaceae (*Otoboa parvifolia* and *Virola sebifera*) and one Lauraceae (*Rhodostemonodaphne kunthiana*), both plant families from the early-diverged magnoliid clade that is known for having thick roots (Valverde-Barrantes *et al.*, 2015a). The presence of these species at 1000 m markedly widens the range of root diameters found here.

A major reason of the high root trait variability in our study region likely is local soil heterogeneity (2). Gradient studies in our study region have shown that local topography is causing considerable small-scale variability in soil fertility and community composition (Wilcke *et al.*, 2008a; Homeier *et al.*, 2010; Wolf *et al.*, 2011; Werner & Homeier, 2015), which is reflected in a higher observed root trait variability along the topographic than along the much longer elevation gradient (Pierick *et al.*, 2021). Even though we aimed at selecting only study plots at mid-slope positions, we cannot exclude the possibility that the chosen plots within an elevation level comprise a broad range of micro-habitats that promote the occurrence of tree species with different belowground strategies in close proximity.

A hint on the role of root fungal partners in promoting the multidimensionality of the root trait spectrum (3) is given by the observation that the environmental influence on root traits was strongest for root N and P concentrations and weaker for the morphological traits. This is supported by the finding of previous studies such as Holdaway *et al.* (2011); Kramer-Walter *et al.* (2016); Wang *et al.* (2018) and Ding *et al.* (2020), which all demonstrated a decoupling of root morphological traits, especially diameter-related traits, from soil fertility gradients, whereas root nutrient contents and sometimes RTD varied more closely in dependence on soil fertility. While this phenomenon has frequently been explained with a stronger phylogenetic signal in diameter-related traits than in root chemical traits (Kong *et al.*, 2014; Wang *et al.*, 2018; Liu *et al.*, 2019), this cannot be valid in our data set, as we found a strong phylogenetic signal in all root traits except for AFRF, and the largest phylogenetic influence for root N concentration.

A strong influence of phylogeny on fine root traits is in agreement with earlier studies demonstrating that many root traits are highly phylogenetically conserved, and that differences found in root traits of extant plant clades mirror key diversification events in the past (Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2017).
Specifically, the evolution of angiosperms was associated with the evolution of thinner roots from primitive thicker roots in the course of adaptation to colder and drier

biomes (Chen *et al.*, 2013; Ma *et al.*, 2018). Consequently, modern species of the ancient magnoliid clade still possess thicker, less branched absorptive roots than species in the evolutionary more derived angiosperm clades (Valverde-Barrantes *et al.*, 2015a), a pattern confirmed by our results. However, root chemical traits also showed a strong phylogenetic signal in our data set. Yet, we found that some families from the later-diverged angiosperm clades (Clusiaceae and Meliaceae) also tend to form thick roots, which have usually been attributed only to the magnoliid clade.

Possibly, the key to explain the weaker relationship of diameter-related traits with the environment compared to chemical traits lies in the gradient of fungal collaboration intensity proposed by Bergmann *et al.* (2020) and further elaborated by Stock *et al.* (2021) and Weigelt *et al.* (2021). This gradient represents a proposed extension of the root economics spectrum to a further dimension related to the intensity of plant-fungal interaction. It attempts to quantify an assumed trade-off between a collaboration strategy with thick roots and a high degree of colonization with mycorrhiza, and a "do-it-yourself strategy" with thin roots and high SRL with low or no support by fungal partners. Both strategies, i.e. either thick roots relying highly on mycorrhizal partners or thin roots acting more independently from them, may support a root system to function in an acquisitive way (Bergmann *et al.*, 2020; Stock *et al.*, 2021; Weigelt *et al.*, 2021). The notion that both thin and thick roots can be acquisitive due to different degrees of mycorrhizal collaboration is supported by calculation with a heuristic model (McCormack & Iversen, 2019). In further support, Lugli *et al.* (2019) and Yaffar *et al.* (2021) showed that a diverse set of species with complementary P acquisition strategies, including both thin- and thick-rooted taxa, can co-exist at highly P-impoverished sites in tropical lowland forests. Such a mechanism related to fungal partners could well offset environmental filtering processes on root diameter and related traits such as SRL and AFRF, and thus be the reason for of weaker dependence of root morphological than chemical traits on environmental factors.

Finally, it is possible that high within-site root trait variation, as observed in our stands, benefits the trees and the community in these highly diverse forests and it might even promote tree diversity (4). The co-existence of species with complementary belowground strategies may allow for the exploitation of distinct spatial, temporal and soil chemical niches in the community (Valverde-Barrantes *et al.*, 2013; Luo *et al.*, 2021; Vleminckx *et al.*, 2021) In addition, this functional diversity could help to avoid the attack by specialized pathogens (Liang *et al.*, 2019; Luo *et al.*, 2021). The phenomenon has been observed and discussed for fine roots in temperate forests

(Valverde-Barrantes *et al.*, 2013), subtropical forests (Luo *et al.*, 2021) and tropical lowland forests (Vleminckx *et al.*, 2021) using different terminologies (competitive trait displacement, limiting similarity, niche segregation).

4.5.4 Belowground functional diversity decreases with elevation

The functional diversity of tree fine roots significantly decreased with increasing elevation, confirming our third hypothesis, and mirroring the main findings of the related study of Pierick *et al.* (2021), i.e. a decrease in community-level FDis from more to less fertile sites along short topographic gradients. In correspondence, Ding *et al.* (2019) also found a decrease in the functional diversity of aboveground plant traits with elevation in tropical montane forests and argued that it was caused by increased environmental filtering at higher elevations. The functional diversity of fine roots has very rarely been investigated so far. St. Martin & Mallik (2021) observed that root functional diversity decreased markedly during the transition from boreal forests to heath vegetation, after a wildfire had reduced N availability and increased soil acidity. The authors argue that harsher conditions and increased resource limitation led to stricter environmental filtering and hence a reduction in belowground functional diversity. We believe that similar processes are involved in our study area, i.e. the growing conditions become increasingly adverse and nutrient-limited at higher elevations, which must lead to a stronger impact of environmental filtering compared to the process of competitive trait displacement. In correspondence, Laughlin *et al.* (2021) concluded that, on the global scale, root trait convergence is more often found in dry and cold climates, whereas the co-existence of a broad range of trait syndromes is prevailing in wet and warm climates. The authors explain their observation by the assumption that many trait-environment relationships may not, as usually assumed, function as trade-offs, but as uni-directional benefits. One consequence would be that, while at one end of an environmental gradient, only a certain extreme trait syndrome is beneficial, at the other end of the gradient, not only the opposite extreme trait syndrome could benefit the plant, but a variety of syndromes might function well. Applied to our elevational gradient, this would mean that a conservative fine root strategy is required under the increasingly unfavorable conditions at higher elevations causing high degrees of trait convergence. A broader range of trait syndromes can be beneficial at the lower sites, allowing for higher functional diversity. Interestingly, only elevation, but not CN_{soil} and P_{av}, were significant predictors of functional dispersion. This may suggest that not nutrient availability itself, but other soil properties that change with elevation, are acting as the environmental filters for species selection. Possible candidates are soil temperature, excess soil water and oxygen availability, and soil acidity and Aluminium concentrations.

4.5.5 Conclusion

Our study with 145 tropical tree species from 47 families shows that functional traits of absorptive fine roots vary from more acquisitive at lower elevations and more fertile sites to more conservative at higher elevations and more infertile sites. These trends were more evident for chemical than for diameter-related morphological traits, which might be linked to the recently proposed idea that different degrees of fungal collaboration allow both thin and thick roots to be acquisitive. However, further studies that also investigate fungal root partners are needed to test if the degree of root-fungus collaboration can explain the co-existence of fine roots with different diameters within communities. We found broad trait variation at all study sites, which in part is a consequence of small-scale soil heterogeneity and spatial niche segregation. For future research in this field, we recommend applying linear mixed models with random effects for species in addition to community-weighted means, because they allow inference about within-site variation and the explanatory power of species identity compared to environmental effects.

Chapter 5

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

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5.1 Abstract

The question whether the strategies of above- and belowground plant organs are coordinated is not fully answered. We aimed to determine the leading dimensions of tree trait variation for above- and belowground functional traits, and test whether they represent spectra of adaptation along environmental gradients in tropical Andean forests. In an unprecedented sampling effort, we measured functional traits and soil nutrient availability for individual trees from 52 species at three elevation levels between 1000 and 3000 m a.s.l.

We found remarkable aboveground–belowground coordination of traits related to the trade-off between resource acquisition and conservation, whereas traits related to root diameter formed an independent axis, confirming the recent collaboration gradient theory. Tree species' position along the acquisition–conservation axis of the trait space was highly associated with soil nitrogen availability. In conclusion, the combined analysis of above- and belowground functional traits can provide deeper insights into different strategies of coexisting species and explain small-scale patterns of community assembly in species-rich tropical forests.

Keywords: Ecuador, fine roots, intraspecific trait variability, microhabitats, plant economics spectrum, soil heterogeneity.

5.2 Introduction

Aboveground and belowground plant organs are functionally integrated through energy, matter and information fluxes as part of the plant's metabolism, and plants thereby link communities and ecosystem processes in the aboveground realm with the belowground compartment of the ecosystem (Porazinska *et al.*, 2003; Wardle *et al.*, 2004; A'Bear *et al.*, 2014). Yet, the question of how resource investment strategies of above- and belowground plant organs influence each other, remains largely unanswered. Investigating plant functional traits is a means to simplify the complexity of highly diverse ecosystems in studies of ecosystem functioning. They can be powerful predictors for plant performance (Poorter & Bongers, 2006), community assembly (Laughlin, 2014; Dantas de Paula *et al.*, 2021), plant-animal interactions (Schleuning *et al.*, 2020), ecosystem processes (Bardgett *et al.*, 2014), and community responses to global change (Suding *et al.*, 2008). A central question of trait-based ecology is, how functional traits are coordinated with each other and with environmental gradients (Westoby & Wright, 2006; Díaz *et al.*, 2016; Bruelheide *et al.*, 2018).

A seminal step forward in identifying general patterns of plant trait coordination was the description of the leaf economics spectrum (LES) (Wright *et al.*, 2004), a framework that contextualizes the coordination of leaf functional traits as trade-off between resource conservation and resource acquisition. Subsequent works integrated the LES, wood traits, plant height and seed mass into multi-dimensional spectra of worldwide plant functioning (Chave *et al.*, 2009; Díaz *et al.*, 2016). However, despite their major relevance for plant and ecosystem functioning, fine root traits have long been studied less than aboveground plant parts and their integration into generalizable trait spectra has proven more challenging (Weemstra *et al.*, 2016; Laliberté, 2017). A major step forward was the plant economics spectrum (PES, Reich, 2014), a comprehensive framework in which functional traits of plant roots, stems and leaves are subject to the same trade-off between a fast, acquisitive strategy and a slow, conservative strategy. 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 more often has pointed towards a multi-dimensional root trait spectrum that is at least partly decoupled from the aboveground PES (Kong *et al.*, 2014; Valverde-Barrantes *et al.*, 2015a; Kramer-Walter *et al.*, 2016; Liese *et al.*, 2017). 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 traits related to root diameter and the degree of reliance on mycorrhiza. Two recent contributions seeked to combine those concepts into multi-dimensional whole-plant trait spectra, reaching at 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 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 represented by their functional traits structure plant communities along environmental gradients through processes of environmental filtering and limiting similarity Tilman (1988); Díaz *et al.* (1998)]), which is why a plenitude of studies on plant trait variation along environmental gradients does exist (e.g., Freschet *et al.*, 2017; Bruelheide *et al.*, 2018). Nutrient availability is thought to be the key driver of the evolution of divergent strategies along the conservation-acquisition axis, with conservative strategies being an adaptation to nutrient scarcity and acquisitive strategies one to nutrient abundance (Reich, 2014). Both above- and belowground functional traits have been shown in many studies to vary with nutrient availability (Pérez-Ramos *et al.*, 2012; de la Riva *et al.*, 2018; Shen *et al.*, 2019). This pattern holds also for leaf traits of tropical rain forest tree species (Asner & Martin, 2016; Ding *et al.*, 2019; Martin *et al.*, 2020; Vleminckx *et al.*, 2021), but the association of root traits with soil fertility seems to be more complex (Lugli *et al.*, 2019; Vleminckx *et al.*, 2021), with their strength and direction highly being dependent on the environmental context, in particular the degree of N and P limitation (Cusack *et al.*, 2021).

Trait variation along environmental gradients can be observed on different aggregation levels, i.e., 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 due to its role in community assembly and ecosystem processes (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 aggregational scales; rather, differing or even reversed relationships of traits with environmental factors on the intra- versus the interspecific level can obscure overall trends (Laughlin *et al.*, 2017; Anderegg *et al.*, 2018; Dong *et al.*, 2020).

Specifically, inferring the existence of relationships on the individual level based on group-level associations constitutes a logical fallacy, the so-called ecological fallacy (Robinson, 1950; Subramanian *et al.*, 2009). It is therefore crucially important to be aware which level of aggregation is studied, and if possible, separate between within- and between-species relationships when describing trait associations with environmental gradients.

As different community assembly processes may operate on different spatial scales, trait-environment associations are often scale-dependent (Mokany & Roxburgh, 2010; Chalmandrier *et al.*, 2017; Saar *et al.*, 2017). Microhabitats within forest patches can harbor 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 has been explored in particular for tropical montane forests in rugged terrain (Inman-Narahari *et al.*, 2014; Werner & Homeier, 2015; Pierick *et al.*, 2021), where small-scale soil heterogeneity was found to contribute to the outstanding species diversity (Homeier *et al.*, 2010; Jones *et al.*, 2011).

We made a comprehensive sampling effort to measure soil nutrient availability in direct vicinity to more than 400 trees of 52 tree species distributed across 9 ha of tropical Andean forest at three elevation levels, and investigate its association with the tree's above- and belowground functional traits.

This study builds on our work in Homeier *et al.* (2021) where we investigated the variation of leaf functional traits of 52 tree species from three elevational levels in highly diverse tropical montane forests in the Andes. Here, we use the same leaf trait data and complement them with individual-level wood and fine root trait data as well as highly resolved data on nutrient availability in order to answer fundamental questions regarding aboveground-belowground trait coordination and trait-environment associations of tropical tree species. We address the following questions:

1. Which are the leading dimensions of trait variation, and are functional traits from fine roots, stems and leaves coordinated with each other? We investigate whether the observed trait coordination most closely 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 N and P availability on the intra- and interspecific level? We expect tree species with more acquisitive functional traits to grow at local habitats with higher nutrient availability, and vice versa.

5.3 Methods

5.3.1 Study area

The study was conducted in tropical montane forests on the eastern slope of the Andes in Southern Ecuador (Figure C.1). Sampling was conducted at three different elevation levels (1000 m, 2000 m and 3000 m a.s.l.) subsequently referred to as ‘sites’ (for their coordinates see Table C.1). The sites at 1000 and 3000 m are located in the Podocarpus National Park, while the 2000 m site lies in the adjacent San Francisco Reserve. The sites are arranged along a pronounced climatic gradient from 1000 m to 3000 m a.s.l., with mean annual temperatures decreasing from 20 °C to 9.5 °C, and annual precipitation increasing from 2000 mm 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 (Emck, 2007; Bendix *et al.*, 2008).

The study sites are characterized by relatively nutrient-poor soils on metamorphic schists and sandstones (1000, 2000 and 3000 m) or granodioritic rocks (1000 m) (Wolf *et al.*, 2011). There is a pronounced decrease in nutrient availability with increasing elevation and also from lower to upper slope positions in the rugged terrain, which is reflected in decreasing forest biomass and productivity along these gradients (Wilcke *et al.*, 2008a; Wolf *et al.*, 2011; Homeier & Leuschner, 2021). The studied forest types can be 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).

5.3.2 Study design

Sampling was conducted in three permanent 1 ha-plots located at 1000 m, 2000 m and 3000 m elevation. We selected 52 tree species in total (20 species each at 1000 m and 2000 m; 12 species at 3000 m, Table C.2) that fulfilled the criteria of a) being common enough to find enough replicates in the plots, and b) covering all major tree functional types including both pioneer and late-successional species, as well as both understory and canopy trees. The latter aspect was supported by taking trait data (specific leaf area, SLA and wood specific gravity, WSG) from previous studies (Báez & Homeier, 2018) into account. Except for one gymnosperm (*Podocarpus oleifolius* at 2000 m), all species were angiosperm trees. All selected species had a restricted elevational distribution, occurring only at one elevational level. Per species, we selected 6-11 replicate individuals (in total 433 trees) by random from the total number of individuals per species found in the plots.

5.3.3 Functional trait measurements

The leaf trait data used in this work are already published in Homeier & Leuschner (2021), and a more detailed description of the methods employed in measuring them is given there. In short, from each tree, one branch was collected in the crown top, and leaf area (LA), specific leaf area (SLA), leaf dry mass content (LDMC), leaf N, and leaf P concentrations were measured on 20 leaves per tree. Leaf thickness and leaf toughness were determined on three additional leaves.

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 (0-10 cm depth). After being collected in the field, the samples were stored in a fridge at 8 °C for no more than two 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 color and surface texture, root diameter, root elasticity, and presence of root hairs, as in McCormack *et al.* (2015), and Chapter 4).

Table 5.1: Trait names, abbreviations, and units. All root traits were measured on the absorptive fine roots.

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

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 a plexiglass tray filled with demineralized water and scanned with a Hewlett Packard Scanjet G4050 scanner at grey-scale and a resolution of 600 dpi. 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 in a next step weighed on an analytic 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 N content was measured with a CN elemental analyzer (Vario EL III, Hanau, Germany), and the P content by ICP analysis (Thermo Scientific iCAP 7000 ICP-OES, Thermo Fisher Scientific, Germany) after HNO_3 digestion of the ground material.

In addition to the leaf and fine root traits, we quantified wood specific gravity (WSG) for each studied tree by collecting a wood core (5 cm length, 5.15 mm diameter) with an increment corer (Haglöf, Sweden) at a stem height of 1.30 m. WSG was obtained by dividing core dry weight by core green volume. A list of all measured functional traits is provided in Table 5.1.

5.3.4 Soil chemical analyses

We measured the chemical properties of the mineral topsoil in close vicinity (distance $< 1\,\text{m}$ from stem) of each of the 433 trees sampled. Samples were taken 0–10 cm depth layer, dried at 40 °C at the field station and transported to Germany for laboratory analyses. Total carbon and nitrogen were measured by elemental analysis via thermal combustion in milled aliquots. Due to high soil acidity, all C was assumed to be organic carbon (SOC). Soil C/N ratios were calculated to estimate the speed of soil organic matter turnover and nutrient supply rate via mineralization. High soil C/N ratios indicate slow turnover of organic matter, resulting in low N availability to plants. Plant-available phosphorus was determined with the Olson method and measured in the $< 2\,\text{mm}$ soil fraction through extraction with 0.5 M $NaHCO_3$ and PO_4^{3-} measurement by continuous flow analysis.

5.3.5 Data analysis

All data analyses were conducted in R version 4.1.0 (R Core Team, 2021).

Aboveground-belowground trait relationships

We calculated three principal component analyses (PCA) with the species-level trait means, one including all 13 measured 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 standardized before running the PCA. Subsequently, the species scores on the first principal components of PCA_{leaf} and PCA_{root} were extracted. To test whether the main axes of root and analyzed for interaction leaf trait variation are coordinated, linear regression was applied.

Trait relationships with local soil nutrient availability

In order 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-group centering (van de Pol & Wright, 2009), which allows discriminating between within-species and between-species effects. 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 standardized, except for WSG, which was not log-transformed. The log transformations were done to address heteroscedasticity and right-skewed trait distributions, while the centering and scaling was done to be able to compare parameter estimates between models. We also centered and scaled both predictors, and additionally log-transformed Olsen P because they were highly right-skewed. The models were fitted in a hierarchical Bayesian framework using R package `brms` V. 2.15.0 (Bürkner, 2017). For details about the model fitting, prior choice, and convergence diagnostics see Methods C.1.

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 $\mathrm{PCA}_{\mathrm{all}}$, $\mathrm{PCA}_{\mathrm{leaf}}$ and $\mathrm{PCA}_{\mathrm{root}}$ in dependency of the mean N and P availabilities measured directly adjacent to the tree individuals of that species.

5.4 Results

5.4.1 Dimensions of the plant economics space

In the principal component analysis performed with all traits ($\mathrm{PCA}_{\mathrm{all}}$, Fig. 5.1), leaf thickness, leaf toughness, WSG, LDMC, and RTD were highly positively associated with the first axis (45 % 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 (19.8 % of variance explained). The species from the three elevational levels did not separate into distinct clusters but formed 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* from 2000 m and *Siparuna muricata* from 3000 m with much more negative scores on PC1 than all other taxa at these sites. In the leaf trait PCA ($\mathrm{PCA}_{\mathrm{leaf}}$, Fig. 5.2 A), the first axis explained 60.7 % and the second axis 14.9 % of variation. Leaf area, SLA, foliar P and foliar N were positively, and leaf toughness, leaf thickness and LDMC, negatively associated with the first axis. Like in $\mathrm{PCA}_{\mathrm{all}}$, there was only a weak differentiation between the species from the three sites, with taxa from 2000 m and 3000 m having lower and species from 1000 m higher values on PC1. In the PCA with root traits

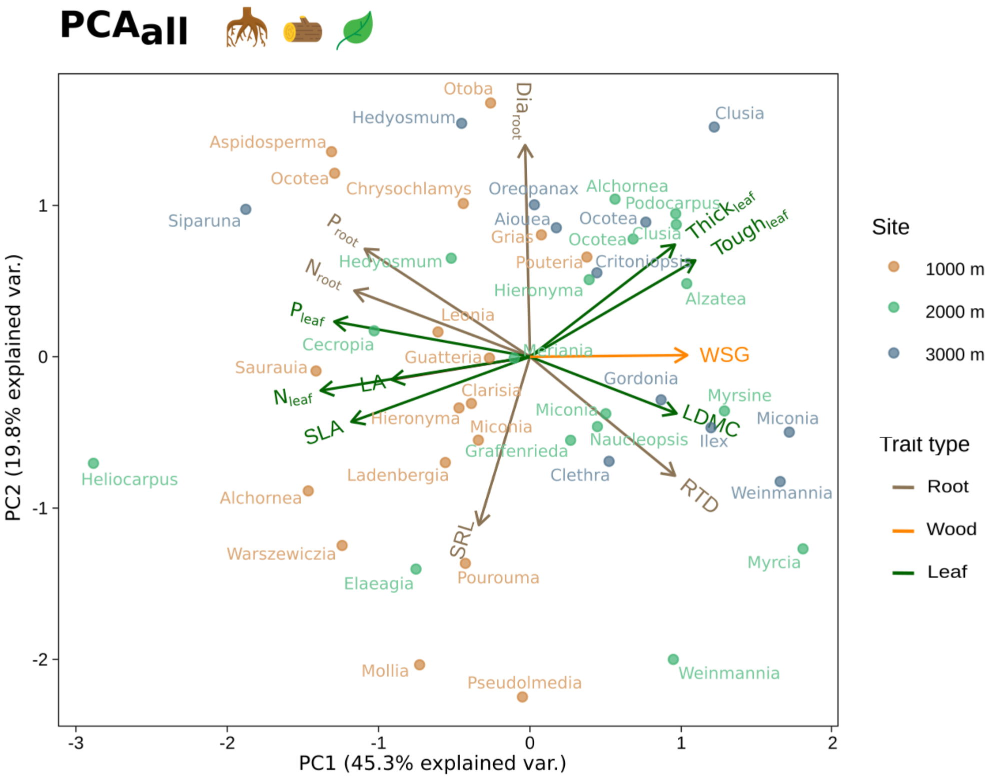


Figure 5.1: Principal component analysis of root, stem and leaf functional traits of 52 tree species from 3 elevational levels. For abbreviations of functional traits, please consult Table 5.1.

(PCA_{root}, Fig. 5.2 B), 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. It 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 leaf economics spectrum 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 significant positive relationship between axes representing the leaf and root economics spectrum ($p = 0.003$, $R^2 = 0.18$, Fig. 5.2 C).

5.4.2 Trait associations with nutrient availability

Soil C/N ratio measured in direct vicinity to the 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

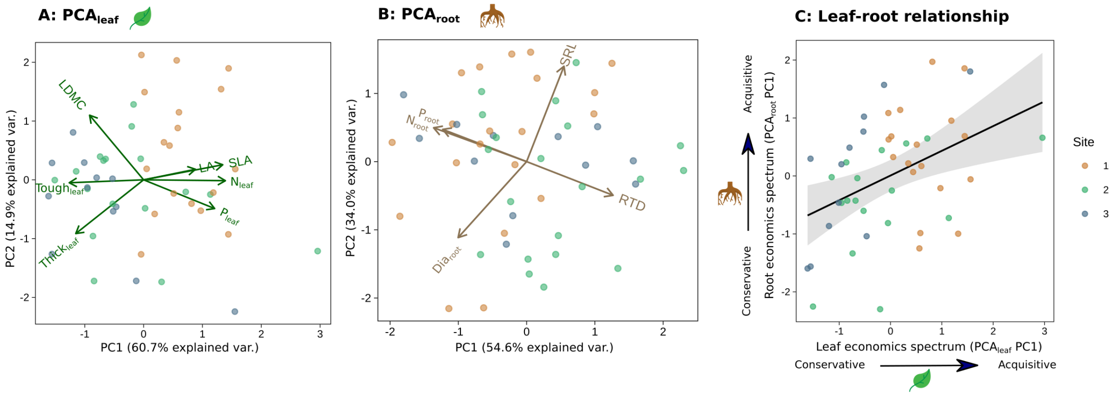


Figure 5.2: Coordination of above- and belowground functional trait dimensions. A) Principal component analysis of leaf functional traits (PCA$_{\text{leaf}}$). B) Principal component analysis of root functional traits (PCA$_{\text{root}}$). C) Relationship between the respective first principal components (PC) from PCA$_{\text{leaf}}$ and PCA$_{\text{root}}$. PCA$_{\text{root}}$PC1 was multiplied with -1 for consistency. The trend line shows the predictions from a linear regression with 95 % confidence intervals ($p = 0.003$, $R^2 = 0.18$). For abbreviations of functional traits, please consult Table 5.1.

14.8) than at 2000 m (9.8–18.9, mean 16.1), revealing no clear elevational trend (Fig. C.2). Topsoil Olsen-P showed highly right-skewed distributions at all three sites, with lower values at 1000 and 2000 m (means around 3 mg kg^{-1}, maxima of 11.5 and 5.9 mg kg^{-1}1, respectively) than at 3000 m (mean 19.1 mg kg^{-1}, maximum 28.4 mg kg^{-1}, Fig. C.2). Soil C/N ratio and Olsen-P were not significantly correlated across the sampling locations ($\rho = -0.15$, Fig. C.3).

Most measured traits, i.e. all leaf traits and RTD and WSG, were credibly associated with soil C/N ratio on the interspecific, but not on the intraspecific level (Fig. 5.3, Table C.3). RTD, DMC, leaf toughness, leaf thickness and WSG increased with soil C/N ratio, whereas leaf area, SLA, foliar N and foliar P decreased with soil C/N ratio. SRL was not associated with soil C/N ratio between species, but declined with increasing C/N at the intraspecific level. Root N and P concentrations declined with increasing soil C/N ratio 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 ratio neither on the intraspecific nor the interspecific level. While all of our models of the 13 traits in dependency of soil N availability had very high explanative power (conditional R^2 values ranging from 66 % for RTD to 95 % for leaf area, Table C.5), a large proportion of the variance in the traits was explained by random variation between experimental units, most importantly by the random species in-

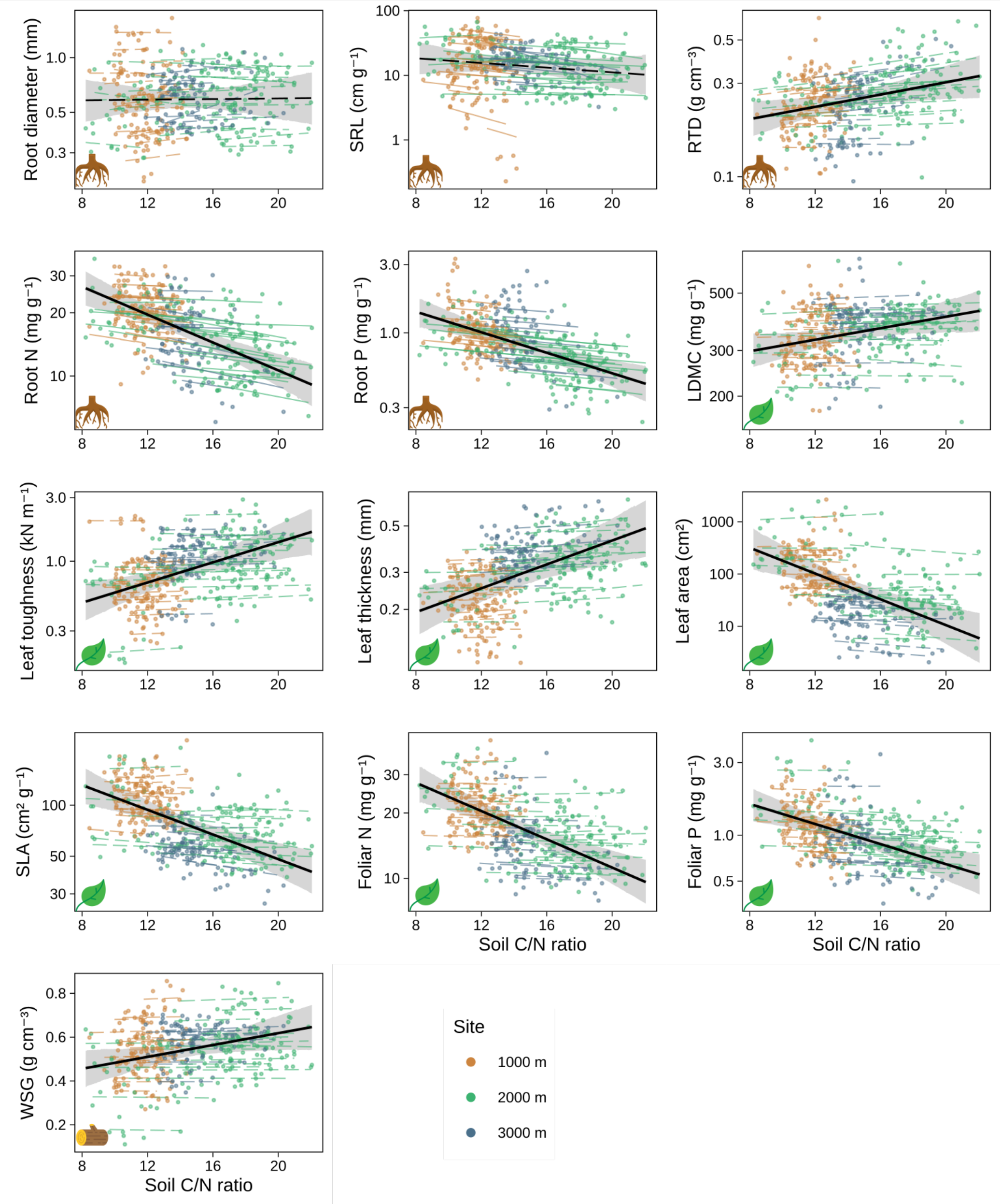


Figure 5.3: Functional traits in dependency of soil C/N ratio. Shown are the data in combination with predictions from mixed models with within-group centering. Each point represents one individual tree. The thin, colorful lines show intraspecific model predictions for the 52 tree species; the black 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. For abbreviations of functional traits, please consult Table 5.1.

tercepts, 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 (both 34 %), and the lowest in the model for root diameter (1 %, Table C.5).

In contrast to the pronounced responses of most traits to soil C/N ratio, there were almost no relationships of traits with Olsen-P in the topsoil on the inter- or intraspecific level (Fig. 5.4, Table C.4). The only exceptions were a positive interspecific trend of leaf thickness, a negative interspecific trend of leaf area, and a positive intraspecific trend of SRL with increasing available P. As in the models with soil C/N ratio, the standard deviations of the random intercepts for species were high in all models, while the random variability between plots and random species-specific differences in slopes were negligible (Table C.4). The variance explained by the whole model was very similar to the models with C/N ratio, 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 Olsen-P: 0.02, Table C.5). The largest marginal R^2 values were found for leaf area and leaf thickness (both 11 %).

5.4.3 Association of the species' position in the trait space with nutrient availability

We found a significant positive relationship between the species scores on the first axis of PCA_{all}, representing the plant economics spectrum (higher values interpretable as conservative and lower values as acquisitive), and the average soil C/N ratio measured in vicinity of the trees ($p < 0.001$, $R^2 = 0.54$, Fig. 5.5). 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 the species related to low C/N 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*, *Elaeagia mollis*, and *Meriania franciscana*) situated in a range largely filled by species from 1000 m. In addition, *Heliocarpus americanus* and *Siparuna muricata* from 2000 m and 3000 m represented striking outliers, with scores on PC1 of PCA_{all} being being unusually low for their average soil C/N ratio compared to the overall trend. We did not find significant relationships of PC2 of PCA_{all} with soil C/N ratio, or of any of the axes with topsoil Olsen-P.

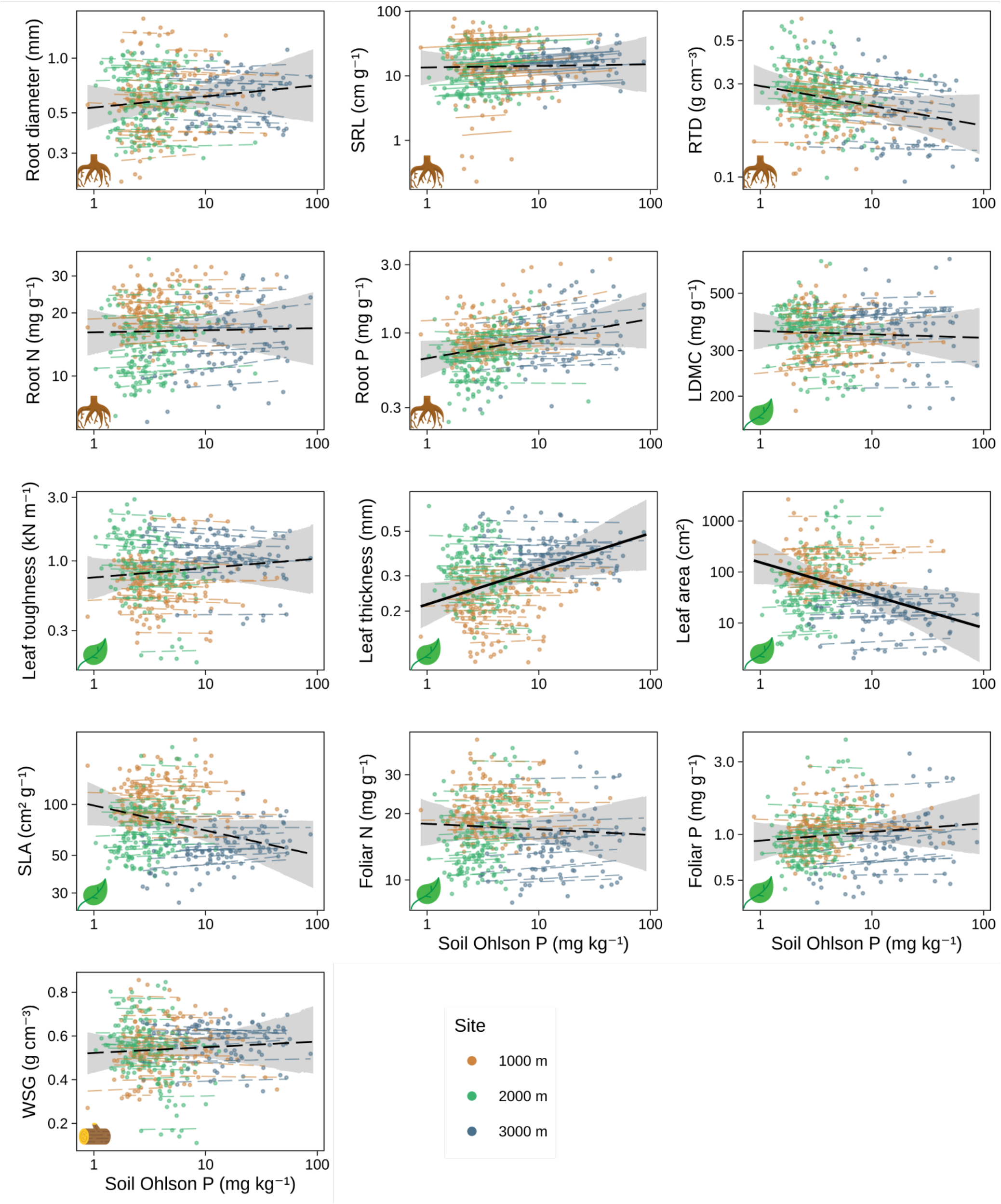


Figure 5.4: Functional traits in dependency of soil Olsen P. Shown are the data in combination with predictions from mixed models with within-group centering. Each point represents one individual tree. The thin, colorful lines show intraspecific model predictions for the 52 tree species; the black lines 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. For abbreviations of functional traits, please consult Table 5.1.

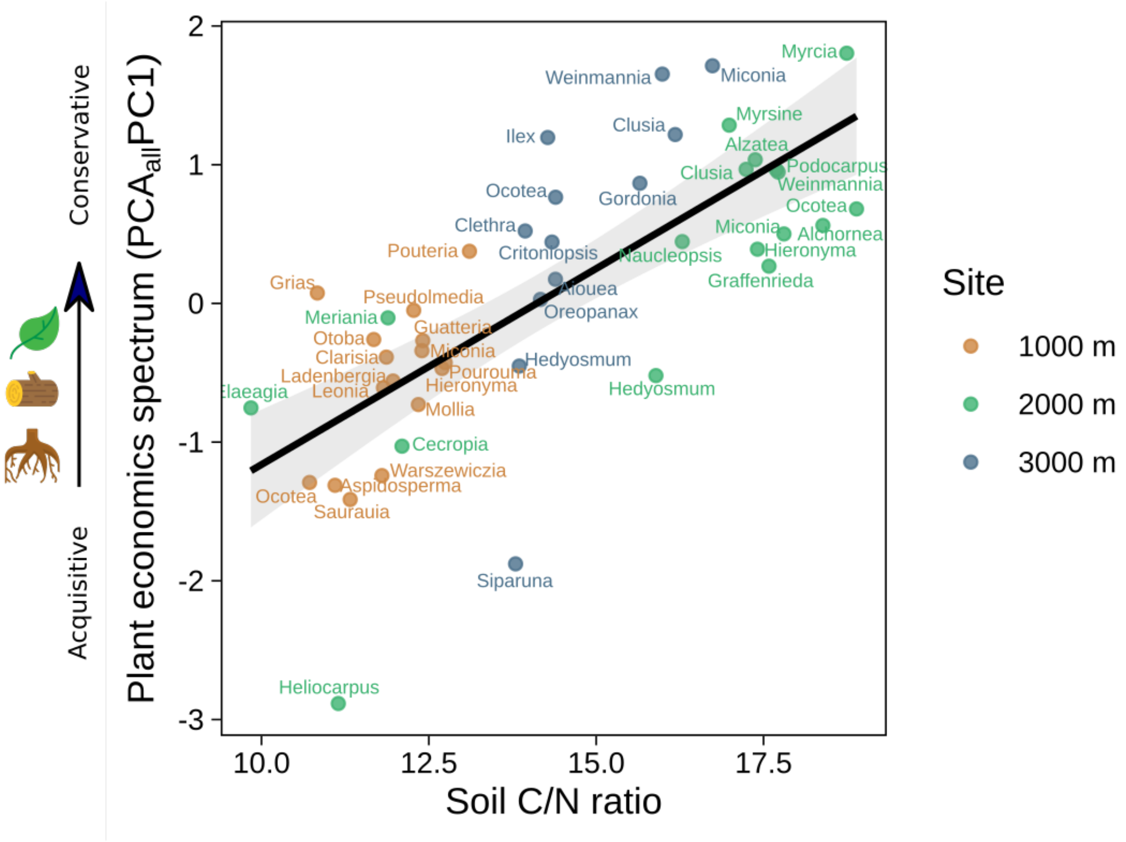


Figure 5.5: Species position in the plant economics space (PCA$_{\text{all}}$PC1) in dependency of mean soil C/N ratio in vicinity of all individuals of the species. The line shows predictions from a linear regression with 95 % confidence intervals ($p < 0.001$, $R^2 = 0.54$)

5.5 Discussion

5.5.1 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 root tissue density (RTD) of 52 tree species in tropical montane forests were coordinated. Root and leaf nutrient concentrations, leaf area and specific leaf area (SLA) were positively correlated with each other, and negatively correlated with RTD, WSG, leaf dry matter content (LDMC), and leaf thickness and toughness. Not only did these traits constitute the first axis of variation when all traits were included in one joint ordination, they also formed the most influential first axes in in separate ordinations for leaf and root traits only. Moreover, the main axes of variation for the leaf and root trait spaces were significantly associated with each other. We interpret thin, large and soft leaves, high leaf and fine root nutrient concentrations, and low tissue densities as indicative of an acquisitive, and a resource use strategy, while a conservative strategy is characterized by opposite properties (Wright *et al.*, 2004; Reich, 2014; Weemstra *et al.*, 2016). The trade-off between resource acquisition and conservation results from the constraint that high investment into 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 into fast growth, high resource acquisition rates and, as a consequence, fast resource return comes at the cost of more vulnerable tissue and shorter tissue life spans (Wright *et al.*, 2004; Reich, 2014; Weemstra *et al.*, 2016). Whether these trade-offs hold for all organs of a plant and therefore lead to trait coordination between leaves, stem and roots is currently still debated.

Our findings represent robust support for the theory that leaves, stem and roots are subject to the same resource acquisition-conservation trade-off, and that traits related to resource economics of all plant organs are correlated with each other (plant economics spectrum, PES, Reich, 2014). Reich (2014) reasons that this is the case because an organ with traits associated with an acquisitive strategy is only advantageous for a plant when its other organs follow the same strategy, as such a strategy is only viable when necessary resources can be supplied fast enough by the other organs. There is broad support for 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., Freschet *et al.*, 2010; Pérez-Ramos *et al.*, 2012; de la Riva *et al.*, 2018; Hu *et al.*, 2019; Shen *et al.*, 2019; Marañón *et al.*, 2020). In a recent review, Weigelt *et al.* (2021) concluded that leaf and root traits related to the resource economics trade-off are generally associated with each other and form an integrated axis from slow to fast resource return. However, a recent analysis based on a global trait database concluded that leaf, root and stem traits were decoupled from each other and in fact form separate dimensions of trait covariation (Carmona *et al.*, 2021). In support, there are other studies reporting a lack of association between aboveground and belowground traits of woody plants (e.g., Valverde-Barrantes *et al.*, 2015a; Burton *et al.*, 2020; Vleminckx *et al.*, 2021). Furthermore, Baraloto *et al.* (2010a); Fortunel *et al.* (2012) and Vleminckx *et al.* (2021) all concluded that the wood traits were decoupled from the leaf economics spectrum in neotropical tree species.

The reasons for these contrasting findings may be of ecological or methodological nature. Comparing different scales, organism groups and environmental contexts can lead to different results concerning trait correlation (Messier *et al.*, 2017). In addition, the most widely used data analysis tools to explore the dimensionality of trait spaces are principal component analysis (PCA) and other ordination methods, which can be problematic, because the results are highly susceptible to the number and correlation structure of the input variables. The outcome of analyses might change dramatically, if certain variables were included or removed. Importantly, as the scores on each axis are computed as a linear combination of all variables in a dataset, comparisons between PCA results based on different sets of input variables are highly questionable.

5.5.2 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) and Liese *et al.* (2017) found that, while root nutrient concentrations and root tissue density were coordinated with traits of the leaf economics spectrum (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. Accordingly, 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 and thereby "outsourcing" part of the costs of soil proliferation and nutrient acquisition to the fungal partners.

This theory is supported by some evidence supporting the assumption 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; Wang *et al.*, 2018; Liu *et al.*, 2019). 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. However, this multi-dimensional perception of the fine root trait space needs validation against empirical data that cover not only root morphology, but also mycorrhizal colonization and fine root functioning, which are still rarely measured in multi-species samples (Freschet *et al.*, 2021a).

Our data support the plant economics spectrum in the form proposed by Weigelt *et al.* (2021), where morphology and nutrient concentrations of leaves and fine roots form a leading dimension of trait covariation driven by the acquisition-conservation trade-off, and traits related to fine root diameter form a separate axis of mycorrhizal collaboration, driven by a trade-off between an outsourcing strategy and a “do-it-yourself” strategy.

5.5.3 Small-scale N availability drives the plant economics spectrum

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 specific root length (SRL) with soil C/N ratio. 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 $\mathrm{PCA_{all}}$). The most likely explanation why conservative strategies are more successful when nitrogen is scarce, and acquisitive strategies are more advantageous upon higher N availability, is that resource conservation is required to survive under infertile conditions, whereas increased competition under fertile conditions makes it advantageous to grow faster than competitors and thus pursue an acquisitive strategy (Reich, 2014). 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 plant economics spectrum.

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 (Homeier *et al.*, 2010; Werner & Homeier, 2015; Pierick *et al.*, 2021). 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 fine root traits (Pierick *et al.*, 2021). The recent study conducted at even finer spatial resolution of soil chemical predictor variables (< 1 m to about 5 m) highlights the relevance small-scale environmental variation for community assembly and trait spectra in topographically complex mountain landscapes.

It is well documented for many biomes that functional traits of communities typically are shifting from more conservative to more acquisitive with increasing N availability (e.g., Pérez-Ramos *et al.*, 2012; Kramer-Walter *et al.*, 2016; de la Riva *et al.*, 2018; Ding *et al.*, 2020). The dependence of aboveground plant functional traits on soil fertility has been demonstrated repeatedly for tropical forests (Asner & Martin, 2016; Ding *et al.*, 2019; Vleminckx *et al.*, 2021), but there is a lack of data on fine root traits for tropical tree species (Cusack *et al.*, 2021). According to Reich (2014), the most likely explanation why conservative strategies are more successful when nitrogen is scarce is that resource conservation is required to enhance survival under infertile conditions. In contrast, acquisitive strategies are assumed to be more successful when nitrogen is more readily available because increased competition under fertile conditions makes it advantageous for a plant to be able to grow faster than its competitors.

We found almost no credible trait associations with available P, 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 (Lugli *et al.*, 2019; Cusack *et al.*, 2021; 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). Therefore, N seems to play a more relevant role than P in structuring the functional composition of tree communities in our study area, which is key to understanding and modeling tropical montane forest vegetation.

Intraspecific trait variation along gradients of nutrient availability did not play a significant role for the majority of traits in our species sample, contrary to our expectation. The only credible intraspecific trait trends observed were negative associations of SRL, root N and root P with soil C/N ratio, and positive associations of SRL with Olsen-P availability. Strikingly, these are all root traits. Roots can be highly plastic both in terms of tissue element contents 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 in dependence on the environment, or from species-specific differences in the direction and magnitude 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. This agrees with the finding that the interspecific component was consistently larger than the intraspecific component of leaf trait variation in our study area (Homeier & Leuschner, 2021). Yet, it contradicts 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 in the study were larger. We judge it plausible that the two factors leading to intraspecific trait variation, genetic adaptation and phenotypic plasticity, are mainly active on larger spatial scales and across larger environmental variation than covered in this study. If valid, this would allow the conclusion that interspecific trait variation along soil fertility gradients seems for most traits to act on a smaller spatial scale than intraspecific trait variation.

Trait relationships with the environment might differ between interspecific and the intraspecific levels, because different underlying processes, i.e. of aggregation selection over evolutionary times vs. within-species adaptation or acclimation and phenotypic plasticity, are causing them (Clark *et al.*, 2011). Furthermore, the strength and direction of intraspecific relationships can vary between species (Anderegg *et al.*, 2018; Weemstra *et al.*, 2020). Both of these phenomena can weaken or reverse patterns of trait association, when inter- and intraspecific effects are not separated from each other (Laughlin *et al.*, 2017; Anderegg *et al.*, 2018; Dong *et al.*, 2020). Within-group centering is a technique that solves this problem elegantly within a mixed-model framework (van de Pol & Wright, 2009), as done here.

5.5.4 Adaptation to edaphic microhabitats promotes coexistence

We found evidence for highly variable soil conditions within plots, and a broad overlap of N and P availability between the three elevational levels. Besides, tree species from different sites were not on average functionally distinct, but occupied largely overlapping areas in the trait space. Conversely, species coexisting within the same plot in close proximity 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 in direct vicinity to 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). Moreover, the position of the tree species within the trait space and their average local N availability may be indicative of the species' role within the community. For example, *Heliocarpus americanus*, *Cecropia angustifolia*, *Hedyosmum goudotianum* (all from 2000 m), *Siparuna muricata*, and *Hedyosmum purpurascens* (both from 3000 m), all fast-growing pioneer species, have more acquisitive traits and on average grow at more N-rich spots than the other species from the same elevational level.

This highlights the importance of paying more attention to small-scale environmental heterogeneity in gradient studies, which usually consider plot or community level means of environmental variables. The approach used here, that measured edaphic predictor variables on the scale of individual trees, performed well in explaining trait variation and provided valuable insights into the community assembly of tree species with diverse functional strategies. Therefore, we encourage field ecologists and modelers in all ecosystems, but especially tropical montane forests, to take small-scale environmental heterogeneity into account in their experimental designs, models, and interpretations of data.

5.5.5 Conclusions

Our investigation of wood, leaf and fine root traits in a species-rich tropical montane forest 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 plots overlaid altitudinal differences and was the most powerful predictor of the species' functional strategy. These findings highlight the advantages of measuring highly resolved environmental predictors 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.

Chapter 6

Synthesis

This chapter summarizes the results found in Chapters 3-5, puts them in perspective to each other and the current state of knowledge, and draws shared conclusions from the unified findings of these chapters. Furthermore, implications and directions for future research projects are presented.

6.1 Leading dimensions of the fine root trait space

The analyses of coordination of root traits in Chapter 3 and 5 both confirm the existence of two main independent dimensions of root trait variation: Firstly, an axis of root nutrient concentrations in negative association with root tissue density (RTD), and secondly an axis where root diameter is negatively correlated with root branching intensity (RBI) and specific root length (SRL) (Fig. 6.1 a). The first axis can be interpreted as a representation of the acquisition–conservation or fast–slow trade-off that constitutes the original root economics spectrum (Kong *et al.*, 2014; Kramer-Walter *et al.*, 2016; Roumet *et al.*, 2016; Weemstra *et al.*, 2016). The second axis can be interpreted as the fungal collaboration gradient, representing a trade-off between outsourcing most of the acquisitive functions to mycorrhizal fungi and pursuing a Do-It-Yourself strategy, the former of which favoring thicker and the latter thinner and highly branched roots (Bergmann *et al.*, 2020; Carmona *et al.*, 2021; Weigelt *et al.*, 2021). However, as no data on the degree of mycorrhizal colonization were measured for this thesis, this interpretation remains speculative. Interestingly, these patterns emerged both in Chapter 3, which only compared species within lower montane forests at roughly 2000 m a.s.l., and in Chapter 5, which covered species from three elevational levels spanning an elevational gradient of 2000 m. This implies that within tropical montane forests, the same trade-offs shape the patterns of tree root trait coordination at different spatial scales. The consistency of the two-dimensional root economics spectrum throughout the chapters of this work provides further support for the emergent theory of the collaboration gradient (Bergmann *et al.*, 2020).

6.2 Aboveground-belowground functional coordination

Chapter 5 showed that tree species with acquisitive root traits also had a high probability of having acquisitive leaf and wood traits, and vice versa with conservative traits (Fig. 6.1 b). There was no such relationship for diameter-related root traits. This partly confirms the seminal framework of the plant economics spectrum (Freschet *et al.*, 2010; Reich, 2014), which states that functional traits related to the acquisition-conservation trade-off in roots, leaves and stems should be correlated with each other and form a single axis of variation. The reasoning behind this is that plants that do not have a consistent strategy within the fast–slow spectrum for all their organs have a reduced fitness due to biophysical constraints (Reich, 2014).

Similar cases of (partly) coordinated above- and belowground functional traits have been reported among others by Freschet *et al.* (2010), Pérez-Ramos *et al.* (2012), Valverde-Barrantes *et al.* (2015a), Kramer-Walter *et al.* (2016), Liese *et al.* (2017) and de la Riva *et al.* (2018). However, while many of these authors acknowledged that not all root traits are aligned with the whole plant economics spectrum (see also Weemstra *et al.* (2016) and Laliberté (2017) for reviews), it was not until the recent introduction of the collaboration gradient by Bergmann *et al.* (2020), that unified theories of a multidimensional plant economics spectrum with a separate dimension for diameter-related root traits, emerged (Carmona *et al.*, 2021; Weigelt *et al.*, 2021). The framework by Carmona *et al.* (2021) states that the two orthogonal dimensions of root trait variation (the fast–slow axis and the collaboration axis) are both independent from the axes of aboveground trait variation. Contrarily, Weigelt *et al.* (2021) propose that there is a shared axis of variation for leaf and root traits that are related to resource acquisition, and an independent collaboration axis encompassing diameter-related root traits. The results in Chapter 5 are a powerful argument for the theory of Weigelt *et al.* (2021), and contradict the view of Carmona *et al.* (2021). In summary, the results in this work provide ample support for the view that leaf, wood and root strategies related to the acquisition–conservation trade-off are coordinated.

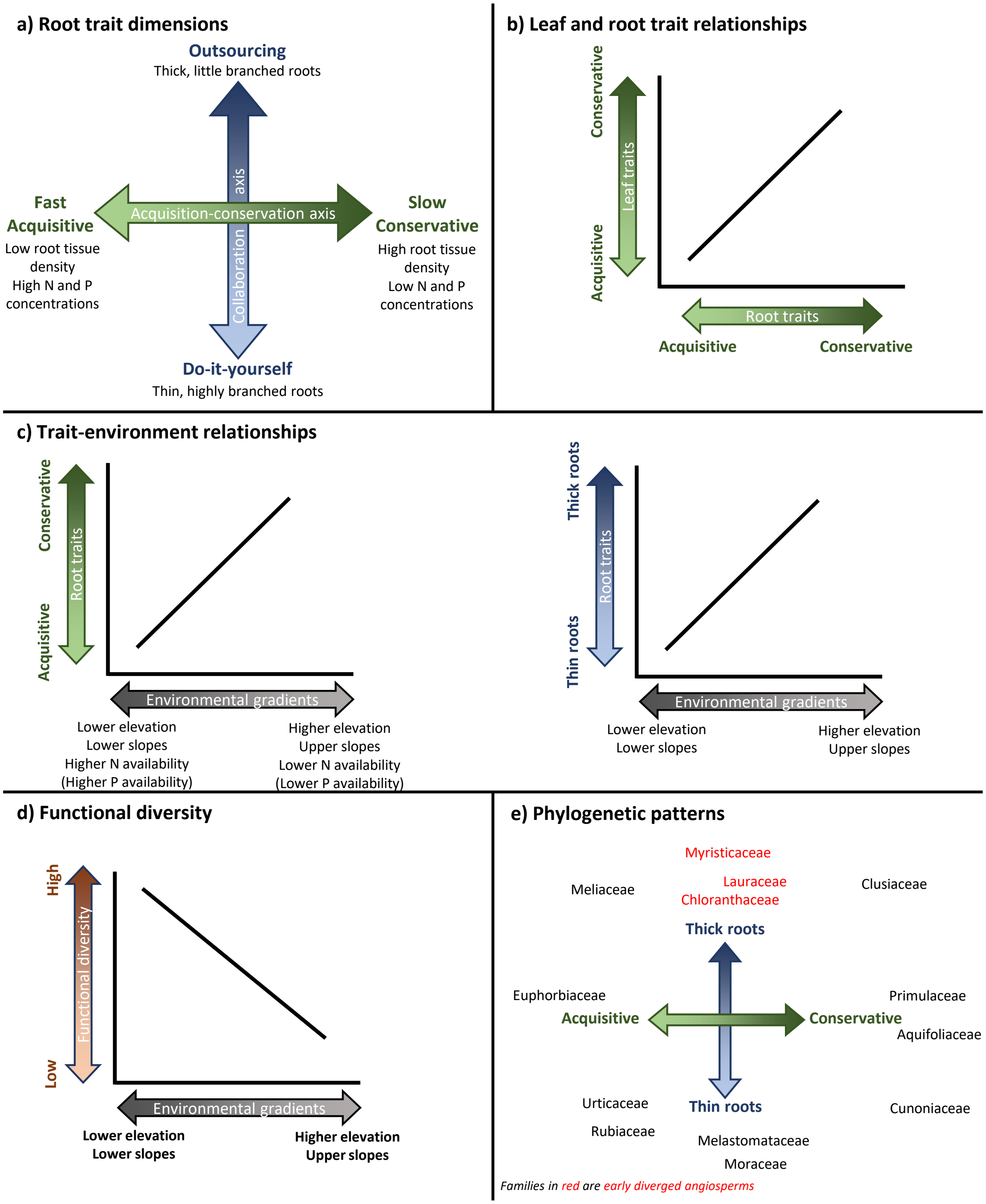


Figure 6.1: Visual summary of the main findings of this thesis.

6.3 Fine root trait variation along environmental gradients

The results from Chapters 3, 4 and 5 concordantly revealed that functional traits of roots varied along gradients of elevation, topography and soil fertility (Fig. 6.1 c). However, which traits showed these patterns depended on the spatial scale, type of gradient (indirect gradient or resource gradient) and the level of aggregation of the analysis (intraspecific, species, or community level). The root functional traits belonging to the acquisition–conservation axis of trait variation (RTD, N_{root}, P_{root}) showed more consistent patterns than those belonging to the collaboration axis (d_{root}, SRL, RBI, AFRF). The observational data from Chapters 3, 4 and 5 indicate roots to be more acquisitive at lower elevations, lower slope positions, and higher nutrient availability, and more conservative at the opposite ends of these gradients. This confirms the predictions by the plant economics spectrum theory that conservative resource use strategies are an adaptation to nutrient scarcity, and acquisitive strategies are an adaptation to nutrient abundance (Reich, 2014). Similar results of root functional trait syndromes changing from acquisitive to conservative with decreasing nutrient availability have been demonstrated e.g. by Pérez-Ramos *et al.* (2012), Kramer-Walter *et al.* (2016), de la Riva *et al.* (2018), Shen *et al.* (2019) and Fort & Freschet (2020).

There is a discrepancy between the results in Chapters 4 and 5 concerning the question whether root traits vary along gradients of N and P availability. Using the highly resolved soil data in Chapter 5, the functional traits were only associated with N availability and showed no trend along P availability, but with the plot-level soil data in Chapter 4, root traits related to the acquisition-conservation trade-off depended both on N and P availability. This can either be attributed to the fact that available P was measured with two different methodologies (resin-exchangeable P in Chapter 4, Olsen P in Chapter 5), or to the different spatial resolution of the environmental predictors. Considering that the results on P availability along the elevational gradient differed greatly between the two chapters (highest P availability at 2000 m in Chapter 4, but at 3000 m in Chapter 5), the first of those two explanations seems more likely. From this, it can be concluded that resin-exchangeable P is presumably a more adequate predictor of root functional traits than Olsen P, and that trends of root traits related to the acquisition-conservation axis along P availability would have maybe been found as well in Chapter 5 if resin-exchangeable P instead of Olsen P would have been measured.

Functional traits related to the collaboration axis of root trait variation were not associated with gradients of N and P availability in almost all cases, but with elevation and topography. Roots at higher elevations and upper slope positions tended to be thicker and less branched than at lower elevations and lower slope positions (Fig. 6.1 c). This is intriguing, because in contrast to the acquisition-conservation axis, there is no consistent evidence or theoretical framework so far on how and why the collaboration axis of root trait variation is associated with environmental gradients (Bergmann *et al.*, 2020; Weigelt *et al.*, 2021). Alternatively, instead of interpreting specific root length (SRL) and root diameter as the collaboration axis, they can also be viewed as part of the acquisition-conservation gradient (McCormack *et al.*, 2013; Roumet *et al.*, 2016), which would explain their trends along the topographic and elevational gradient, but not the absence of association with nitrogen availability. Both topography and elevation are indirect gradients (Garnier *et al.*, 2016) along which several edaphic, hydrologic and (micro-)climatic factors co-vary. Without manipulative experiments or larger observational datasets that cover more naturally occurring combinations of confounding covariates, it will be impossible to disentangle the causal relationships behind these patterns.

The trait associations with environmental gradients described above were observable on the community or interspecific level, while on the intraspecific level, trait–environment associations were mostly absent. This supports the conclusion that the community-level trait changes along environmental gradients observed in Chapters 3 and 4 are driven by species turnover between communities induced by environmental filtering, and not by intraspecific trait variation.

Both in Chapter 3 and 4, it became apparent that there was a large amount of within-community root trait variation, and that the differences between communities explained only minor proportions of the overall trait variance compared to differences between species. This lead to the assumption that species with diverse belowground strategies can coexist within communities, which could be verified in Chapter 5. There, we could show that species have preferences for different edaphic microhabitats and are adapted to them with matching trait syndromes on the acquisition-conservation axis. One of the most astonishing and relevant outcomes of this work is the high degree of interspecific root trait coordination with nitrogen availability on the local scale and individual level in Chapter 5. In combination, all of these findings highlight that small-scale edaphic heterogeneity and adaptations of tree species to different microhabitats are essential to the diversity and functional composition of tropical montane forests.

6.4 Functional diversity along environmental gradients

Functional diversity of root traits decreased from lower to upper slopes, and from lower to higher elevations (Chapters 3 and 4). Presumably, this is the case because the conditions at upper slopes and higher elevations are harsher, more nutrient limited, and less beneficial for plant growth, which leads to stronger environmental filtering (Leuschner *et al.*, 2007; Homeier *et al.*, 2010; Werner & Homeier, 2015). This allows only for a reduced set of viable trait combinations and causes trait convergence towards conservative strategies. Under the more beneficial conditions at lower elevations and lower slopes, trees with several belowground strategies can coexist successfully. These findings coincide with similar evidence for leaf functional diversity by Mason *et al.* (2012), Liu *et al.* (2014), Spasojevic *et al.* (2014), and Ding *et al.* (2019), but are novel for roots.

6.5 Phylogenetic conservation of root traits

Both morphological and chemical root functional traits had high phylogenetic signal (Chapter 3 and 4). In Chapter 3, phylogeny was the most important component in explaining trait variation, exceeding phylogenetically independent species effects and environmental factors. Also in Chapter 5, more closely related species tended to have more similar root traits. The fact that phylogeny played such an important role for all measured root traits, morphological and chemical, confirms observations by Valverde-Barrantes *et al.* (2015a), Liese *et al.* (2017) and Valverde-Barrantes *et al.* (2017). This contradicts statements by Kong *et al.* (2014), Wang *et al.* (2018), Liu *et al.* (2019) and Fort & Freschet (2020), who assumed that only root diameter and related morphological root traits are highly phylogenetically conserved, whereas chemical traits (and partly RTD) tend to be less conserved and to respond more plastically to the environment.

Several well-represented plant families had characteristic root trait syndromes throughout all the datasets analyzed in this thesis. A schematic figure showing their positioning within the root trait space is given in Fig. 6.1 e. Three of the typically thick-rooted families, Myristicaceae, Chloranthaceae and Lauraceae, are early diverged angiosperms (magnoliid clade and close relatives). It has been shown repeatedly in the literature that older angiosperm taxa on average have larger root diameters (Chen *et al.*, 2013; Comas *et al.*, 2014; Valverde-Barrantes *et al.*, 2015a;

Ma *et al.*, 2018). The fine roots of the first angiosperms are assumed to have been thick and highly reliant on arbuscular mycorrhizal fungi (Chen *et al.*, 2013; Bardgett *et al.*, 2014; Ma *et al.*, 2018). Thinner, more branched roots and other types of mycorrhizal associations evolved presumably during the angiosperm radiation as adaptations to a changing climate (Chen *et al.*, 2013; Bardgett *et al.*, 2014; Ma *et al.*, 2018). As the results of this work confirm, a legacy of this evolutionary history is still visible in the thick fine roots of extant magnoliid tree species. However, with Meliaceae and Clusiaceae, two later-diverged angiosperm families had similarly high fine root diameters as the early diverged angiosperms. This is probably a result of convergent evolution, and shows that the large angiosperm clades can contain plant groups with very different belowground strategies.

6.6 Implications

The root functional traits featured in this thesis are closely associated with root decomposition, respiration, growth rates, life spans and resource uptake rates (Comas *et al.*, 2002; McCormack *et al.*, 2013; Roumet *et al.*, 2016; See *et al.*, 2019; Freschet *et al.*, 2021b). They are furthermore relevant for a complex network of belowground interactions, because they can impact root–root competition (Mommer *et al.*, 2016), root herbivory both directly and via their relationships with defensive secondary compounds (Xia *et al.*, 2021), and the microbial communities of the rhizosphere via their relationship with exudation (Wen *et al.*, 2019; Spitzer *et al.*, 2021; Sun *et al.*, 2021; Williams *et al.*, 2021). In other words, they are both response and effect traits. Accordingly, the observed trait-environment associations imply that many of these plant functions and ecosystem processes also vary along the environmental gradients. One likely example of a potential effect of root traits in the study area is the impact of fine root litter quality on decomposition and soil fertility. In analogy to leaf litter (Werner & Homeier, 2015), the poor fine root litter quality at less fertile sites, which is in parts a result of high root tissue densities and low root nitrogen concentrations (i.e., a conservative strategy that represents an adaptation to low nutrient availability), could have a feedback effect on decomposition and thus reinforce the low soil fertility (Werner & Homeier, 2015).

The robust support for the existence of an axis of root trait covariation related to a growth–survival trade-off, and its strong association with nutrient availability and aboveground traits, highlights the root economics spectrum theory as a framework that is simplified, but of great predictive value for plant functioning and community assembly along environmental gradients. The work by Dantas de Paula *et al.* (2021) is an example from the study area that demonstrates how functional traits can be successfully integrated into dynamic vegetation models to improve the predictions of ecosystem functioning along gradients of nutrient availability. However, one has to stay aware that dimensionality reduction of the trait space might be a useful simplification in some applications, but should not be extrapolated universally. For example, the findings from this work demonstrate that trait–environment associations depend on the level of aggregation, spatial scale, and spatial resolution of the environmental data. This underlines that it is crucial to take these factors into account when studying trait-environment relationships.

By showing that niche differentiation causes adaptation of tree species to different microhabitats in close spatial proximity, especially the results from Chapter 5 contribute valuable aspects to the understanding of community assembly and maintenance of biodiversity in species-rich tree communities. They highlight that for understanding these processes, it can be insightful to zoom in into local spatial scales and highly resolved environmental data. This finding is especially important for tropical montane forests with their highly heterogeneous topography, but can also be extrapolated to other ecosystems.

6.7 Conclusions

By measuring the previously unexplored fine root traits of more than a hundred tropical tree species, this work helps answering several vividly debated questions related to the dimensionality of the plant economics space and functional trait distribution along environmental gradients. The results obtained in this thesis do not support the hypothesis that root traits are aligned along a single axis of variation that mirrors the leaf economics spectrum. Rather, they provide important evidence in favor of recent theories claiming that the root economics spectrum is formed by two main axes of fine root trait variation, one related to resource economics and driven by a growth-survival trade-off, and one related to root diameter. Whether in accordance with a recent hypothesis the diameter-related axis can be understood as a gradient of dependency on mycorrhizal fungi could not be tested in the framework of this study. It thus remains a central question for subsequent research. The conservation–acquisition axis of root trait variation was strongly coordinated with aboveground functional traits such as wood density, and leaf traits of the leaf economics spectrum. This reinforces one of the central tenets of functional trait theory, namely that there are selective pressures that favor coordinated functioning of different plant organs. The mounting evidence that trait syndromes are coordinated in a consistent fashion across plant organs is of crucial importance for the parametrization of trait-based models of plant and ecosystem functioning.

Many common tropical tree families displayed consistent trait combinations within this two-dimensional trait spectrum, and considerable phylogenetic signal was found for all traits. Contrary to previous findings, high root diameters were not only restricted to early-diverged plant families, but also found in later-diverged angiosperm clades.

In general, the observed variation of traits along environmental gradients implies that strong environmental filters at higher elevations and upper slopes allow only for the persistence of plants with a limited set of strategies, leading to trait convergences towards more conservative trait syndromes. At lower elevations and lower slopes, root trait syndromes were on average more acquisitive, but the higher belowground functional diversity observed there indicates the coexistence of species with a wider range of strategies within these communities. These findings suggest that environmental filtering acts on belowground strategies of trees both on the larger spatial scale of the elevational gradient, and on the smaller spatial scale of the topographic gradient, but it also implies that the relative importance of niche differentiation for community assembly might increase towards more fertile sites. Within the scope of this descriptive study, it was not possible to determine which of the many environmental factors that vary along the indirect gradients, elevation and topography, have a direct causal effect on the root trait distributions along these gradients. Identifying such causal trait-environment relationships is a future challenge that will require more mechanistically orientated methodological approaches. Nevertheless, the correlative patterns found in this study suggest that nitrogen availability could play a crucial role in the distribution of root functional strategies along elevation and topography.

Even though the trends along elevation and topography were robust, they explained only small proportions of overall root trait variation, because tree species with many different root trait syndromes coexist within communities. Highly resolved, small-scale soil data resolved this previously unexplained root trait variation, and led to the insight that topography-induced, small-scale soil heterogeneity allows the coexistence of many species adapted to slightly different microhabitats in tropical montane forests. The root economics spectrum proved to be a useful concept with high predictive power in explaining the microhabitat preferences of tree species.

Appendix A

Root traits along topography

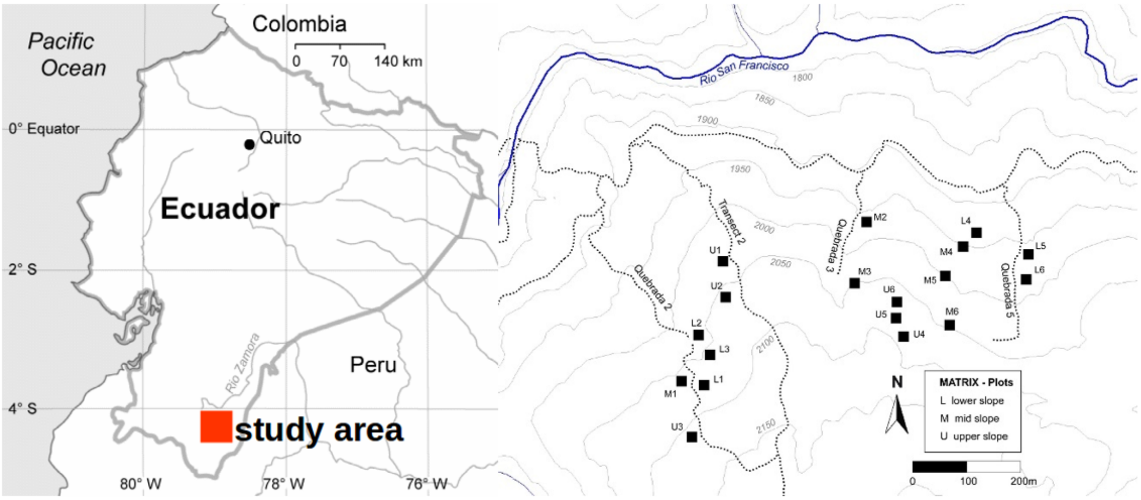


Figure A.1: Map of (a) the location of the study area in Ecuador and (b) the location of the study plots in the Reserva Biológica San Francisco

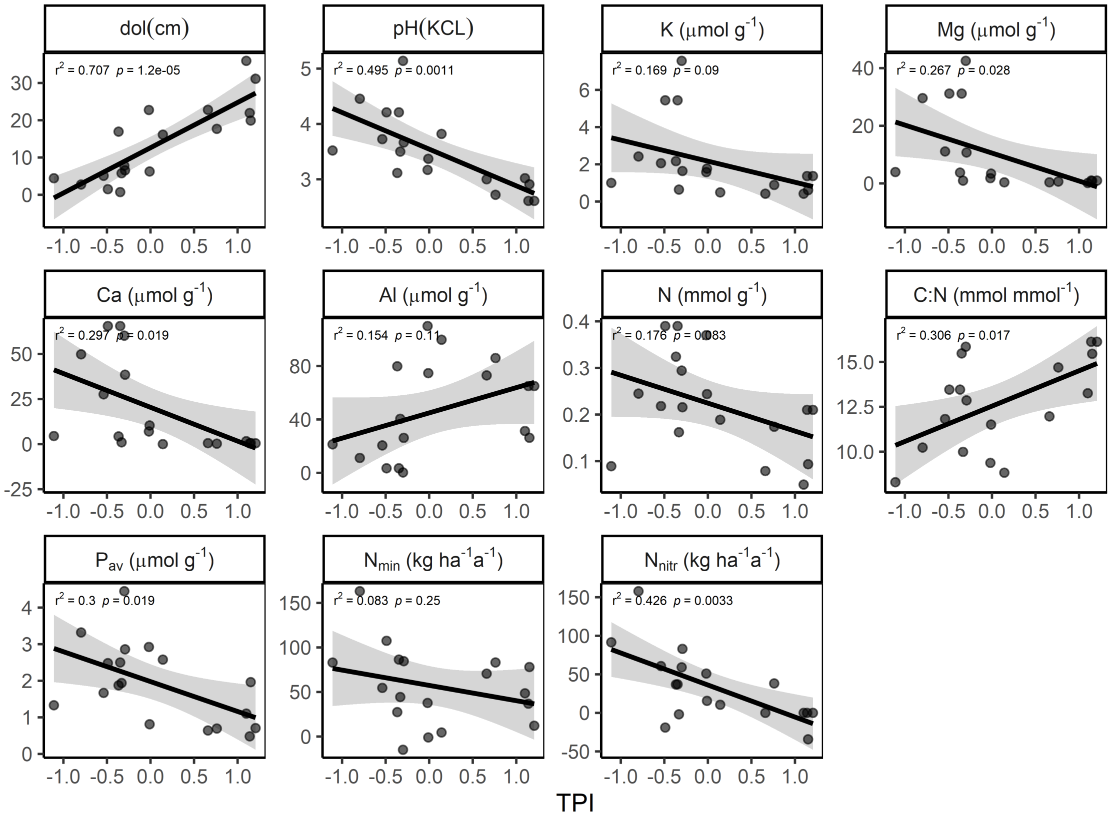


Figure A.2: Coordination of soil properties with the Topographic Position Index (TPI) in the 18 study plots. Soil properties: Depth of organic layer (dol), pH value, concentrations of K, Mg, Ca, Al and N, C:N ratio, plant available phosphorus (P_{av}), nitrogen mineralization rate (N_{min}) and nitrogen nitrification rate (N_{nitr}). Data from Wolf et al. (2011).

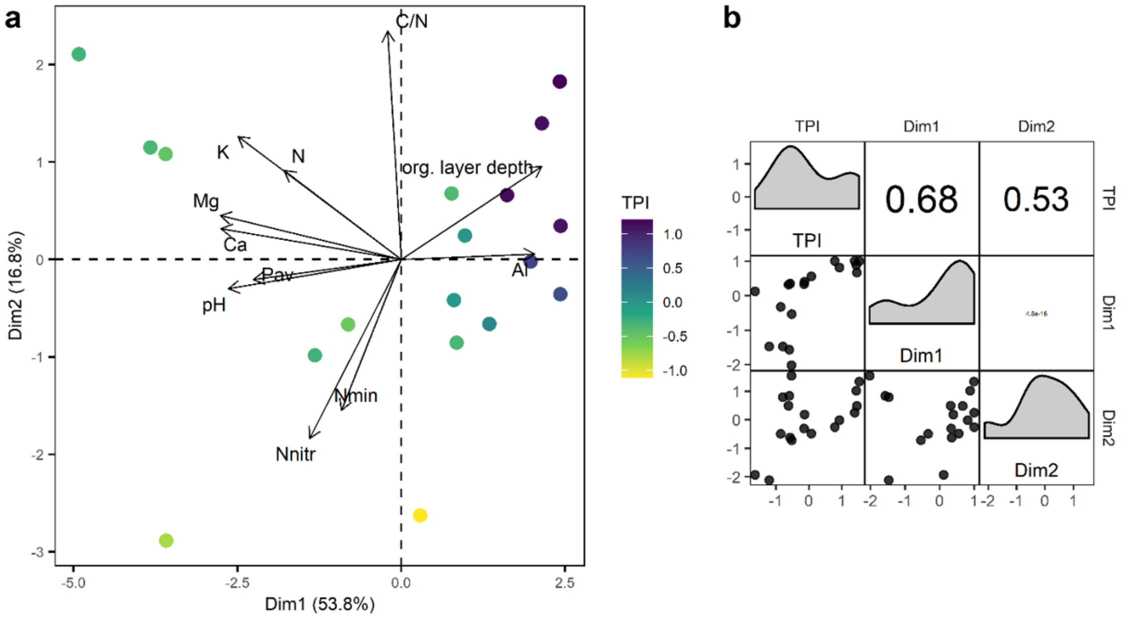


Figure A.3: Principal component analysis (PCA) of the soil properties Depth of organic layer (dol), pH value, concentrations of K, Mg, Ca, Al and N, C:N ratio, plant available phosphorus (P_{av}), nitrogen mineralization rate (N_{min}) and nitrogen nitrification rate (N_{nitr}) in the 18 study plots. The variables were centered and scaled. a) Biplot of the PCA with topographic position index (TPI) indicated by color. b) Relationships between the first two PCA dimensions and TPI. Upper triangle: Pearson's correlation coefficient; diagonal: density distribution; lower triangle: scatterplots of the respective variable pairs. Data from Wolf et al. (2011).

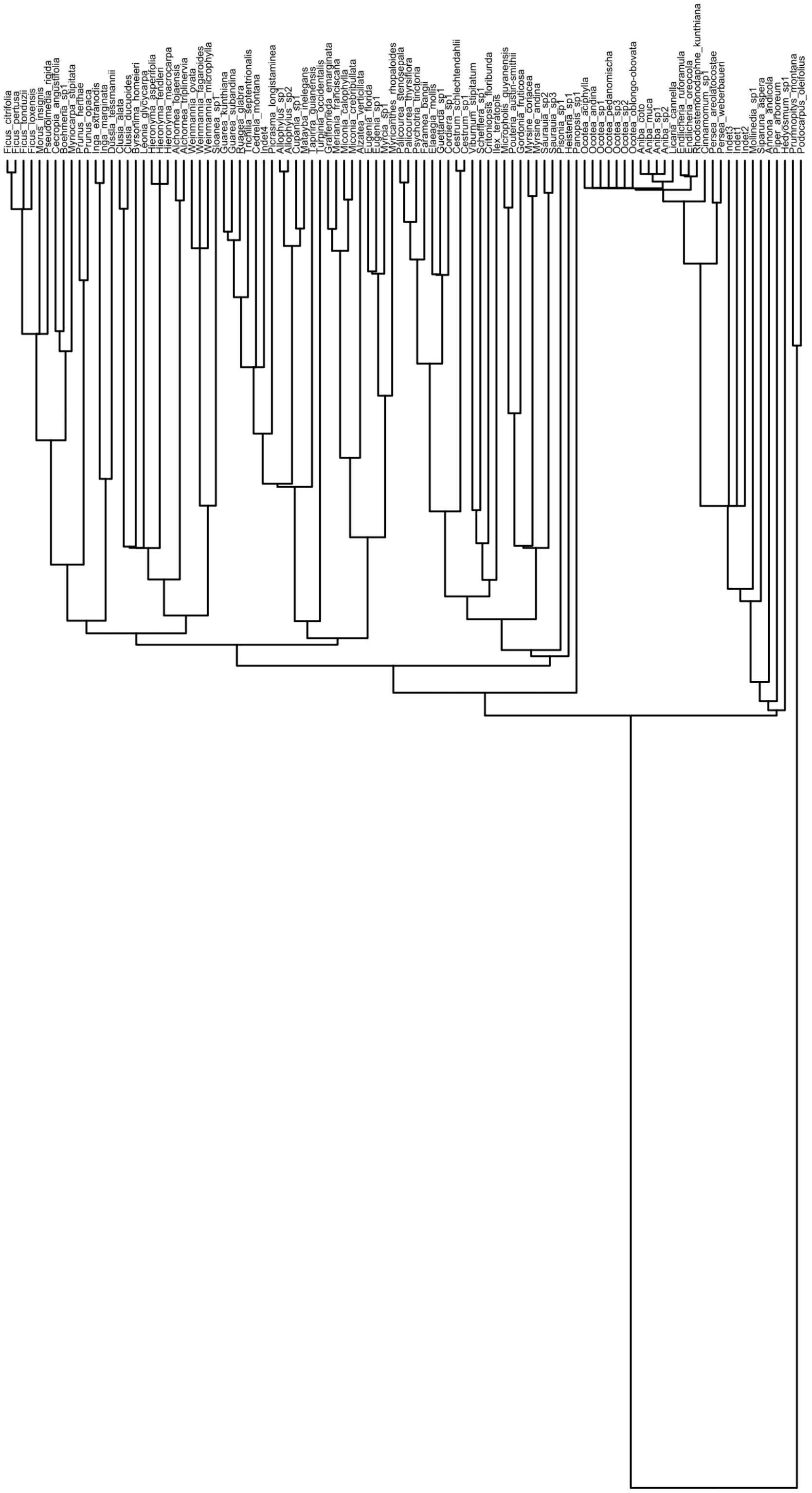


Figure A.4: Phylogenetic tree of the studied species.

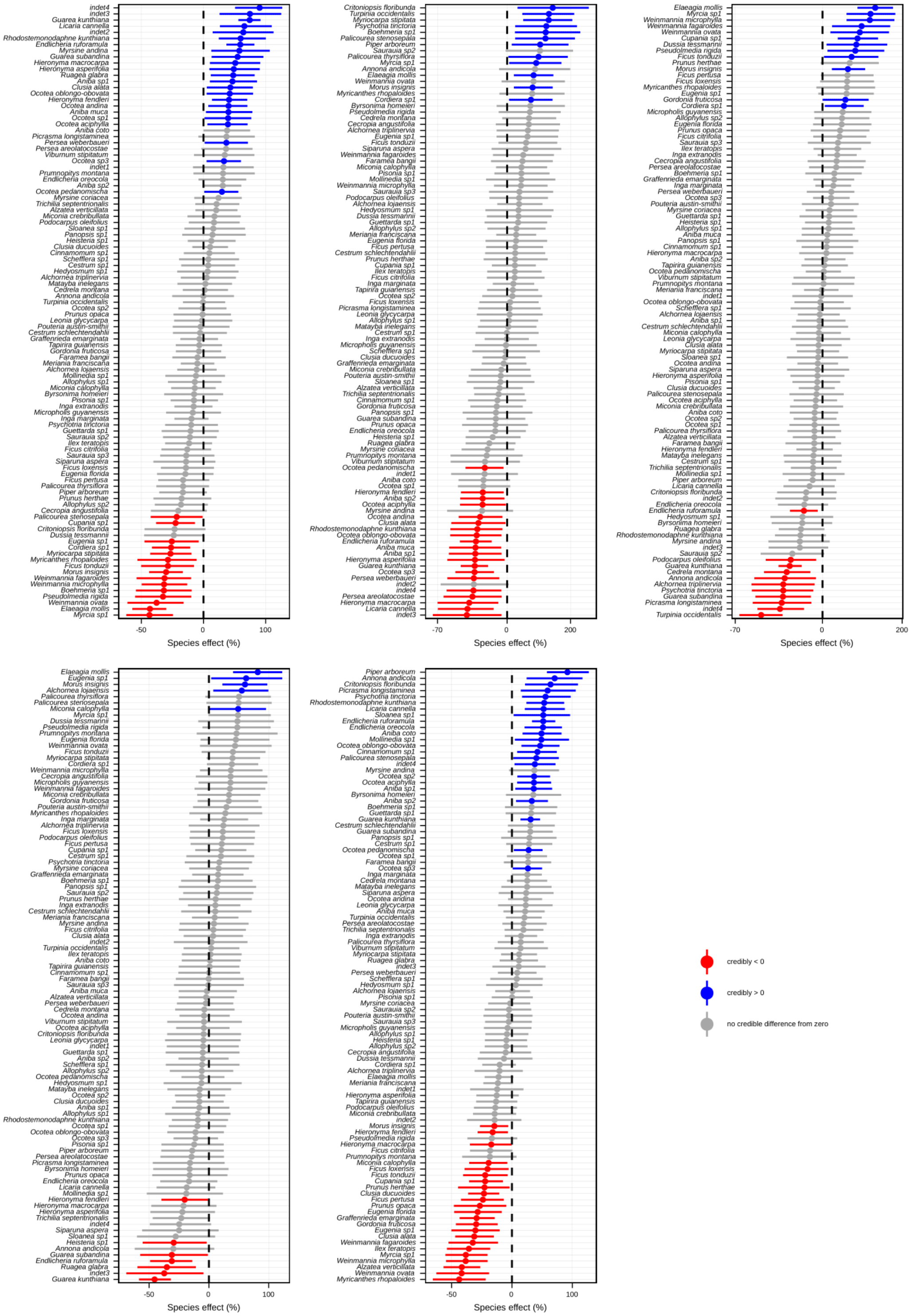
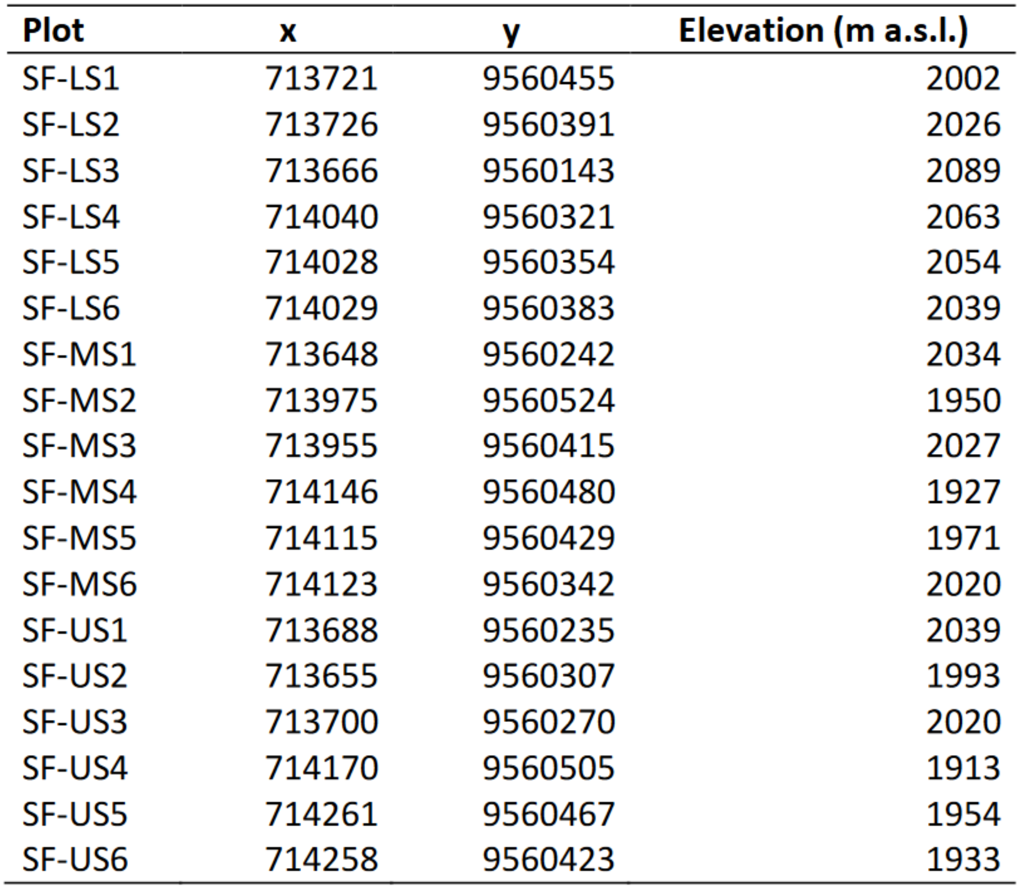


Figure A.5: Random effects of the studied species in Bayesian Phylogenetic Mixed Models for the traits root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), root branching intensity (RBI), and root nitrogen concentration (N_{root}). Displayed are posterior means and highest density intervals of the combined phylogenetic species effects and phylogenetically independent species effects as relative effects on the response scale (%).

Table A.1: Positions (UTM coordiantes) and altitudes of the plots.



Plot	x	y	Elevation (m a.s.l.)
SF-LS1	713721	9560455	2002
SF-LS2	713726	9560391	2026
SF-LS3	713666	9560143	2089
SF-LS4	714040	9560321	2063
SF-LS5	714028	9560354	2054
SF-LS6	714029	9560383	2039
SF-MS1	713648	9560242	2034
SF-MS2	713975	9560524	1950
SF-MS3	713955	9560415	2027
SF-MS4	714146	9560480	1927
SF-MS5	714115	9560429	1971
SF-MS6	714123	9560342	2020
SF-US1	713688	9560235	2039
SF-US2	713655	9560307	1993
SF-US3	713700	9560270	2020
SF-US4	714170	9560505	1913
SF-US5	714261	9560467	1954
SF-US6	714258	9560423	1933

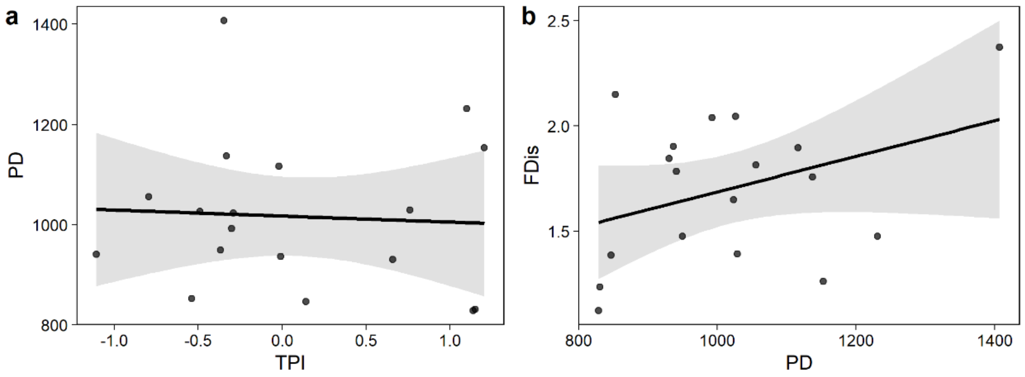
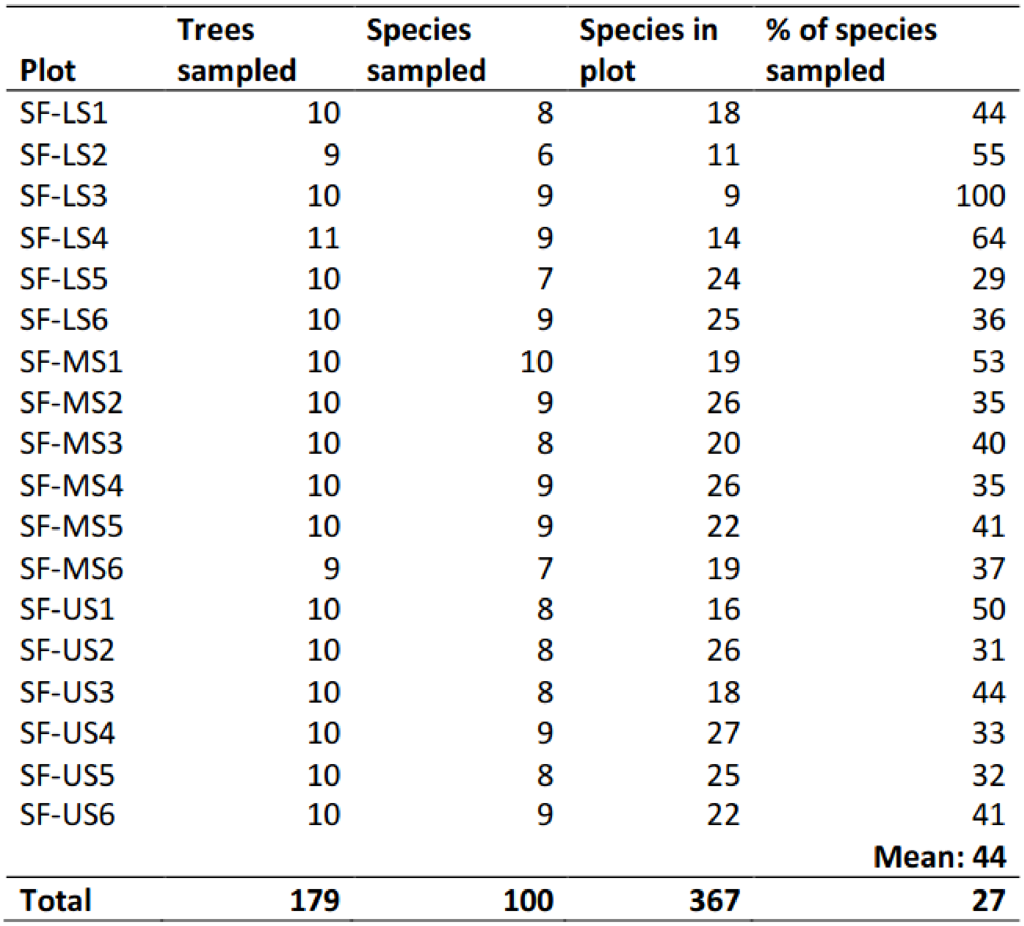


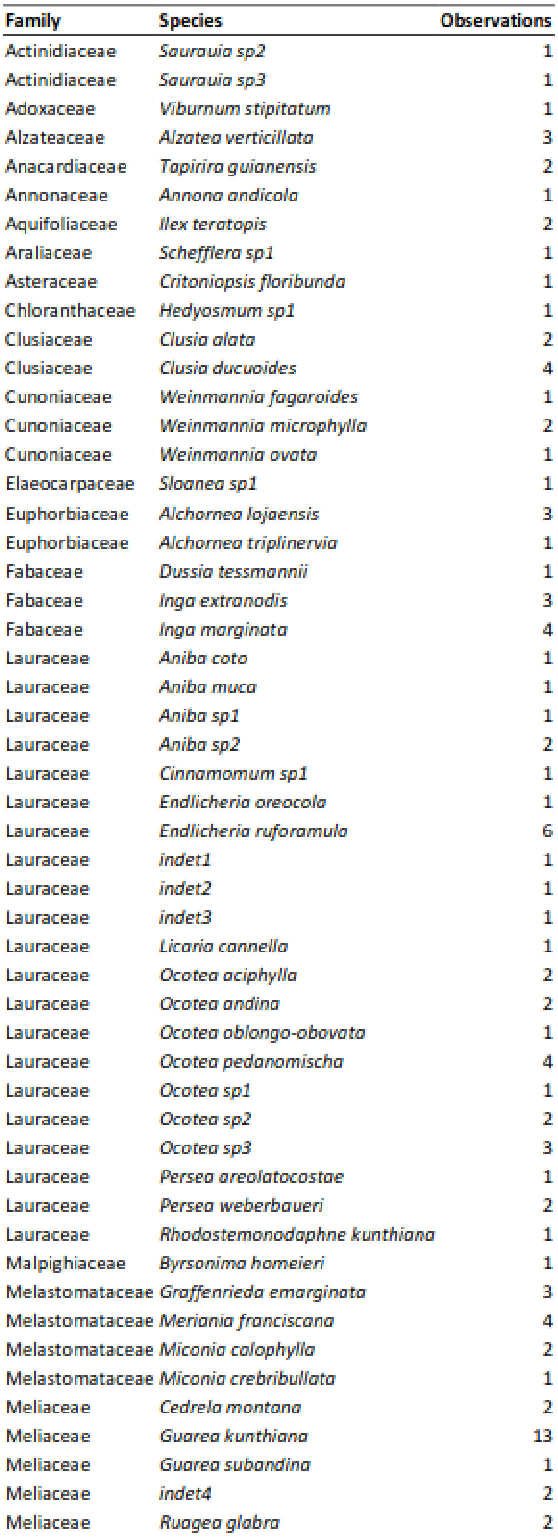
Figure A.6: Relationships of (a) phylogenetic diversity (PD) with the topographic position index (TPI) ($p = 0.81$, $R^2 = 0.003$) and (b) of functional dispersion (FDis) with PD ($p = 0.13$, $R^2 = 0.14$). Grey ribbons show the 95 % confidence intervals.

Table A.2: List of the plots with number of sampled trees and species, and the coverage of the tree species present in the plots (diameter at breast height ≥ 10cm, 2016) by our sampling procedure.



Plot	Trees sampled	Species sampled	Species in plot	% of species sampled
SF-LS1	10	8	18	44
SF-LS2	9	6	11	55
SF-LS3	10	9	9	100
SF-LS4	11	9	14	64
SF-LS5	10	7	24	29
SF-LS6	10	9	25	36
SF-MS1	10	10	19	53
SF-MS2	10	9	26	35
SF-MS3	10	8	20	40
SF-MS4	10	9	26	35
SF-MS5	10	9	22	41
SF-MS6	9	7	19	37
SF-US1	10	8	16	50
SF-US2	10	8	26	31
SF-US3	10	8	18	44
SF-US4	10	9	27	33
SF-US5	10	8	25	32
SF-US6	10	9	22	41
				Mean: 44
Total	**179**	**100**	**367**	**27**

Table A.3: List the sampled tree species with the corresponding sampling size.



Family	Species	Observations
Actinidiaceae	*Saurauia sp2*	1
Actinidiaceae	*Saurauia sp3*	1
Adoxaceae	*Viburnum stipitatum*	1
Alzateaceae	*Alzatea verticillata*	3
Anacardiaceae	*Tapirira guianensis*	2
Annonaceae	*Annona andicola*	1
Aquifoliaceae	*Ilex teratopis*	2
Araliaceae	*Schefflera sp1*	1
Asteraceae	*Critoniopsis floribunda*	1
Chloranthaceae	*Hedyosmum sp1*	1
Clusiaceae	*Clusia alata*	2
Clusiaceae	*Clusia ducuoides*	4
Cunoniaceae	*Weinmannia fagaroides*	1
Cunoniaceae	*Weinmannia microphylla*	2
Cunoniaceae	*Weinmannia ovata*	1
Elaeocarpaceae	*Sloanea sp1*	1
Euphorbiaceae	*Alchornea lojaensis*	3
Euphorbiaceae	*Alchornea triplinervia*	1
Fabaceae	*Dussia tessmannii*	1
Fabaceae	*Inga extranodis*	3
Fabaceae	*Inga marginata*	4
Lauraceae	*Aniba coto*	1
Lauraceae	*Aniba muca*	1
Lauraceae	*Aniba sp1*	1
Lauraceae	*Aniba sp2*	2
Lauraceae	*Cinnamomum sp1*	1
Lauraceae	*Endlicheria oreocola*	1
Lauraceae	*Endlicheria ruforamula*	6
Lauraceae	*indet1*	1
Lauraceae	*indet2*	1
Lauraceae	*indet3*	1
Lauraceae	*Licaria cannella*	1
Lauraceae	*Ocotea aciphylla*	2
Lauraceae	*Ocotea andina*	2
Lauraceae	*Ocotea oblongo-obovata*	1
Lauraceae	*Ocotea pedanomischa*	4
Lauraceae	*Ocotea sp1*	1
Lauraceae	*Ocotea sp2*	2
Lauraceae	*Ocotea sp3*	3
Lauraceae	*Persea areolatocostae*	1
Lauraceae	*Persea weberbaueri*	2
Lauraceae	*Rhodostemonodaphne kunthiana*	1
Malpighiaceae	*Byrsonima homeieri*	1
Melastomataceae	*Graffenrieda emarginata*	3
Melastomataceae	*Meriania franciscana*	4
Melastomataceae	*Miconia calophylla*	2
Melastomataceae	*Miconia crebribullata*	1
Meliaceae	*Cedrela montana*	2
Meliaceae	*Guarea kunthiana*	13
Meliaceae	*Guarea subandina*	1
Meliaceae	*indet4*	2
Meliaceae	*Ruagea glabra*	2

Meliaceae	*Trichilia septentrionalis*	2
Monimiaceae	*Mollinedia sp1*	1
Moraceae	*Ficus citrifolia*	1
Moraceae	*Ficus loxensis*	1
Moraceae	*Ficus pertusa*	1
Moraceae	*Ficus tonduzii*	1
Moraceae	*Morus insignis*	5
Moraceae	*Pseudolmedia rigida*	1
Myrtaceae	*Eugenia florida*	1
Myrtaceae	*Eugenia sp1*	1
Myrtaceae	*Myrcia sp1*	2
Myrtaceae	*Myricanthes rhopaloides*	1
Nyctaginaceae	*Pisonia sp1*	2
Olacaceae	*Heisteria sp1*	2
Phyllanthaceae	*Hieronyma asperifolia*	1
Phyllanthaceae	*Hieronyma fendleri*	4
Phyllanthaceae	*Hieronyma macrocarpa*	1
Piperaceae	*Piper arboreum*	2
Podocarpaceae	*Podocarpus oleifolius*	2
Podocarpaceae	*Prumnopitys montana*	1
Primulaceae	*Myrsine andina*	1
Primulaceae	*Myrsine coriacea*	2
Proteaceae	*Panopsis sp1*	1
Rosaceae	*Prunus herthae*	1
Rosaceae	*Prunus opaca*	1
Rubiaceae	*Cordiera sp1*	3
Rubiaceae	*Elaeagia mollis*	5
Rubiaceae	*Faramea bangii*	1
Rubiaceae	*Guettarda sp1*	1
Rubiaceae	*Palicourea stenosepala*	1
Rubiaceae	*Palicourea thyrsiflora*	1
Rubiaceae	*Psychotria tinctoria*	1
Sapindaceae	*Allophylus sp1*	1
Sapindaceae	*Allophylus sp2*	1
Sapindaceae	*Cupania sp1*	3
Sapindaceae	*Matayba inelegans*	1
Sapotaceae	*Micropholis guyanensis*	1
Sapotaceae	*Pouteria austin-smithii*	1
Simaroubaceae	*Picrasma longistaminea*	1
Siparunaceae	*Siparuna aspera*	1
Solanaceae	*Cestrum schlechtendahlii*	1
Solanaceae	*Cestrum sp1*	1
Staphyleaceae	*Turpinia occidentalis*	3
Theaceae	*Gordonia fruticosa*	2
Urticaceae	*Boehmeria sp1*	1
Urticaceae	*Cecropia angustifolia*	1
Urticaceae	*Myriocarpa stipitata*	3
Violaceae	*Leonia glycycarpa*	1

Table A.4: Inference and diagnostics from the Bayesian Phylogenetic Multilevel Models. For each parameter (for explanation of parameter symbols, see Methods S1), the point estimate posterior mean, its standard error, highest posterior density intervals (HDI), Rhat convergence diagnostic and effective sample size (ESS).

Parameter	Estimate	Standard error	HDI low	HDI high	$\hat{R}$	ESS
Root diameter						
α_0	-0.37	0.28	-0.93	0.16	1.00	4432
β	0.09	0.05	-0.00	0.17	1.00	6732
τ_{ind}	0.14	0.05	0.02	0.23	1.00	937
τ_{phyl}	0.43	0.08	0.28	0.59	1.00	1841
τ_{plot}	0.04	0.03	0.00	0.08	1.00	3666
σ	0.21	0.02	0.17	0.24	1.00	2557
Specific root length						
α_0	2.13	0.42	1.31	2.98	1.00	7750
β	-0.25	0.09	-0.42	-0.07	1.00	8108
τ_{ind}	0.25	0.09	0.04	0.40	1.00	1018
τ_{phyl}	0.63	0.15	0.35	0.93	1.00	2118
τ_{plot}	0.14	0.06	0.01	0.26	1.00	2743
σ	0.38	0.03	0.32	0.45	1.00	2115
Root tissue density						
α_0	-1.12	0.33	-1.78	-0.48	1.00	5179
β	0.05	0.06	-0.09	0.17	1.00	7558
τ_{ind}	0.21	0.07	0.06	0.34	1.00	751
τ_{phyl}	0.50	0.12	0.26	0.72	1.00	1216
τ_{plot}	0.11	0.05	0.01	0.19	1.00	2227
σ	0.25	0.02	0.21	0.29	1.00	1524
Root branching intensity						
α_0	0.62	0.29	0.03	1.18	1.00	5852
β	-0.24	0.10	-0.43	-0.05	1.00	5730
τ_{ind}	0.16	0.06	0.03	0.28	1.00	1384
τ_{phyl}	0.43	0.11	0.21	0.64	1.00	1774
τ_{plot}	0.25	0.06	0.14	0.36	1.00	3850
σ	0.30	0.02	0.26	0.34	1.00	3951
Root nitrogen concentration						
α_0	2.79	0.32	2.18	3.44	1.00	3691
β	-0.18	0.04	-0.27	-0.10	1.00	5380
τ_{ind}	0.10	0.05	0.00	0.18	1.01	640
τ_{phyl}	0.50	0.08	0.35	0.66	1.00	1425
τ_{plot}	0.05	0.03	0.00	0.10	1.00	2571
σ	0.18	0.02	0.15	0.21	1.00	1955

A.1 Method: Phylogenetic multilevel models

Five Phylogenetic Multilevel Models with identical structures, one for each fine root trait, were fit following Bürkner (2020).

Model equation:

$$\log(Y_i) \sim \text{Normal}\left(\mu_i, \sigma\right)$$

$$\mu_{ijk} = \alpha_0 + \beta \cdot TPI_i + \alpha_{plot[j]} + \alpha_{species[k]}$$

The log-transformed response variable Y (a fine root trait) followed a normal distribution around the varying mean μ with a standard deviation of σ.The predicted value for observation i in plot j and of species k equals the sum of an overall intercept α_0, a slope parameter β multiplied with the Topographic Position Index (TPI), a random intercept for plot j ($\alpha_{plot[j]}$) and a random intercept for species k ($\alpha_{species[k]}$).

Random plot effects:

$$\alpha_{plot[j]} \sim \text{Normal}\left(0, \tau_{plot}\right)$$

Random species effects:

$$\alpha_{species[k]} \sim \text{MVN}\left(0, \Sigma_{phyl}\right)$$

$$\Sigma_{phyl[m,n]} = \begin{cases} \tau^2_{phyl} + \tau^2_{ind} & \text{if } m = n \\ \tau^2_{phyl}\, \rho_{phyl[m,n]} & \text{else} \end{cases}$$

While the random plot effects where drawn from a normal distribution with standard deviation τ_{plot}, like done for random intercept effects in standard Linear Mixed Models, the random species effects were build from two components: A phylogenetic species effect that incorporated the phylogenetic non-independence of residuals, and an independent species effect that accounted for additional variance among species independent from phylogeny. The random species intercepts stem from a multivariate normal distribution with a covariance of Σ_{phyl}. $\Sigma_{phyl[m,n]}$ is a matrix with $\tau^2_{phyl} + \tau^2_{ind}$ (Variances of the phylogenetic species effect and the independent species effect) on the diagonal and τ^2_{phyl} times the correlation $\rho_{phyl[m,n]}$ between the two species m and n everywhere else.

Prior probabilities of regression coefficients: The intercept was assigned a weakly informative Student t prior with a scale of 10 and 3 degrees of freedom, thus placing the bulk of probability mass at values around zero while not ruling out more extreme values.

$$\alpha_0 \sim \mathrm{Student-t}\,(\mu = 0, \nu = 3, \sigma = 10)$$

The effect of topographic position β_{TPI} was assigned a noniformative improper uniform prior over the real line.

All variance components were assigned half-t priors with a scale of 10 and 3 degrees of freedom.

$$\sigma \sim \mathrm{half-t}\,(\mu = 0,\ \nu = 3,\ \sigma = 10)$$

$$\tau_{plot} \sim \mathrm{half-t}\,(\mu = 0,\ \nu = 3,\ \sigma = 10)$$

$$\tau_{phyl} \sim \mathrm{half-t}\,(\mu = 0,\ \nu = 3,\ \sigma = 10)$$

$$\tau_{spec} \sim \mathrm{half-t}\,(\mu = 0,\ \nu = 3,\ \sigma = 10)$$

Models were fit with Hamiltonian Monte Carlo (HMC, Betancourt & Girolami (2015)) via the Stan probabilistic programming language (Carpenter *et al.*, 2017) using R package `brms` (Bürkner, 2017). Sampling was performed on 4 chains for each 5000 iterations, discarding the first 2500 iterations of each chain for warmup. The settings used for the HMC algorithm were adapt_delta = 0.95 and a maximum tree depth of 15.

Appendix B

Elevational trends of fine root traits

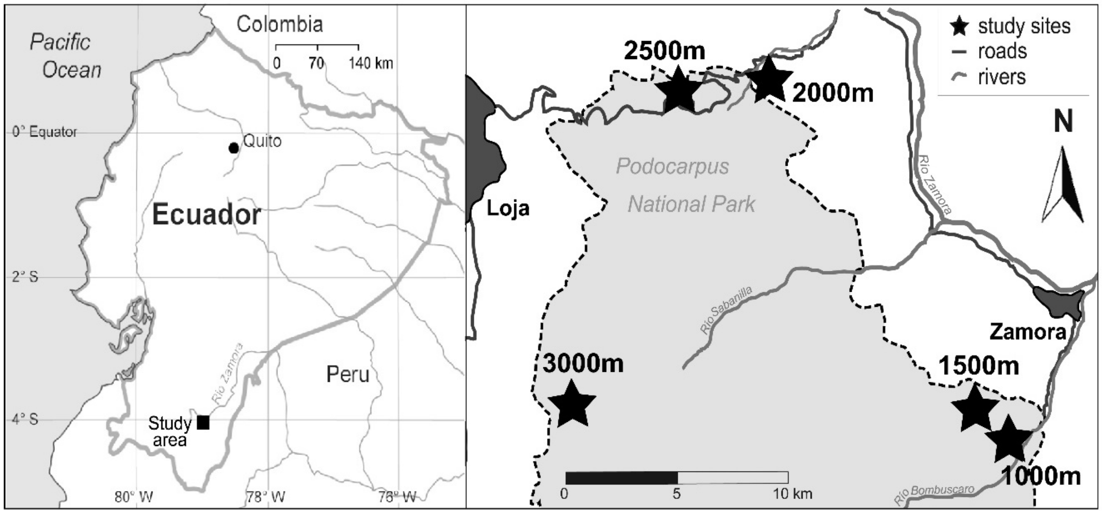


Figure B.1: Map of the study area.

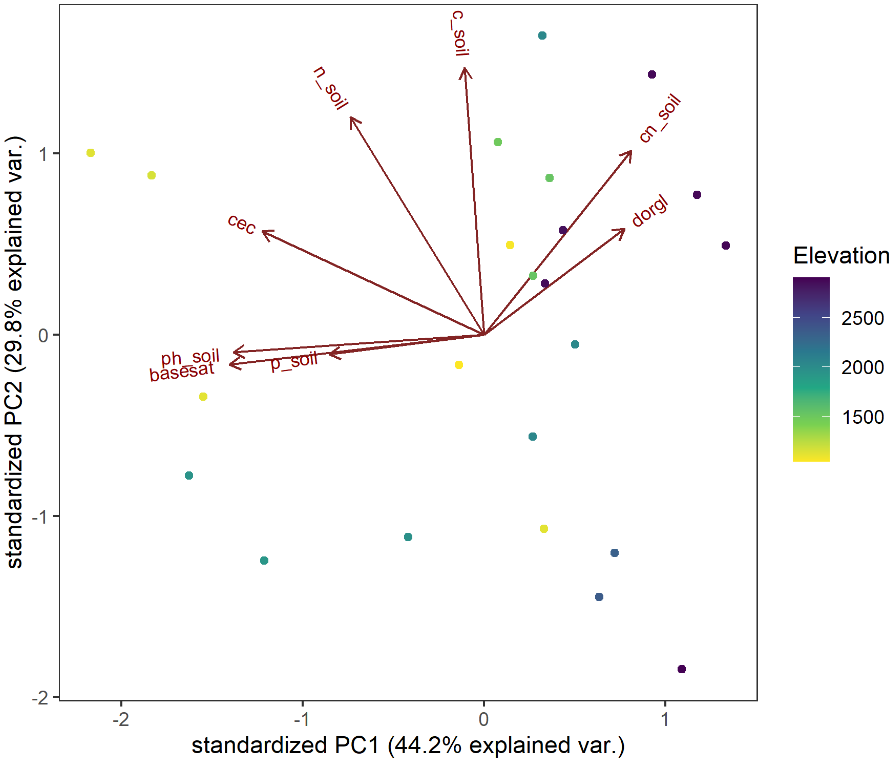


Figure B.2: Biplot of the plot scores of the first two principal components of the principal component analysis with soil parameters for 23 plots, overlaid with the loadings for the analyzed soil properties. Included variables are: Plant available phosphorus, base saturation, soil pH value, cation exchange capacity, nitrogen concentration, carbon concentration, soil C:N ratio, and depth of the organic layer. All variables were standardized prior to the analysis. Color indicates plot elevation in m a.s.l.

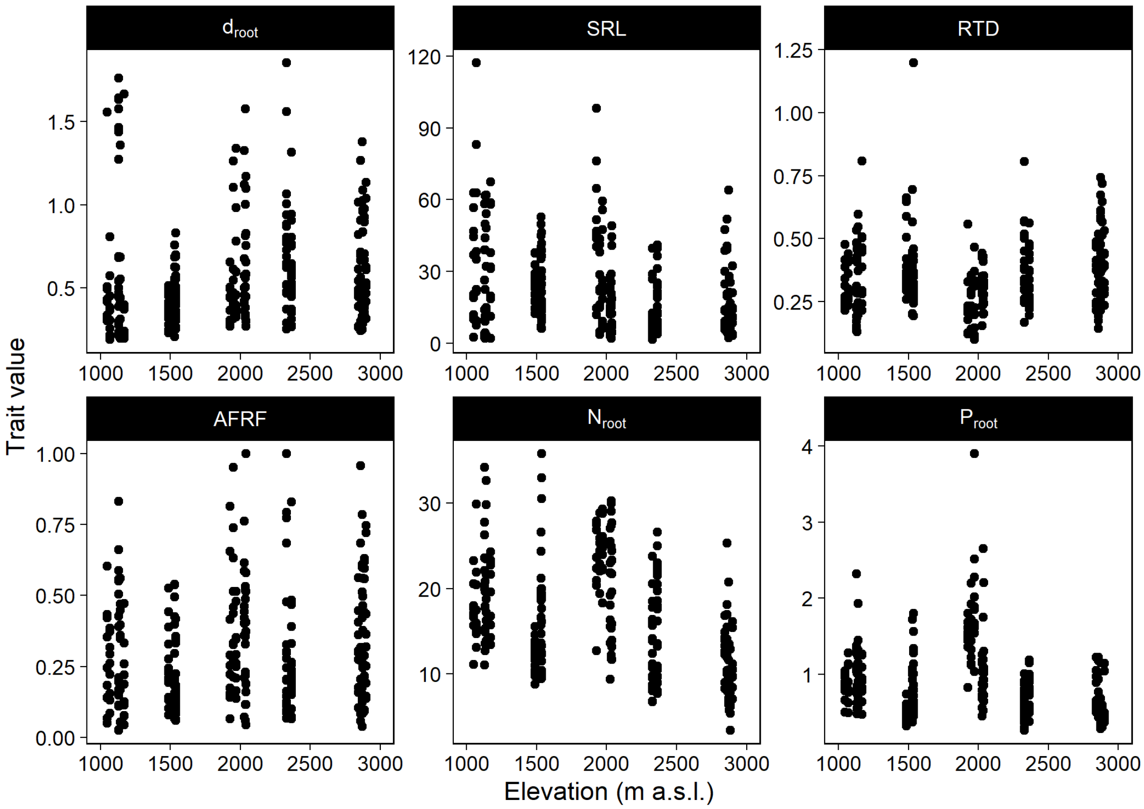


Figure B.3: Fine root functional traits (raw data, each dot represents one tree) along the elevational gradient. Data are shown for average root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), absorptive fine root fraction (AFRF), root nitrogen concentration (N_{root}) and root phosphorus concentration (P_{root}). Trait units can be found in Tab. 1 in the main article.

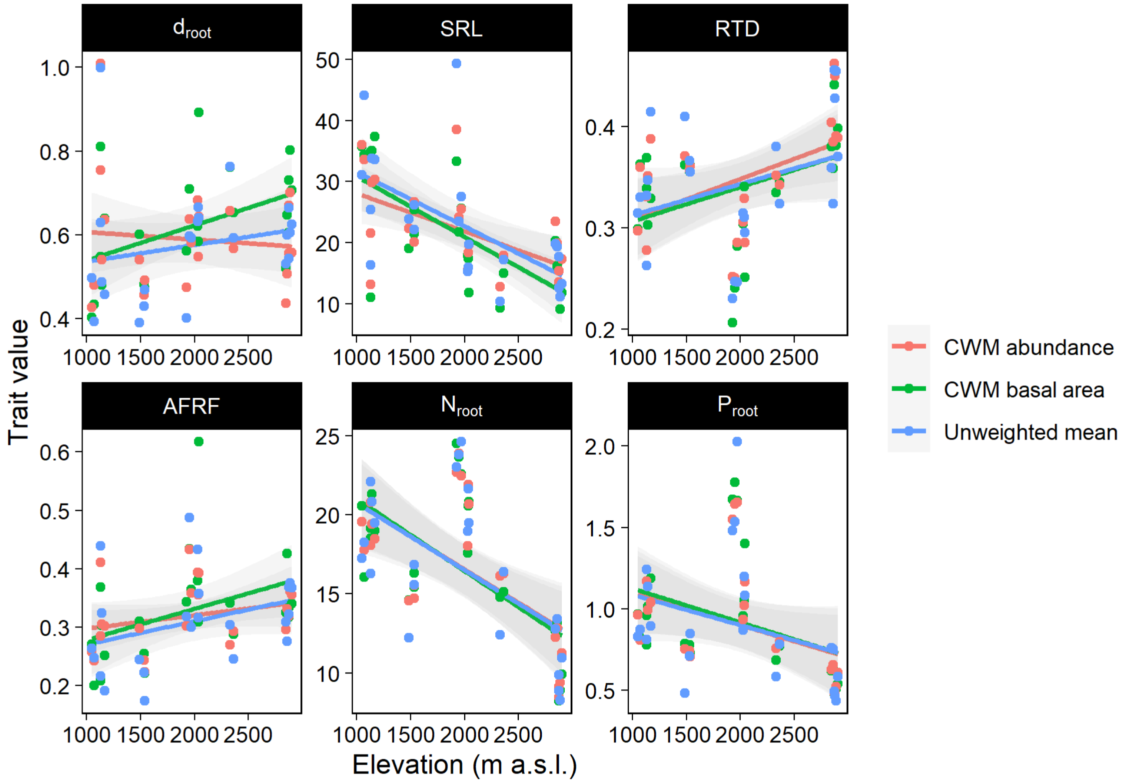


Figure B.4: Different types of plot means of root trait values in dependency of elevation. Each dot represents one plot mean, with colors distinguishing community-weighted means (CWM) calculated with the number of individuals per species as weights, CWM calculated with the species' total basal area as weights, and the mean calculated with all the randomly selected trees from the plot. Data are shown for average root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), absorptive fine root fraction (AFRF), root nitrogen concentration (N_{root}) and root phosphorus concentration (P_{root}). Trait units can be found in Tab. 1 in the main article.

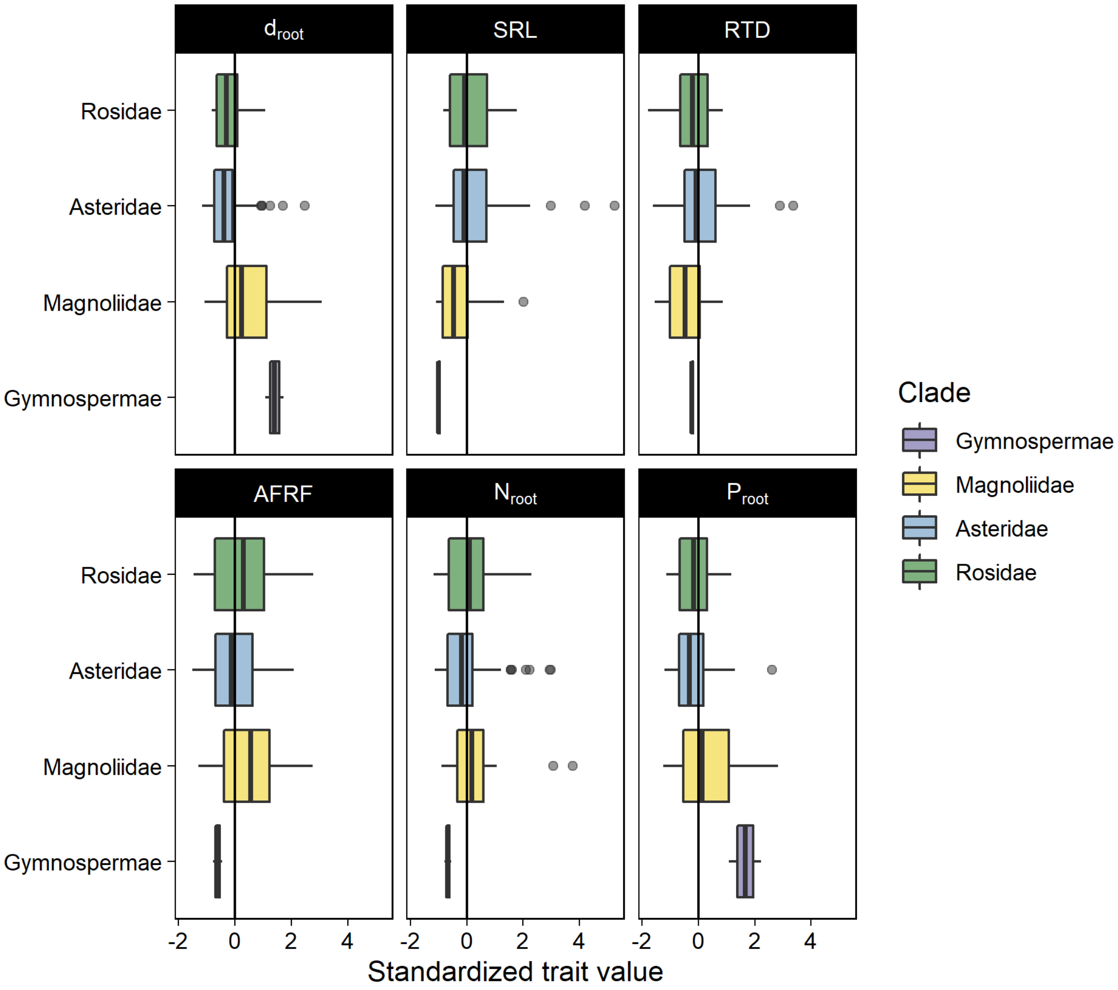
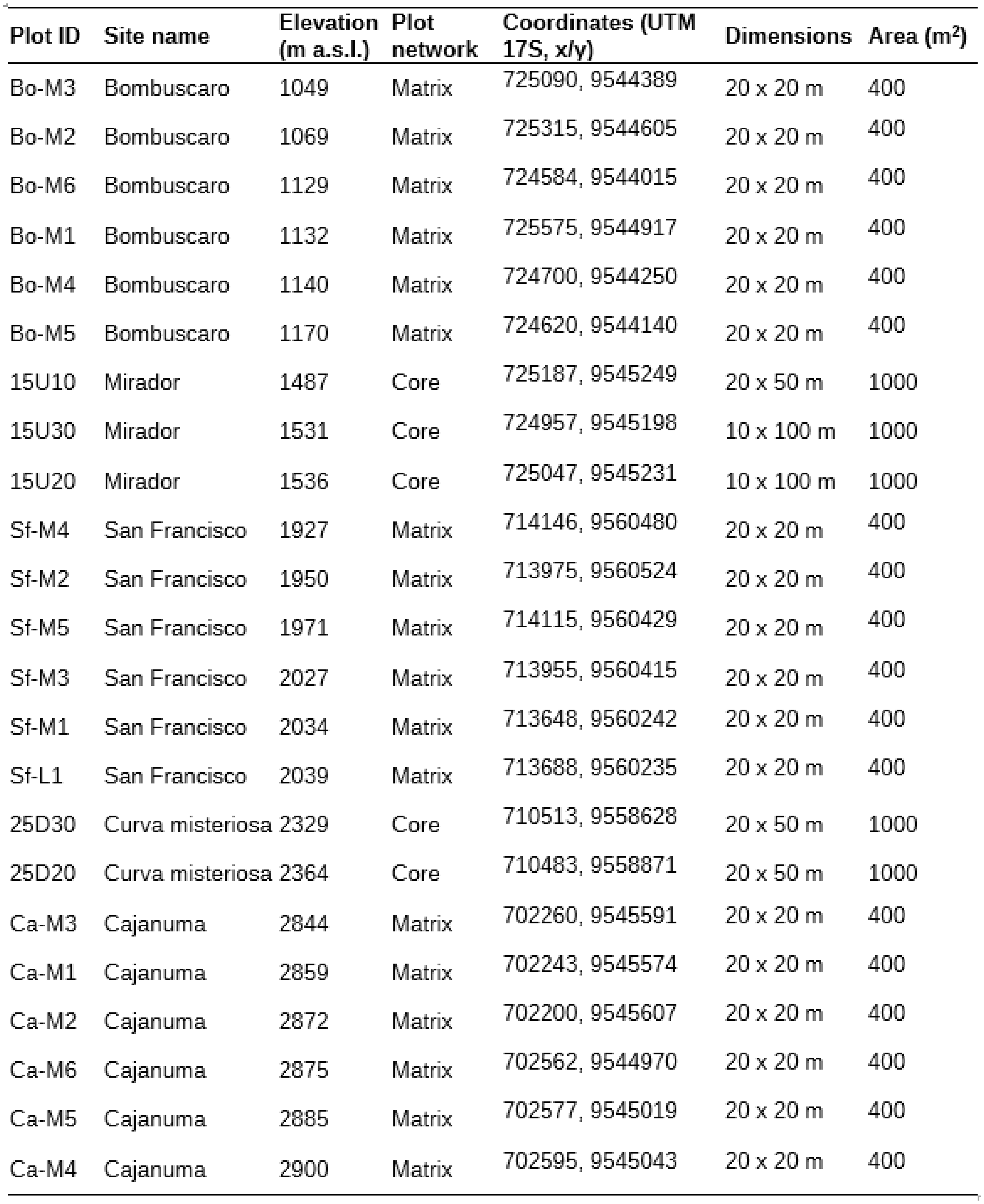


Figure B.5: Fine root functional traits of large phylogenetic clades. Results are shown for average root diameter (d_{root}), specific root length (SRL), root tissue density (RTD), absorptive fine root fraction (AFRF), root nitrogen concentration (N_{root}) and root phosphorus concentration (P_{root}). All traits were centered and scaled.

Table B.1: Locations and extents of the plots.



Plot ID	Site name	Elevation (m a.s.l.)	Plot network	Coordinates (UTM 17S, x/y)	Dimensions	Area (m^2)
Bo-M3	Bombuscaro	1049	Matrix	725090, 9544389	20 x 20 m	400
Bo-M2	Bombuscaro	1069	Matrix	725315, 9544605	20 x 20 m	400
Bo-M6	Bombuscaro	1129	Matrix	724584, 9544015	20 x 20 m	400
Bo-M1	Bombuscaro	1132	Matrix	725575, 9544917	20 x 20 m	400
Bo-M4	Bombuscaro	1140	Matrix	724700, 9544250	20 x 20 m	400
Bo-M5	Bombuscaro	1170	Matrix	724620, 9544140	20 x 20 m	400
15U10	Mirador	1487	Core	725187, 9545249	20 x 50 m	1000
15U30	Mirador	1531	Core	724957, 9545198	10 x 100 m	1000
15U20	Mirador	1536	Core	725047, 9545231	10 x 100 m	1000
Sf-M4	San Francisco	1927	Matrix	714146, 9560480	20 x 20 m	400
Sf-M2	San Francisco	1950	Matrix	713975, 9560524	20 x 20 m	400
Sf-M5	San Francisco	1971	Matrix	714115, 9560429	20 x 20 m	400
Sf-M3	San Francisco	2027	Matrix	713955, 9560415	20 x 20 m	400
Sf-M1	San Francisco	2034	Matrix	713648, 9560242	20 x 20 m	400
Sf-L1	San Francisco	2039	Matrix	713688, 9560235	20 x 20 m	400
25D30	Curva misteriosa	2329	Core	710513, 9558628	20 x 50 m	1000
25D20	Curva misteriosa	2364	Core	710483, 9558871	20 x 50 m	1000
Ca-M3	Cajanuma	2844	Matrix	702260, 9545591	20 x 20 m	400
Ca-M1	Cajanuma	2859	Matrix	702243, 9545574	20 x 20 m	400
Ca-M2	Cajanuma	2872	Matrix	702200, 9545607	20 x 20 m	400
Ca-M6	Cajanuma	2875	Matrix	702562, 9544970	20 x 20 m	400
Ca-M5	Cajanuma	2885	Matrix	702577, 9545019	20 x 20 m	400
Ca-M4	Cajanuma	2900	Matrix	702595, 9545043	20 x 20 m	400

Table B.2: Species list, including number of individuals sampled per elevational level.

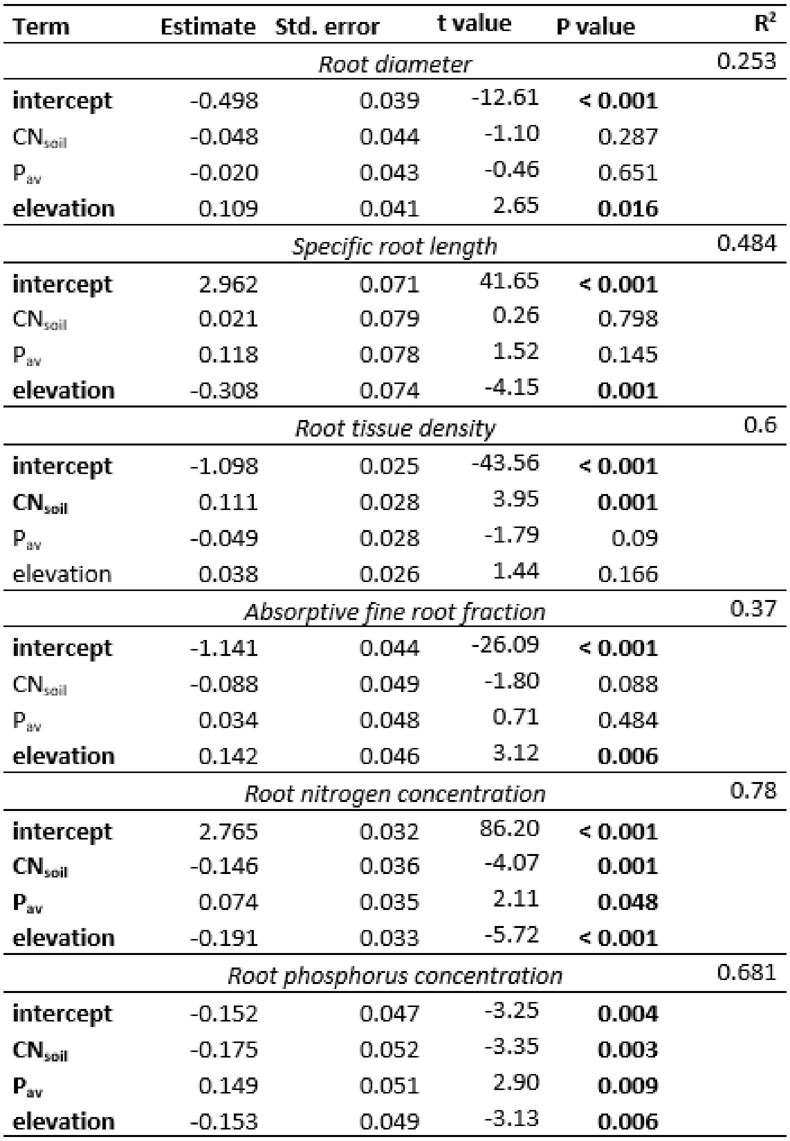
Family	**Species**	**1000 m**	**1500 m**	**2000 m**	**2500 m**	**3000 m**
Actinidiaceae	*Saurauia cf herthae*	0	0	1	0	0
Actinidiaceae	*Saurauia sp 1*	0	0	1	0	0
Adoxaceae	*Viburnum stipitatum*	0	0	1	0	0
Anacardiaceae	*Tapirira guianensis*	2	4	1	0	0
Annonaceae	*Guatteria oblongifolia*	0	2	0	0	0
Aquifoliaceae	*Ilex hippocrateoides*	0	0	0	2	0
Aquifoliaceae	*Ilex laurina*	0	0	0	0	2
Aquifoliaceae	*Ilex rupicola*	0	0	0	0	1
Aquifoliaceae	*Ilex teratopis*	0	0	0	0	2
Aquifoliaceae	*Ilex weberlingii*	0	0	0	0	2
Araliaceae	*Oreopanax sessiliflorus*	0	0	0	0	1
Araliaceae	*Schefflera cf acuminata*	0	0	0	1	0
Asteraceae	*Critoniopsis floribunda*	0	0	1	0	0
Asteraceae	*Critoniopsis pycnantha*	0	0	0	4	2
Burseraceae	*Burseraceae sp 1*	0	1	0	0	0
Burseraceae	*Dacryodes cf peruviana*	1	0	0	0	0
Burseraceae	*Protium sp 1*	0	2	0	0	0
Burseraceae	*Trattinnickia aff lawrancei*	1	0	0	0	0
Celastraceae	*Maytenus JH5772*	1	0	0	0	0
Chloranthaceae	*Hedyosmum purpurascens*	0	0	0	0	1
Chloranthaceae	*Hedyosmum sp 1*	0	0	0	1	0
Chrysobalanaceae	*Licania harlingii*	3	0	0	0	0
Clusiaceae	*Clusia alata*	0	0	0	0	5
Clusiaceae	*Clusia cf latipes*	0	0	0	0	1
Clusiaceae	*Clusia ducoides*	0	0	1	0	1
Clusiaceae	*Clusia elliptica*	0	0	0	6	5
Clusiaceae	*Clusia sp 1*	0	0	0	1	0
Clusiaceae	*Clusia sp 2*	0	0	0	4	0
Clusiaceae	*Clusia sp 3*	0	1	0	0	0
Combretaceae	*Terminalia amazonia*	1	0	0	0	0
Cunoniaceae	*Weinmannia cf magnifolia*	0	0	0	1	0
Cunoniaceae	*Weinmannia elliptica*	0	0	0	0	4
Cunoniaceae	*Weinmannia loxensis*	0	0	0	0	1
Cunoniaceae	*Weinmannia ovata*	0	0	0	0	4
Elaeocarpaceae	*Sloanea aff grandiflora*	1	0	0	0	0
Elaeocarpaceae	*Sloanea cf rufa*	1	0	0	0	0
Elaeocarpaceae	*Sloanea sp 1*	0	2	0	0	0
Euphorbiaceae	*Alchornea lojaensis*	0	0	0	7	0
Euphorbiaceae	*Alchornea triplinervia*	0	3	0	0	0
Euphorbiaceae	*Chaetocarpus sp 1*	0	4	0	0	0
Euphorbiaceae	*Sapium stylare*	0	0	1	0	0
Fabaceae	*Inga cf extra-nodis*	0	0	2	0	0
Fabaceae	*Inga marginata*	0	0	1	0	0
Fabaceae	*Inga nobilis*	1	0	0	0	0
Fabaceae	*Inga umbellifera*	1	0	0	0	0

Lauraceae	*Aiouea dubia*	0	0	0	0	1
Lauraceae	*Aniba cf coto*	0	0	2	0	0
Lauraceae	*Aniba sp 1*	0	0	1	0	0
Lauraceae	*Aniba sp 2*	1	0	0	0	0
Lauraceae	*Cinnamomum cf triplinerve*	1	0	0	0	0
Lauraceae	*Cinnamomum sp nov*	0	0	1	0	0
Lauraceae	*Endlicheria cf ruforamula*	0	0	2	0	0
Lauraceae	*Lauraceae sp 1*	0	1	0	0	0
Lauraceae	*Lauraceae sp 2*	0	2	0	0	0
Lauraceae	*Lauraceae sp 3*	0	2	0	0	0
Lauraceae	*Licaria sp 1*	0	0	0	3	0
Lauraceae	*Lauraceae sp 4*	0	0	2	0	1
Lauraceae	*Ocotea infrafoveolata*	0	0	0	0	2
Lauraceae	*Ocotea sp 1*	0	0	1	0	0
Lauraceae	*Persea areolatocostae*	0	0	1	0	0
Lauraceae	*Persea cf areolatocostae*	1	0	0	0	0
Lauraceae	*Persea ferruginea*	0	0	0	0	2
Lauraceae	*Persea sp 1*	0	1	0	0	0
Lauraceae	*Persea sp 2*	0	0	0	1	0
Lauraceae	*Rhodostemonodaphne kunthiana*	1	0	0	0	0
Lecythidaceae	*Eschweilera sessilis*	0	0	0	1	0
Lecythidaceae	*Grias peruviana*	1	0	0	0	0
Linaceae	*Roucheria colombiana*	0	1	0	0	0
Malvaceae	*Mollia gracilis*	2	0	0	0	0
Melastomataceae	*Centronia laurifolia*	3	1	0	0	0
Melastomataceae	*Graffenrieda aff uribei*	0	7	0	0	0
Melastomataceae	*Graffenrieda emarginata*	0	0	1	0	0
Melastomataceae	*Graffenrieda harlingii*	0	0	0	0	2
Melastomataceae	*Graffenrieda sp 1*	0	1	0	0	0
Melastomataceae	*Graffenrieda sp 2*	1	3	0	0	0
Melastomataceae	*Graffenrieda sp 3*	0	4	0	0	0
Melastomataceae	*Meriania franciscana*	0	0	4	0	0
Melastomataceae	*Meriania sp 1*	0	0	0	2	0
Melastomataceae	*Miconia cf pilgeriana*	1	0	0	0	0
Melastomataceae	*Miconia cf punctata*	0	3	0	0	0
Melastomataceae	*Miconia jahnii*	0	0	0	0	5
Melastomataceae	*Miconia sp 1*	0	0	0	0	1
Melastomataceae	*Miconia radula*	0	0	0	0	1
Melastomataceae	*Andesanthus lepidotus*	0	0	0	2	0
Melastomataceae	*Tibouchina ochypetala*	0	1	0	0	0
Meliaceae	*Cedrela montana*	0	0	1	0	0
Meliaceae	*Guarea kunthiana*	0	0	3	0	0
Meliaceae	*Guarea macrophylla*	1	0	0	0	0
Meliaceae	*Guarea subandina*	0	0	2	0	0
Meliaceae	*Trichilia septentrionalis*	0	0	3	0	0
Moraceae	*Clarisia biflora*	2	0	0	0	0

Moraceae	*Clarisia racemosa*	2	0	0	0	0
Moraceae	*Ficus apollinaris*	1	0	0	0	0
Moraceae	*Ficus tonduzii*	0	0	1	0	0
Moraceae	*Helicostylis tomentosa*	1	0	0	0	0
Moraceae	*Helicostylis tovarensis*	0	0	0	3	0
Moraceae	*Morus insignis*	0	0	4	0	0
Moraceae	*Pseudolmedia laevigata*	0	5	0	0	0
Moraceae	*Pseudolmedia laevis*	5	0	0	0	0
Moraceae	*Pseudolmedia rigida*	0	0	1	0	0
Myricaceae	*Morella pubescens*	0	0	0	1	0
Myricaceae	*Myrica pubescens*	0	0	0	0	2
Myristicaceae	*Otoba parvifolia*	7	0	0	0	0
Myristicaceae	*Virola sebifera*	1	0	0	0	0
Myrtaceae	*Eugenia florida*	0	0	2	0	0
Myrtaceae	*Myrcia sp 1*	0	0	0	1	0
Nyctaginaceae	*Neea sp 1*	0	2	0	0	0
Nyctaginaceae	*Pisonia sp 1*	0	0	2	0	0
Olacaceae	*Heisteria sp 1*	0	0	1	0	0
Pentaphylacaceae	*Ternstroemia cf jelskii*	0	0	0	1	0
Pentaphylacaceae	*Ternstroemia macrocarpa*	0	0	0	0	1
Phyllanthaceae	*Hieronyma asperifolia*	0	0	0	3	0
Phyllanthaceae	*Hieronyma macrocarpa*	1	0	0	0	0
Phyllanthaceae	*Hieronyma oblonga*	2	0	0	0	0
Picramniaceae	*Picramnia cf latifolia*	1	0	0	0	0
Piperaceae	*Piper arboreum*	0	0	1	0	0
Podocarpaceae	*Podocarpus oleifolius*	0	0	0	1	4
Podocarpaceae	*Prumnopitys montana*	0	0	0	0	1
Primulaceae	*Geissanthus vanderwerfii*	0	0	0	0	1
Primulaceae	*Myrsine andina*	0	0	0	0	3
Primulaceae	*Myrsine coriacea*	0	0	0	3	0
Rosaceae	*Hesperomeles obtusifolia*	0	0	0	0	1
Rubiaceae	*Cordiera montana*	0	0	1	0	0
Rubiaceae	*Dioicodendron dioicum*	0	0	0	1	0
Rubiaceae	*Ladenbergia cf riveroana*	0	1	0	0	0
Rubiaceae	*Ladenbergia oblongifolia*	2	0	0	0	0
Rubiaceae	*Palicourea sp 1*	1	0	0	0	0
Rubiaceae	*Warszewiczia coccinea*	1	0	0	0	0
Salicaceae	*Banara nitida*	1	0	0	0	0
Sapindaceae	*Allophylus sp 1*	0	0	3	0	0
Sapindaceae	*Cupania sp 1*	0	0	1	0	0
Sapindaceae	*Matayba peruviana*	0	4	0	0	0
Sapotaceae	*Micropholis guyanensis*	0	0	1	0	0
Sapotaceae	*Pouteria bilocularis*	3	0	0	0	0
Solanaceae	*Solanum nutans*	0	0	0	1	0
Staphyleaceae	*Turpinia occidentalis*	0	0	3	0	0
Symplocaceae	*Symplocos bogotensis*	0	0	0	0	1
Theaceae	*Gordonia fruticosa*	0	1	1	0	0

Thymelaeaceae	*Daphnopsis sp 1*	0	0	1	0	0
Urticaceae	*Myriocarpa stipitata*	0	0	1	0	0
Violaceae	*Leonia cf glycycarpa*	0	0	1	0	0
Violaceae	*Leonia crassa*	1	0	0	0	0

Table B.3: Results from linear models for six fine root functional traits in dependency of soil C:N ratio (CN_{soil}), plant available phosphorus (P_{av}) and elevation. Models were fitted on the level of community weighted means for 23 plots. Parameters that are different from zero on a $p < 0.05$ level are highlighted.



Term	Estimate	Std. error	t value	P value	R^2
		Root diameter			0.253
intercept	-0.498	0.039	-12.61	**< 0.001**	
CN_{soil}	-0.048	0.044	-1.10	0.287	
P_{av}	-0.020	0.043	-0.46	0.651	
elevation	0.109	0.041	2.65	**0.016**	
		Specific root length			0.484
intercept	2.962	0.071	41.65	**< 0.001**	
CN_{soil}	0.021	0.079	0.26	0.798	
P_{av}	0.118	0.078	1.52	0.145	
elevation	-0.308	0.074	-4.15	**0.001**	
		Root tissue density			0.6
intercept	-1.098	0.025	-43.56	**< 0.001**	
CN_{soil}	0.111	0.028	3.95	**0.001**	
P_{av}	-0.049	0.028	-1.79	0.09	
elevation	0.038	0.026	1.44	0.166	
		Absorptive fine root fraction			0.37
intercept	-1.141	0.044	-26.09	**< 0.001**	
CN_{soil}	-0.088	0.049	-1.80	0.088	
P_{av}	0.034	0.048	0.71	0.484	
elevation	0.142	0.046	3.12	**0.006**	
		Root nitrogen concentration			0.78
intercept	2.765	0.032	86.20	**< 0.001**	
CN_{soil}	-0.146	0.036	-4.07	**0.001**	
P_{av}	0.074	0.035	2.11	**0.048**	
elevation	-0.191	0.033	-5.72	**< 0.001**	
		Root phosphorus concentration			0.681
intercept	-0.152	0.047	-3.25	**0.004**	
CN_{soil}	-0.175	0.052	-3.35	**0.003**	
P_{av}	0.149	0.051	2.90	**0.009**	
elevation	-0.153	0.049	-3.13	**0.006**	

Table B.4: Results from linear mixed models for six fine root functional traits in dependency of soil C:N ratio (CN_{soil}), plant available phosphorus (P_{av}) and elevation. Models were fitted on the level of individual trees (n = 288), with plot nested in site, and species, as random effects. Significant parameters ($p < 0.05$) are highlighted. “sd” stands for standard deviation.

Effect	Term	Estimate	Std. error	z value	P value	$R^2_{marginal}$	$R^2_{conditional}$
		Root diameter				0.031	0.636
fixed	**intercept**	-0.727	0.036	-20.04	**< 0.001**		
	elevation	0.073	0.038	1.91	0.056		
	CN_{soil}	-0.042	0.031	-1.36	0.175		
	P_{av}	0.024	0.028	0.88	0.381		
random	plot:site (intercepts sd)	$1e^{-5}$					
	site (intercepts sd)	$1e^{-7}$					
	Species (intercepts sd)	0.362					
	residual sd	0.281					
		Specific root length				0.04	0.696
fixed	**intercept**	2.845	0.067	42.38	**< 0.001**		
	elevation	-0.174	0.07	-2.48	**0.013**		
	CN_{soil}	-0.008	0.056	-0.14	0.886		
	P_{av}	0.028	0.051	0.55	0.58		
random	plot:site (intercepts sd)	0.072					
	site (intercepts sd)	$1e^{-5}$					
	Species (intercepts sd)	0.672					
	residual sd	0.46					
		Root tissue density				0.154	0.526
fixed	**intercept**	-1.148	0.029	-40.01	**< 0.001**		
	elevation	0.037	0.03	1.22	0.222		
	CN_{soil}	0.101	0.028	3.68	**< 0.001**		
	P_{av}	-0.082	0.026	-3.15	**0.002**		
random	plot:site (intercepts sd)	0.056					
	site (intercepts sd)	$1e^{-6}$					
	Species (intercepts sd)	0.226					
	residual sd	0.262					
		Absorptive fine root fraction				0.076	0.292
fixed	**intercept**	-1.457	0.053	-27.26	**< 0.001**		
	elevation	0.122	0.056	2.17	**0.03**		
	CN_{soil}	-0.025	0.053	-0.47	0.636		
	P_{av}	0.174	0.051	3.38	**0.001**		
random	plot:site (intercepts sd)	0.095					
	site (intercepts sd)	$1e^{-5}$					
	Species (intercepts sd)	0.328					
	residual sd	0.617					
		Root nitrogen concentration				0.293	0.708
fixed	**intercept**	2.741	0.045	61.04	**< 0.001**		
	elevation	-0.171	0.047	-3.60	**< 0.001**		
	CN_{soil}	-0.086	0.036	-2.42	**0.015**		
	P_{av}	0.092	0.038	2.39	**0.017**		

random	plot:site (intercepts sd)	0.090					
	site (intercepts sd)	0.070					
	Species (intercepts sd)	0.231					
	residual sd	0.216					
		Root phosphorus concentration				0.396	0.638
fixed	**intercept**	-0.241	0.053	-4.47	**< 0.001**		
	elevation	-0.135	0.054	-2.51	**0.012**		
	$\mathrm{CN}_{\mathrm{soil}}$	-0.177	0.043	-4.08	**< 0.001**		
	P_{av}	0.162	0.065	2.47	**0.013**		
random	plot:site (intercepts sd)	0.136					
	site (intercepts sd)	0.073					
	Species (intercepts sd)	0.175					
	residual sd	0.285					

Appendix C

Above- and belowground strategies

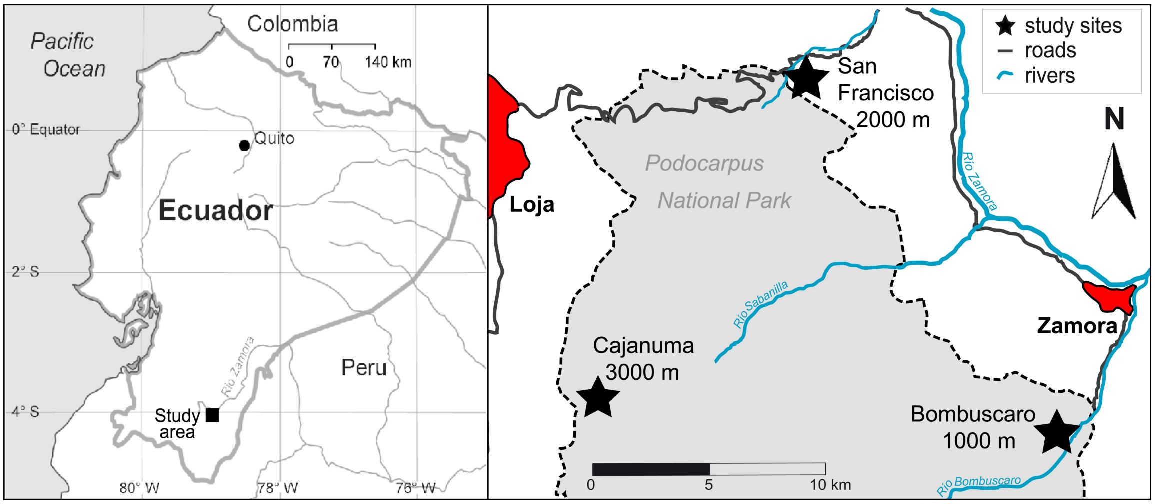


Figure C.1: Map of the study area.

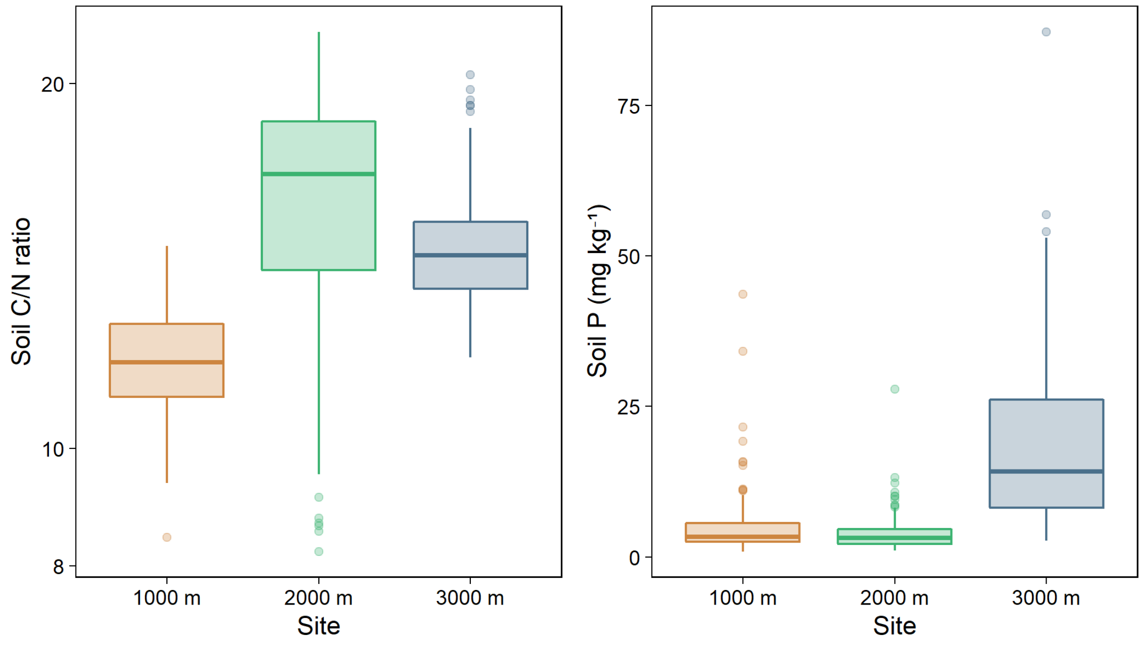


Figure C.2: Soil C/N ratio and soil Olsen P measured in vicinity to the sampled trees at three elevational levels.

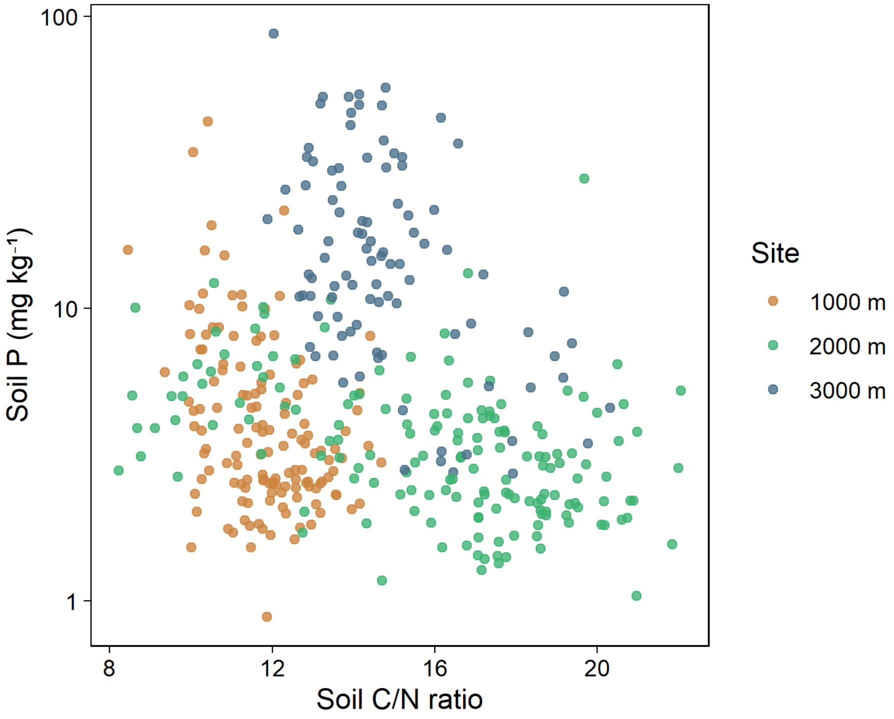
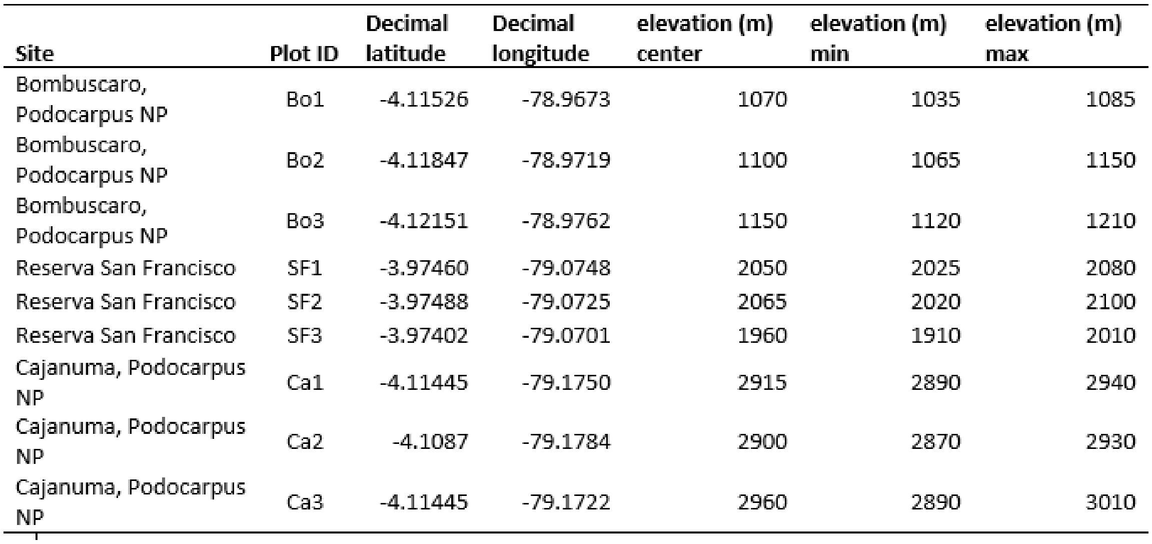


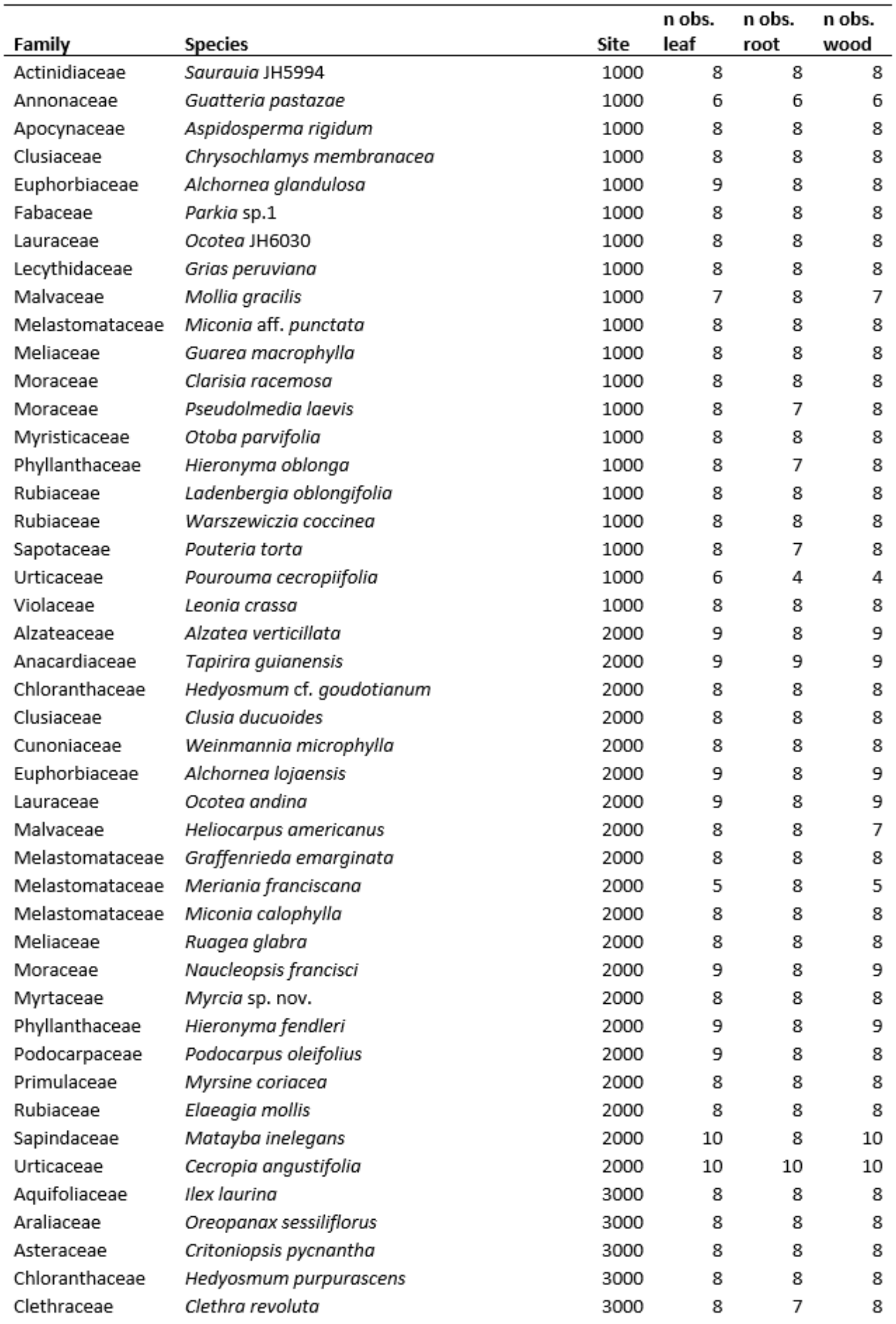
Figure C.3: Relationship between soil C/N ratio and soil Olsen P measured in vicinity to the sampled trees at three elevational levels.

Table C.1: List of permanent plots, their coordinates, and elevations.



Site	Plot ID	Decimal latitude	Decimal longitude	elevation (m) center	elevation (m) min	elevation (m) max
Bombuscaro, Podocarpus NP	Bo1	-4.11526	-78.9673	1070	1035	1085
Bombuscaro, Podocarpus NP	Bo2	-4.11847	-78.9719	1100	1065	1150
Bombuscaro, Podocarpus NP	Bo3	-4.12151	-78.9762	1150	1120	1210
Reserva San Francisco	SF1	-3.97460	-79.0748	2050	2025	2080
Reserva San Francisco	SF2	-3.97488	-79.0725	2065	2020	2100
Reserva San Francisco	SF3	-3.97402	-79.0701	1960	1910	2010
Cajanuma, Podocarpus NP	Ca1	-4.11445	-79.1750	2915	2890	2940
Cajanuma, Podocarpus NP	Ca2	-4.1087	-79.1784	2900	2870	2930
Cajanuma, Podocarpus NP	Ca3	-4.11445	-79.1722	2960	2890	3010

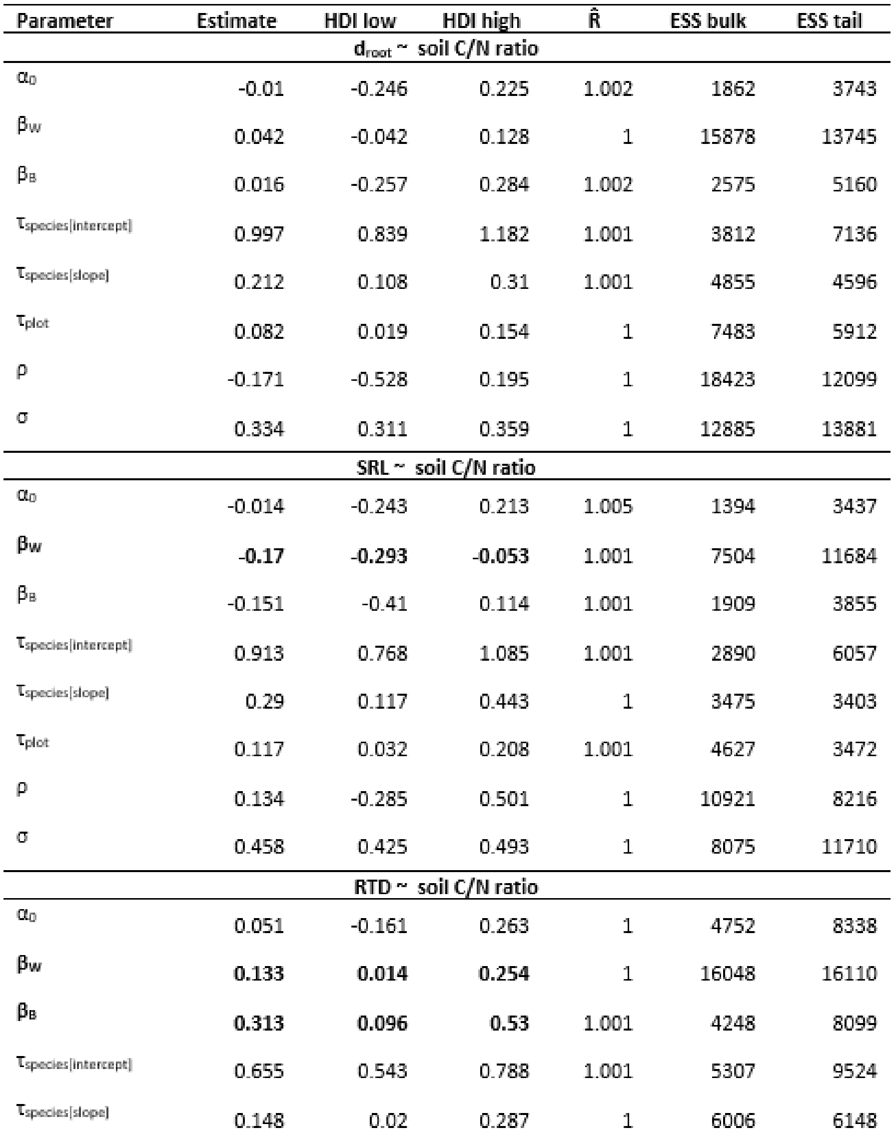
Table C.2: List of tree species with the number of replicates on which leaf, root and wood functional traits were measured.



Family	Species	Site	n obs. leaf	n obs. root	n obs. wood
Actinidiaceae	*Saurauia* JH5994	1000	8	8	8
Annonaceae	*Guatteria pastazae*	1000	6	6	6
Apocynaceae	*Aspidosperma rigidum*	1000	8	8	8
Clusiaceae	*Chrysochlamys membranacea*	1000	8	8	8
Euphorbiaceae	*Alchornea glandulosa*	1000	9	8	8
Fabaceae	*Parkia* sp.1	1000	8	8	8
Lauraceae	*Ocotea* JH6030	1000	8	8	8
Lecythidaceae	*Grias peruviana*	1000	8	8	8
Malvaceae	*Mollia gracilis*	1000	7	8	7
Melastomataceae	*Miconia* aff. *punctata*	1000	8	8	8
Meliaceae	*Guarea macrophylla*	1000	8	8	8
Moraceae	*Clarisia racemosa*	1000	8	8	8
Moraceae	*Pseudolmedia laevis*	1000	8	7	8
Myristicaceae	*Otoba parvifolia*	1000	8	8	8
Phyllanthaceae	*Hieronyma oblonga*	1000	8	7	8
Rubiaceae	*Ladenbergia oblongifolia*	1000	8	8	8
Rubiaceae	*Warszewiczia coccinea*	1000	8	8	8
Sapotaceae	*Pouteria torta*	1000	8	7	8
Urticaceae	*Pourouma cecropiifolia*	1000	6	4	4
Violaceae	*Leonia crassa*	1000	8	8	8
Alzateaceae	*Alzatea verticillata*	2000	9	8	9
Anacardiaceae	*Tapirira guianensis*	2000	9	9	9
Chloranthaceae	*Hedyosmum* cf. *goudotianum*	2000	8	8	8
Clusiaceae	*Clusia ducuoides*	2000	8	8	8
Cunoniaceae	*Weinmannia microphylla*	2000	8	8	8
Euphorbiaceae	*Alchornea lojaensis*	2000	9	8	9
Lauraceae	*Ocotea andina*	2000	9	8	9
Malvaceae	*Heliocarpus americanus*	2000	8	8	7
Melastomataceae	*Graffenrieda emarginata*	2000	8	8	8
Melastomataceae	*Meriania franciscana*	2000	5	8	5
Melastomataceae	*Miconia calophylla*	2000	8	8	8
Meliaceae	*Ruagea glabra*	2000	8	8	8
Moraceae	*Naucleopsis francisci*	2000	9	8	9
Myrtaceae	*Myrcia* sp. nov.	2000	8	8	8
Phyllanthaceae	*Hieronyma fendleri*	2000	9	8	9
Podocarpaceae	*Podocarpus oleifolius*	2000	9	8	8
Primulaceae	*Myrsine coriacea*	2000	8	8	8
Rubiaceae	*Elaeagia mollis*	2000	8	8	8
Sapindaceae	*Matayba inelegans*	2000	10	8	10
Urticaceae	*Cecropia angustifolia*	2000	10	10	10
Aquifoliaceae	*Ilex laurina*	3000	8	8	8
Araliaceae	*Oreopanax sessiliflorus*	3000	8	8	8
Asteraceae	*Critoniopsis pycnantha*	3000	8	8	8
Chloranthaceae	*Hedyosmum purpurascens*	3000	8	8	8
Clethraceae	*Clethra revoluta*	3000	8	7	8

Clusiaceae	*Clusia elliptica*	3000	8	7	8
Cunoniaceae	*Weinmannia elliptica*	3000	8	7	8
Lauraceae	*Aiouea dubia*	3000	8	7	8
Lauraceae	*Ocotea rotundata*	3000	8	7	8
Melastomataceae	*Miconia* cf. *jahnii*	3000	8	7	8
Siparunaceae	*Siparuna muricata*	3000	8	8	8
Theaceae	*Gordonia fruticosa*	3000	9	7	9

Table C.3: Inference and diagnostics from mixed models describing the dependency of functional traits on soil C/N ratio. α_0: Intercept. β_W: Within-species slope. β_B: Between-species slope. τ: Standard deviation parameters of random effects. ρ: Correlation between random slopes and intercepts. σ: residual variance. For more information on the model structure, see Method refmeth2. Shown are the posterior mean (Estimate) and the 95 % highest density intervals (HDI low and high) of each parameter. Slope parameters are considered credibly different from zero when the 95 % HDI does not include zero, in which case they are highlighted in bold case. As indicators of model convergence, $\hat{R}$, and bulk and tail effective sample sizes (ESS) are given.



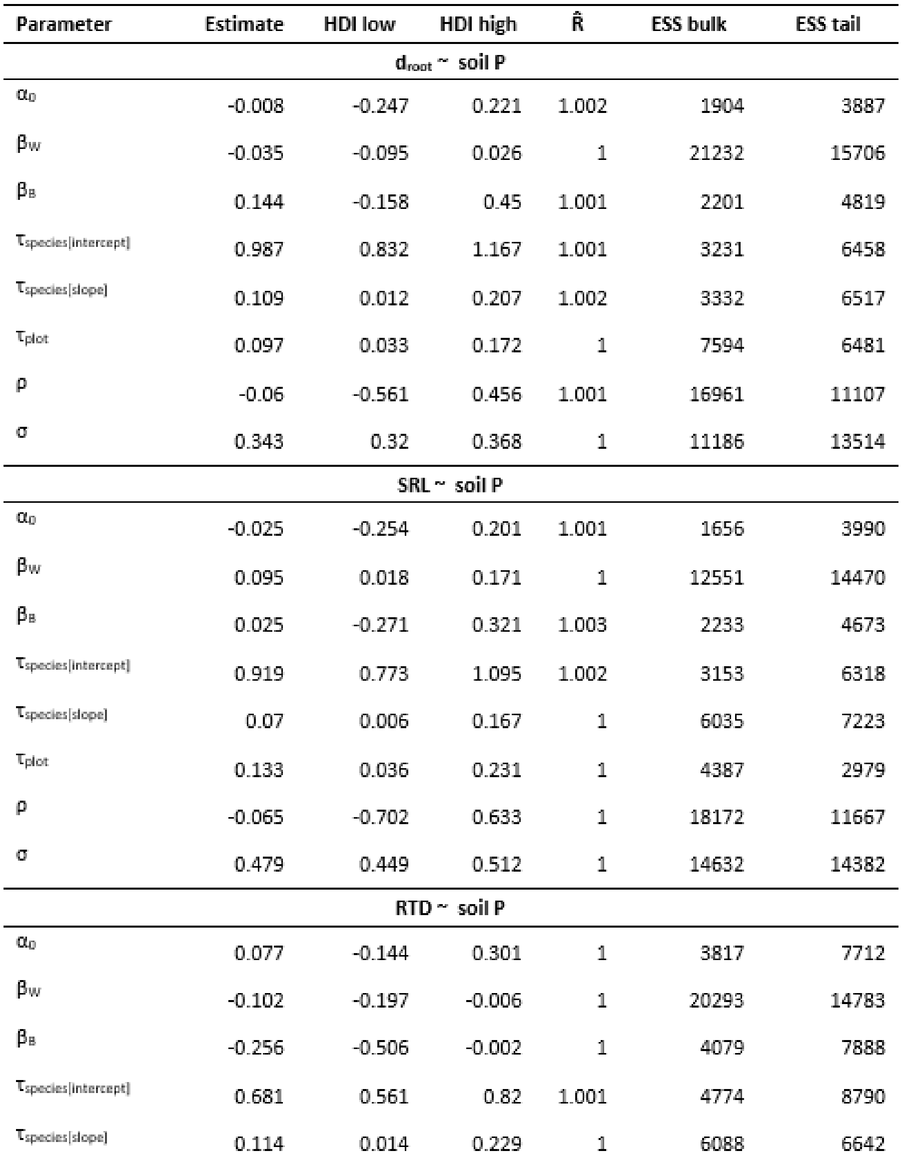
Parameter	Estimate	HDI low	HDI high	$\hat{R}$	ESS bulk	ESS tail
			d_{root} ~ soil C/N ratio			
α_0	-0.01	-0.246	0.225	1.002	1862	3743
β_W	0.042	-0.042	0.128	1	15878	13745
β_B	0.016	-0.257	0.284	1.002	2575	5160
$\tau_{species\|intercept}$	0.997	0.839	1.182	1.001	3812	7136
$\tau_{species\|slope}$	0.212	0.108	0.31	1.001	4855	4596
τ_{plot}	0.082	0.019	0.154	1	7483	5912
ρ	-0.171	-0.528	0.195	1	18423	12099
σ	0.334	0.311	0.359	1	12885	13881
			SRL ~ soil C/N ratio			
α_0	-0.014	-0.243	0.213	1.005	1394	3437
β_W	**-0.17**	**-0.293**	**-0.053**	1.001	7504	11684
β_B	-0.151	-0.41	0.114	1.001	1909	3855
$\tau_{species\|intercept}$	0.913	0.768	1.085	1.001	2890	6057
$\tau_{species\|slope}$	0.29	0.117	0.443	1	3475	3403
τ_{plot}	0.117	0.032	0.208	1.001	4627	3472
ρ	0.134	-0.285	0.501	1	10921	8216
σ	0.458	0.425	0.493	1	8075	11710
			RTD ~ soil C/N ratio			
α_0	0.051	-0.161	0.263	1	4752	8338
β_W	**0.133**	**0.014**	**0.254**	1	16048	16110
β_B	**0.313**	**0.096**	**0.53**	1.001	4248	8099
$\tau_{species\|intercept}$	0.655	0.543	0.788	1.001	5307	9524
$\tau_{species\|slope}$	0.148	0.02	0.287	1	6006	6148

τ_{plot}	0.25	0.172	0.338	1.001	11098	12697
ρ	0.348	-0.269	0.816	1	16149	10471
σ	0.575	0.538	0.614	1	19265	14637
N_{root} ~ soil C/N ratio						
α_0	-0.026	-0.2	0.148	1.001	2272	5082
β_W	**-0.154**	**-0.251**	**-0.05**	1	11518	12524
β_B	**-0.656**	**-0.861**	**-0.449**	1.001	2177	4232
$\tau_{species\|intercept\|}$	0.69	0.575	0.827	1.001	3567	7145
$\tau_{species\|slope\|}$	0.173	0.026	0.319	1.002	3479	4670
τ_{plot}	0.087	0.01	0.186	1.001	4474	6568
ρ	0.223	-0.309	0.677	1	10210	9005
σ	0.448	0.418	0.479	1	11269	14534
P_{root} ~ soil C/N ratio						
α_0	-0.034	-0.237	0.167	1.001	4550	7882
β_W	**-0.167**	**-0.267**	**-0.068**	1	19851	14995
β_B	**-0.576**	**-0.774**	**-0.375**	1.001	4202	7456
$\tau_{species\|intercept\|}$	0.562	0.464	0.68	1.001	4689	9164
$\tau_{species\|slope\|}$	0.067	0.005	0.168	1	9135	9420
τ_{plot}	0.271	0.198	0.356	1	11556	13002
ρ	0.107	-0.627	0.761	1	22034	12972
σ	0.504	0.473	0.538	1	20194	15010
LDMC ~ soil C/N ratio						
α_0	0.027	-0.162	0.22	1.002	2413	4615
β_W	0.017	-0.08	0.112	1	27587	15364
β_B	**0.306**	**0.086**	**0.528**	1.002	2316	4765
$\tau_{species\|intercept\|}$	0.788	0.658	0.94	1.001	3798	7601
$\tau_{species\|slope\|}$	0.103	0.009	0.229	1.001	6811	7743
τ_{plot}	0.044	0.003	0.112	1	10193	9396
ρ	0.184	-0.494	0.749	1	20790	13008
σ	0.53	0.497	0.565	1	19103	14063
$Tough_{leaf}$ ~ soil C/N ratio						
α_0	-0.018	-0.23	0.199	1.002	1561	3758
β_W	0.039	-0.02	0.099	1	16414	14975
β_B	**0.523**	**0.279**	**0.769**	1.003	2039	4003
$\tau_{species\|intercept\|}$	0.888	0.747	1.053	1.003	3556	6326
$\tau_{species\|slope\|}$	0.089	0.015	0.161	1.001	5112	5396
τ_{plot}	0.094	0.028	0.17	1	6385	5932

ρ	-0.156	-0.667	0.41	1	21037	12818
σ	0.265	0.247	0.283	1	18717	14893
Thick$_{leaf}$ ~ soil C/N ratio						
α_0	0.048	-0.22	0.333	1.001	5445	7598
β_W	0.059	-0.011	0.127	1	20235	13582
β_B	**0.505**	**0.265**	**0.737**	1.001	3613	6597
$\tau_{species[intercept]}$	0.638	0.521	0.781	1.001	3077	7006
$\tau_{species[slope]}$	0.103	0.012	0.204	1	4433	8275
τ_{plot}	0.394	0.13	0.765	1.001	1889	5290
ρ	0.005	-0.543	0.553	1	20512	12580
σ	0.3	0.28	0.321	1	14714	15414
LA ~ soil C/N ratio						
α_0	0.008	-0.201	0.223	1.002	1311	2781
β_W	-0.036	-0.089	0.019	1	13708	13230
β_B	**-0.627**	**-0.878**	**-0.375**	1.003	1792	3748
$\tau_{species[intercept]}$	0.849	0.708	1.017	1.001	2979	5871
$\tau_{species[slope]}$	0.112	0.04	0.178	1.001	4669	3834
τ_{plot}	0.026	0.002	0.072	1	9606	10877
ρ	0.161	-0.257	0.555	1	10711	10675
σ	0.228	0.212	0.245	1	12026	14053
SLA ~ soil C/N ratio						
α_0	-0.047	-0.236	0.142	1	2691	5307
β_W	-0.077	-0.159	0.008	1	11994	14072
β_B	**-0.595**	**-0.802**	**-0.381**	1.002	2674	5225
$\tau_{species[intercept]}$	0.68	0.555	0.825	1.001	2673	5593
$\tau_{species[slope]}$	0.141	0.032	0.242	1.001	4705	5405
τ_{plot}	0.164	0.068	0.281	1	2972	5390
ρ	0.282	-0.221	0.718	1	12393	10954
σ	0.372	0.348	0.398	1	13305	13079
N$_{leaf}$ ~ soil C/N ratio						
α_0	-0.01	-0.195	0.17	1.003	2112	4068
β_W	-0.02	-0.087	0.047	1	15654	15247
β_B	**-0.674**	**-0.885**	**-0.458**	1.003	2086	3881
$\tau_{species[intercept]}$	0.753	0.631	0.897	1.002	3132	5430
$\tau_{species[slope]}$	0.074	0.007	0.162	1.001	5857	7347
τ_{plot}	0.089	0.029	0.162	1.001	5852	4733
ρ	0.24	-0.436	0.774	1	17399	12324

σ	0.333	0.311	0.355	1	16312	15048
P_{leaf} ~ soil C/N ratio						
α_0	-0.023	-0.237	0.195	1.001	2913	5845
β_W	-0.062	-0.153	0.03	1	16261	13472
β_B	**-0.568**	**-0.8**	**-0.338**	1.001	3044	5579
$\tau_{species(intercept)}$	0.727	0.602	0.875	1.001	3210	6679
$\tau_{species(slope)}$	0.101	0.009	0.225	1.001	5084	8075
τ_{plot}	0.224	0.151	0.311	1	7680	12556
ρ	0.136	-0.534	0.699	1	18516	10728
σ	0.423	0.396	0.451	1.001	15987	15818
WSG ~ soil C/N ratio						
α_0	-0.006	-0.225	0.215	1.001	2367	5162
β_W	0.015	-0.057	0.088	1	22613	15567
β_B	**0.331**	**0.079**	**0.586**	1.001	3123	5230
$\tau_{species(intercept)}$	0.92	0.772	1.093	1.001	4036	7263
$\tau_{species(slope)}$	0.069	0.005	0.159	1	7614	7989
τ_{plot}	0.087	0.018	0.169	1	6707	6806
ρ	0.188	-0.518	0.765	1	23679	11849
σ	0.369	0.345	0.394	1	20154	14523

Table C.4: Inference and diagnostics from mixed models describing the dependency of functional traits on soil Olsen P. α_0: Intercept. β_W: Within-species slope. β_B: Between-species slope. τ: Standard deviation parameters of random effects. ρ: Correlation between random slopes and intercepts. σ: residual variance. For more information on the model structure, see Method refmeth2. Shown are the posterior mean (Estimate) and the 95 % highest density intervals (HDI low and high) of each parameter. Slope parameters are considered credibly different from zero when the 95 % HDI does not include zero, in which case they are highlighted in bold case. As indicators of model convergence, $\hat{R}$, and bulk and tail effective sample sizes (ESS) are given.



Parameter	Estimate	HDI low	HDI high	$\hat{R}$	ESS bulk	ESS tail
d_{root} ~ soil P						
α_0	-0.008	-0.247	0.221	1.002	1904	3887
β_W	-0.035	-0.095	0.026	1	21232	15706
β_B	0.144	-0.158	0.45	1.001	2201	4819
$\tau_{species\|intercept}$	0.987	0.832	1.167	1.001	3231	6458
$\tau_{species\|slope}$	0.109	0.012	0.207	1.002	3332	6517
τ_{plot}	0.097	0.033	0.172	1	7594	6481
ρ	-0.06	-0.561	0.456	1.001	16961	11107
σ	0.343	0.32	0.368	1	11186	13514
SRL ~ soil P						
α_0	-0.025	-0.254	0.201	1.001	1656	3990
β_W	0.095	0.018	0.171	1	12551	14470
β_B	0.025	-0.271	0.321	1.003	2233	4673
$\tau_{species\|intercept}$	0.919	0.773	1.095	1.002	3153	6318
$\tau_{species\|slope}$	0.07	0.006	0.167	1	6035	7223
τ_{plot}	0.133	0.036	0.231	1	4387	2979
ρ	-0.065	-0.702	0.633	1	18172	11667
σ	0.479	0.449	0.512	1	14632	14382
RTD ~ soil P						
α_0	0.077	-0.144	0.301	1	3817	7712
β_W	-0.102	-0.197	-0.006	1	20293	14783
β_B	-0.256	-0.506	-0.002	1	4079	7888
$\tau_{species\|intercept}$	0.681	0.561	0.82	1.001	4774	8790
$\tau_{species\|slope}$	0.114	0.014	0.229	1	6088	6642

τ_{plot}	0.251	0.17	0.341	1	11622	12345
ρ	-0.276	-0.784	0.341	1	15436	10661
σ	0.576	0.539	0.614	1	19177	13929
N_{root} ~ soil P						
α_0	-0.051	-0.279	0.18	1	3216	6402
β_W	0.054	-0.025	0.132	1	12819	14300
β_B	0.025	-0.258	0.307	1.001	3095	6131
$\tau_{species[intercept]}$	0.86	0.706	1.037	1.001	3783	6188
$\tau_{species[slope]}$	0.11	0.015	0.206	1	5467	7207
τ_{plot}	0.177	0.061	0.294	1.001	3386	3488
ρ	-0.2	-0.708	0.363	1	16347	13124
σ	0.453	0.424	0.484	1	14109	13923
P_{root} ~ soil P						
α_0	-0.071	-0.303	0.16	1.001	3956	7448
β_W	0.061	-0.027	0.15	1	16820	14883
β_B	0.28	0.018	0.538	1.003	3162	6713
$\tau_{species[intercept]}$	0.637	0.522	0.775	1.001	3880	7781
$\tau_{species[slope]}$	0.145	0.032	0.245	1	4026	2884
τ_{plot}	0.313	0.231	0.404	1	8694	11755
ρ	0.188	-0.296	0.639	1	11519	10612
σ	0.497	0.465	0.532	1	13914	14274
LDMC ~ soil P						
α_0	0.031	-0.172	0.234	1.002	2011	3879
β_W	0.064	-0.017	0.147	1	15687	15271
β_B	-0.046	-0.303	0.213	1.001	1985	3903
$\tau_{species[intercept]}$	0.832	0.696	0.993	1.001	3203	5829
$\tau_{species[slope]}$	0.109	0.01	0.234	1	4182	6383
τ_{plot}	0.058	0.004	0.146	1.001	5968	8226
ρ	-0.073	-0.631	0.542	1	13344	10998
σ	0.526	0.492	0.562	1	15278	13857
$Tough_{leaf}$ ~ soil P						
α_0	-0.013	-0.249	0.223	1.003	1352	2669
β_W	-0.042	-0.091	0.009	1	11079	13789
β_B	0.124	-0.166	0.418	1.004	1685	3645
$\tau_{species[intercept]}$	0.996	0.84	1.183	1.003	2148	4297
$\tau_{species[slope]}$	0.104	0.057	0.154	1	8134	7173

τ_{plot}	0.065	0.008	0.14	1	5109	6534
ρ	-0.251	-0.63	0.157	1	16685	14420
σ	0.26	0.243	0.278	1	16483	14428
			$Thick_{leaf}$ ~ soil P			
α_0	0.013	-0.197	0.216	1.002	2822	5111
β_W	-0.002	-0.057	0.052	1	19369	15669
β_B	0.397	0.14	0.653	1.001	2818	5133
$\tau_{species[intercept]}$	0.774	0.632	0.94	1.002	2677	4751
$\tau_{species[slope]}$	0.068	0.007	0.143	1	5012	7891
τ_{plot}	0.182	0.096	0.288	1.002	4208	7802
ρ	-0.065	-0.662	0.534	1.001	23140	12030
σ	0.302	0.282	0.322	1	18073	14704
			LA ~ soil P			
α_0	0.015	-0.222	0.252	1.002	1007	2592
β_W	0.037	0.001	0.074	1	18883	14710
β_B	-0.412	-0.696	-0.128	1.002	1803	3578
$\tau_{species[intercept]}$	0.957	0.802	1.143	1.001	2342	4954
$\tau_{species[slope]}$	0.035	0.003	0.085	1	6839	7380
τ_{plot}	0.028	0.002	0.074	1	9775	8352
ρ	-0.241	-0.807	0.486	1	19079	12908
σ	0.235	0.22	0.251	1	19972	14701
			SLA ~ soil P			
α_0	-0.053	-0.274	0.172	1.001	3502	6412
β_W	0.028	-0.04	0.098	1	13974	13184
β_B	-0.304	-0.572	-0.04	1.001	3500	6569
$\tau_{species[intercept]}$	0.781	0.628	0.958	1.001	3527	7555
$\tau_{species[slope]}$	0.085	0.012	0.165	1	6007	8303
τ_{plot}	0.21	0.102	0.331	1.001	3382	6804
ρ	-0.309	-0.81	0.309	1	21774	12775
σ	0.375	0.351	0.4	1	20918	15196
			N_{leaf} ~ soil P			
α_0	-0.018	-0.245	0.211	1.002	1753	3887
β_W	0.037	-0.018	0.09	1	20935	15356
β_B	-0.066	-0.347	0.223	1	2411	4763
$\tau_{species[intercept]}$	0.956	0.802	1.136	1.002	3355	6763
$\tau_{species[slope]}$	0.061	0.007	0.126	1	7736	7539

τ_{plot}	0.084	0.02	0.162	1	6689	6505
ρ	-0.293	-0.804	0.364	1	25946	13895
σ	0.332	0.311	0.355	1	24181	14152
P_{leaf} ~ soil P						
α_0	-0.035	-0.268	0.198	1.002	2861	5577
β_W	0.039	-0.044	0.119	1	13959	14367
β_B	0.125	-0.16	0.409	1.003	2806	5217
$\tau_{species[intercept]}$	0.855	0.712	1.025	1.001	3528	6260
$\tau_{species[slope]}$	0.144	0.048	0.233	1.001	4639	4709
τ_{plot}	0.215	0.139	0.306	1.001	9505	13023
ρ	-0.2	-0.626	0.244	1	15730	12469
σ	0.416	0.388	0.445	1	11353	13369
WSG ~ soil P						
α_0	0.002	-0.232	0.236	1.002	2195	4468
β_W	-0.014	-0.077	0.049	1	20359	15139
β_B	0.08	-0.222	0.385	1.001	2798	5301
$\tau_{species[intercept]}$	0.972	0.818	1.154	1.001	4359	7733
$\tau_{species[slope]}$	0.1	0.018	0.181	1.001	5598	7114
τ_{plot}	0.077	0.013	0.153	1	7085	7897
ρ	-0.163	-0.692	0.427	1	14987	13005
σ	0.365	0.341	0.39	1	17264	14251

Table C.5: Marginal and conditional R^2 values for all models of functional traits in dependency of soil C/N ratio and Olsen P.

Model	**R^2 marginal**	**R^2 conditional**
d_{root} ~ soil C/N ratio	0.01	0.89
SRL ~ soil C/N ratio	0.03	0.79
RTD ~ soil C/N ratio	0.08	0.66
N_{root} ~ soil C/N ratio	0.34	0.80
P_{root} ~ soil C/N ratio	0.28	0.75
LDMC ~ soil C/N ratio	0.08	0.70
$Tough_{leaf}$ ~ soil C/N ratio	0.20	0.93
$Thick_{leaf}$ ~ soil C/N ratio	0.24	0.90
LA ~ soil C/N ratio	0.29	0.95
SLA ~ soil C/N ratio	0.30	0.86
N_{leaf} ~ soil C/N ratio	0.34	0.89
P_{leaf} ~ soil C/N ratio	0.23	0.82
WSG ~ soil C/N ratio	0.08	0.87
d_{root} ~ soil P	0.02	0.89
SRL ~ soil P	0.01	0.77
RTD ~ soil P	0.05	0.66
N_{root} ~ soil P	0.01	0.80
P_{root} ~ soil P	0.05	0.75
LDMC ~ soil P	0.01	0.70
$Tough_{leaf}$ ~ soil P	0.01	0.93
$Thick_{leaf}$ ~ soil P	0.11	0.90
LA ~ soil P	0.11	0.95
SLA ~ soil P	0.06	0.86
N_{leaf} ~ soil P	0.01	0.89
P_{leaf} ~ soil P	0.02	0.83
WSG ~ soil P	0.01	0.87

C.1 Method: Within-group centering multilevel models

In order to test for associations between traits and N and P availability, we used mixed models with the technique of within-group centering (van de Pol & Wright, 2009), which allows to discriminate between effects within and between groups (in our case, species). We fitted one model for each combination of the 13 functional traits and the two predictors Soil C/N ratio and Soil P, leading to a total of 26 models. We chose this approach instead of fitting models with both predictors at once 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 log-transformed, centered and scaled, except for WSG, which was not log-transformed. The log transformations were done to deal with issues of heteroscedasticity and right-skewed trait distributions, while the centering and scaling was done to be able to compare parameter estimates between models. We also centered and scaled both predictors, and additionally log-transformed soil P because it was highly right-skewed. The models were fitted in a hierarchical Bayesian framework.

We assumed the observed trait values y_{ijk} for observation i, species j and plot k to be normally distributed across their conditional mean μ_{ijk} with residual standard deviation σ :

$$y_{ijk} \sim \text{Normal}(\mu_{ijk}, \sigma)$$

Here, the conditional mean μ_{ijk} is expressed as a linear function of both the group-centered predictors $x_{ij} - \bar{x}_j$ and the species level averages $\bar{x}_j$.

$$\mu_{ijk} = \alpha_0 + \alpha_{species[j]} + \alpha_{plot[k]} + (\beta_W + \beta_{W[species][j]})(x_{ij} - \bar{x}_j) + \beta_B \bar{x}_j$$

where $alpha_0$ is the overall intercept, $\alpha_{species[j]}$ and $\alpha_{plot[k]}$ ar random intercepts for species and plot, respecively, β_W and β_B are the average within- and between-species slopes and $\beta_{W[species][j]}$ is a species-specific random within-species slope.

On the parameter level, we assumed plot-specific random intercepts to be normally distributed with a mean of zero and a standard deviation τ_{plot}, while the species-specific random intercept and slope were assumed to be distributed according to a multivariate normal distribution with mean 0 and covariance matrix Σ containing the random effects standard deviations $\tau_{species[slope]}$ and $\tau_{species[intercept]}$ and their correlation ρ.

$$\alpha_{plot} \sim \text{Normal}(0, \tau_{plot})$$

$$\begin{bmatrix} \alpha_{species} \\ \beta_{W[species]} \end{bmatrix} \sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \Sigma \right)$$

We assigned moderately informative priors to all model parameters that were intended to constrain the parameters to reasonable ranges and assuring convergence without overpowering the posterior.

$$\alpha_0 \sim \text{normal}\,(\mu = 0, \sigma = 1)$$

$$\beta \sim \text{normal}\,(\mu = 0, \sigma = 1)$$

$$\tau_{species[intercept]} \sim \text{normal}\,(\mu = 0, \sigma = 1)$$

$$\tau_{species[slope]} \sim \text{normal}\,(\mu = 0, \sigma = 0.2)$$

$$\tau_{plot} \sim \text{normal}\,(\mu = 0, \sigma = 0.1)$$

$$\rho \sim \text{LKJ}\,(\eta = 2)$$

The models were fit with the R package `brms` (Bürkner, 2017), which performs Hamilton Monte Carlo (HMC) sampling (Betancourt & Girolami, 2015) based on the probabilistic programming language Stan (Carpenter *et al.*, 2017). For each model, we fitted 4 parallel chains with 10000 iterations each, of which the first 5000 were used for warm-up. We set the adapt_delta value to 0.95 and the maximum tree depth to 15. Convergence was assessed by the inspection of the $\hat{R}$ criterion (Vehtari *et al.*, 2021) and visual inspection of trace plots for the main model parameters. Further, we used approximate leave-one-out cross validation (LOO CV) based on Pareto-smoothed importance sampling (Vehtari *et al.*, 2017) to identify highly influential observations. The samples for all main parameters in all models reached $\hat{R}$ below 1.004 (indicating full convergence) and achieved an effective sample size of > 3000 (Tables C.3 and C.4). In LOO CV, no model hat any observations with a Pareto tail shape parameter $k > 0.7$ (indicating problematic model fits). We assumed parameters to be credibly different from zero when their 95 %% highest posterior density interval (Kruschke, 2011) excluded zero.

References

A'Bear AD, Johnson SN, Jones TH. **2014**. Putting the "upstairs–downstairs" into ecosystem service: What can aboveground–belowground ecology tell us? *Biological Control* **75**: 97–107.

Adams TS, McCormack ML, Eissenstat DM. **2013**. Foraging strategies in trees of different root morphology: The role of root lifespan. *Tree Physiology* **33**: 940–948.

Addo-Danso SD, Defrenne CE, McCormack ML, Ostonen I, Addo-Danso A, Foli EG, Borden KA, Isaac ME, Prescott CE. **2020**. Fine-root morphological trait variation in tropical forest ecosystems: An evidence synthesis. *Plant Ecology* **221**: 1–13.

Albrecht J, Classen A, Vollstädt MGR, Mayr A, Mollel NP, Costa DS, Dulle HI, Fischer M, Hemp A, Howell KM, *et al.* **2018**. Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. *Nature Communications* **9**: 3177.

Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J. **2018**. Within-species patterns challenge our understanding of the leaf economics spectrum (J Penuelas, Ed.). *Ecology Letters* **21**: 734–744.

Apaza-Quevedo A, Lippok D, Hensen I, Schleuning M, Both S. **2015**. Elevation, Topography, and Edge Effects Drive Functional Composition of Woody Plant Species in Tropical Montane Forests. *Biotropica* **47**: 449–458.

Asefa M, Cao M, Zhang G, Ci X, Li J, Yang J. **2017**. Environmental filtering structures tree functional traits combination and lineages across space in tropical tree assemblages. *Scientific Reports* **7**: 132.

Asner GP, Martin RE. **2016**. Convergent elevation trends in canopy chemical traits of tropical forests. *Global Change Biology* **22**: 2216–2227.

Asner GP, Martin RE, Tupayachi R, Anderson CB, Sinca F, Carranza-Jimenez L, Martinez P. **2014**. Amazonian functional diversity from forest canopy chemical assembly. *Proceedings of the National Academy of Sciences* **111**: 5604–5609.

Assefa D, Godbold DL, Belay B, Abiyu A, Rewald B. **2018**. Fine root morphology, biochemistry and litter quality indices of fast- and slow-growing woody species in ethiopian highland forest. *Ecosystems* **21**: 482–494.

Báez S, Homeier J. **2018**. Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: Insights from a long-term nutrient manipulation experiment. *Global Change Biology* **24**: 399–409.

Báez S, Jaramillo L, Cuesta F, Donoso DA. **2016**. Effects of climate change on Andean biodiversity: A synthesis of studies published until 2015. *Neotropical Biodiversity* **2**: 181–194.

Báez S, Malizia A, Carilla J, Blundo C, Aguilar M, Aguirre N, Aquirre Z, Álvarez E, Cuesta F, Duque Á, *et al.* **2015**. Large-scale patterns of turnover and basal area change in Andean forests. *PLOS ONE* **10**: e0126594.

Bañares-de-Dios G, Macía MJ, Granzow-de la Cerda Í, Arnelas I, Martins de Carvalho G, Espinosa CI, Salinas N, Swenson NG, Cayuela L. **2020**. Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests. *Ecology* **101**: e03058.

Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, Domenach A-M, Hérault B, Patiño S, Roggy J-C, Chave J. **2010a**. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* **13**: 1338–1347.

Baraloto C, Timothy Paine CE, Patiño S, Bonal D, Hérault B, Chave J. **2010b**. Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology* **24**: 208–216.

Bardgett RD, Mommer L, De Vries FT. **2014**. Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution* **29**: 692–699.

Beck E, Makeschin F, Haubrich F, Richter M, Bendix J, Valerezo C. **2008**. The ecosytem (Reserva Biológica San Francisco). In: Ecological Studies. Gradients in a tropical mountain ecosystem of Ecuador. Berlin, Heidelberg: Springer, 1–13.

Beck E, Richter M. **2008**. Ecological aspcets of a biodiversity hotspot in the Andes of southern Ecuador. In: Gradstein SR, Homeier J, Gansert D, eds. The tropical mountain forest. Patterns and processes in a biodiversity hotspot. Göttingen: Univ.-Verl. Göttingen, 195–217.

Bendix J, Aguire N, Beck E, Bräuning A, Brandl R, Breuer L, Böhning-Gaese K, de Paula MD, Hickler T, Homeier J, *et al.* **2021**. A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. *Oecologia* **195**: 589–600.

Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W (Eds.). **2013**. *Ecosystem Services, Biodiversity and Environmental Change in a*

Tropical Mountain Ecosystem of South Ecuador. Springer Science & Business Media.

Bendix J, Rollenbeck RT, Richter M, Fabian P, Emck P. **2008**. Climate. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer Berlin Heidelberg, 63–73.

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM, *et al.* **2020**. The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**: eaba3756.

Betancourt M, Girolami M. **2015**. Hamiltonian Monte Carlo for Hierarchical Models. In: Dipak US, Dey K, Loganathan A, eds. Current Trends in Bayesian Methodology with Applications. Boca Raton (FL, USA), London (GB), New York (NY, USA): Chapman & Hall/CRC Pres.

Blanchard G, Munoz F, Ibanez T, Hequet V, Vandrot H, Girardi J, Birnbaum P. **2019**. Regional rainfall and local topography jointly drive tree community assembly in lowland tropical forests of New Caledonia. *Journal of Vegetation Science.*

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. **2011**. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* **26**: 183–192.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM. **2017**. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal* **9**: 378–400.

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, Jansen F, *et al.* **2018**. Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**: 1906.

Bruijnzeel LA, Scatena FN, Hamilton LS. **2011**. *Tropical Montane Cloud Forests: Science for Conservation and Management.* Cambridge University Press.

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C. **2015**. How tree roots respond to drought. *Frontiers in Plant Science* **6**.

Bürkner P-C. **2017**. Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**: 1–28.

Bürkner P-C. **2020**. Estimating phylogenetic multilevel models with brms.

Burton JI, Perakis SS, Brooks JR, Puettmann KJ. **2020**. Trait integration and functional differentiation among co-existing plant species. *American Journal of*

Botany **107**: 628–638.

Butterfield BJ, Suding KN. **2013**. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* **101**: 9–17.

Cadotte MW, Carscadden K, Mirotchnick N. **2011**. Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**: 1079–1087.

Cárate-Tandalla D, Camenzind T, Leuschner C, Homeier J. **2018**. Contrasting species responses to continued nitrogen and phosphorus addition in tropical montane forest tree seedlings. *Biotropica* **50**: 234–245.

Carmona CP, Bueno CG, Toussaint A, Träger S, Díaz S, Moora M, Munson AD, Pärtel M, Zobel M, Tamme R. **2021**. Fine-root traits in the global spectrum of plant form and function. *Nature* **597**: 683–687.

Carmona CP, Rota C, Azcárate FM, Peco B. **2015**. More for less: Sampling strategies of plant functional traits across local environmental gradients. *Functional Ecology* **29**: 579–588.

Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A. **2017**. Stan : A Probabilistic Programming Language. *Journal of Statistical Software* **76**.

Chalmandrier L, Münkemüller T, Colace M-P, Renaud J, Aubert S, Carlson BZ, Clément J-C, Legay N, Pellet G, Saillard A, *et al.* **2017**. Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. *Journal of Ecology* **105**: 277–287.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. **2009**. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. **2016**. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences* **113**: 8741–8746.

Chen W, Zeng H, Eissenstat DM, Guo D. **2013**. Variation of first-order root traits across climatic gradients and evolutionary trends in geological time: Root trait variation and evolution. *Global Ecology and Biogeography* **22**: 846–856.

Clark JS, Bell DM, Hersh MH, Kwit MC, Moran E, Salk C, Stine A, Valle D, Zhu K. **2011**. Individual-scale variation, species-scale differences: Inference needed to understand diversity. *Ecology Letters* **14**: 1273–1287.

Comas L, Bouma T, Eissenstat D. **2002**. Linking root traits to potential growth rate in six temperate tree species. *Oecologia* **132**: 34–43.

Comas LH, Callahan HS, Midford PE. **2014**. Patterns in root traits of woody species hosting arbuscular and ectomycorrhizas: Implications for the evolution of belowground strategies. *Ecology and Evolution* **4**: 2979–2990.

Comas LH, Eissenstat DM. **2004**. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **18**: 388–397.

Craine JM, Lee WG. **2003**. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia* **134**: 471–478.

Curatola Fernández GF, Obermeier WA, Gerique A, López Sandoval MF, Lehnert LW, Thies B, Bendix J. **2015**. Land cover change in the Andes of southern Ecuador—patterns and drivers. *Remote Sensing* **7**: 2509–2542.

Cusack DF, Addo-Danso SD, Agee EA, Andersen KM, Arnaud M, Batterman SA, Brearley FQ, Ciochina MI, Cordeiro AL, Dallstream C, *et al.* **2021**. Tradeoffs and synergies in tropical forest root traits and dynamics for nutrient and water acquisition: Field and modeling advances. *Frontiers in Forests and Global Change* **4**: 704469.

Dantas de Paula M, Forrest M, Langan L, Bendix J, Homeier J, Velescu A, Wilcke W, Hickler T. **2021**. Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot. *New Phytologist* **232**: 551–566.

de Bello F, Lepš J, Sebastià M-T. **2006**. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* **29**: 801–810.

de la Cruz-Amo L, Bañares-de-Dios G, Cala V, Granzow-de la Cerda Í, Espinosa CI, Ledo A, Salinas N, Macía MJ, Cayuela L. **2020**. Trade-offs among aboveground, belowground, and soil organic carbon stocks along altitudinal gradients in Andean tropical montane forests. *Frontiers in Plant Science* **11**.

de la Riva EG, Marañón T, Pérez-Ramos IM, Navarro-Fernández CM, Olmo M, Villar R. **2018**. Root traits across environmental gradients in Mediterranean woody communities: Are they aligned along the root economics spectrum? *Plant and Soil* **424**: 35–48.

De Bello F, Carmona CP, Dias ATC, Götzenberger L, Moretti M, Berg MP. **2021**. *Handbook of Trait-Based Ecology: From Theory to R Tools.* Cambridge University Press.

Defrenne CE, Abs E, Longhi Cordeiro A, Dietterich L, Hough M, Jones

JM, Kivlin SN, Chen W, Cusack D, Franco ALC, *et al.* 2021. The Ecology Underground coalition: Building a collaborative future of belowground ecology and ecologists. *New Phytologist* **229**: 3058–3064.

Delpiano CA, Prieto I, Loayza AP, Carvajal DE, Squeo FA. **2020**. Different responses of leaf and root traits to changes in soil nutrient availability do not converge into a community-level plant economics spectrum. *Plant and Soil* **450**: 436–478.

Díaz S, Cabido M. **2001**. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* **16**: 646–655.

Díaz S, Cabido M, Casanoves F. **1998**. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* **9**: 113–122.

Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, *et al.* 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I, *et al.* 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Díaz S, Lavorel S, Bello F de, Quétier F, Grigulis K, Robson TM. **2007**. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* **104**: 20684–20689.

Ding J, Kong D, Zhang Z, Cai Q, Xiao J, Liu Q, Yin H. **2020**. Climate and soil nutrients differentially drive multidimensional fine root traits in ectomycorrhizal-dominated alpine coniferous forests. *Journal of Ecology* **108**: 2544–2556.

Ding Y, Zang R, Lu X, Huang J, Xu Y. **2019**. The effect of environmental filtering on variation in functional diversity along a tropical elevational gradient. *Journal of Vegetation Science* **30**: 973–983.

Dong N, Prentice IC, Wright IJ, Evans BJ, Togashi HF, Caddy-Retalic S, McInerney FA, Sparrow B, Leitch E, Lowe AJ. **2020**. Components of leaf-trait variation along environmental gradients. *New Phytologist* **228**: 82–94.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, *et al.* 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27–46.

Duque A, Peña MA, Cuesta F, González-Caro S, Kennedy P, Phillips OL, Calderón-Loor M, Blundo C, Carilla J, Cayola L, *et al.* 2021. Mature Andean forests as globally important carbon sinks and future carbon refuges. *Nature*

Communications **12**: 2138.

Duque A, Stevenson PR, Feeley KJ. **2015**. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences* **112**: 10744–10749.

Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. **2015**. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114–124.

Emck P. **2007**. A climatology of South Ecuador - with special focus on the major Andean ridge as Atlantic-Pacific climate divide.

Enquist BJ, Norberg J, Bonser SP, Violle C, Webb CT, Henderson A, Sloat LL, Savage VM. **2015**. Scaling from Traits to Ecosystems. In: Advances in Ecological Research. Elsevier, 249–318.

Fadrique B, Báez S, Duque Á, Malizia A, Blundo C, Carilla J, Osinaga-Acosta O, Malizia L, Silman M, Farfán-Ríos W, *et al.* **2018**. Widespread but heterogeneous responses of Andean forests to climate change. *Nature* **564**: 207–212.

Faith DP. **1992**. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**: 1–10.

Fort F, Freschet GT. **2020**. Plant ecological indicator values as predictors of fine-root trait variations (H Kroon, Ed.). *Journal of Ecology* **108**: 1565–1577.

Fortunel C, Fine PVA, Baraloto C. **2012**. Leaf, stem and root tissue strategies across 758 Neotropical tree species (J Dalling, Ed.). *Functional Ecology* **26**: 1153–1161.

Fotis AT, Murphy SJ, Ricart RD, Krishnadas M, Whitacre J, Wenzel JW, Queenborough SA, Comita LS. **2018**. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. *Journal of Ecology* **106**: 561–570.

Freschet GT, Cornelissen JHC, van Logtestijn RSP, Aerts R. **2010**. Evidence of the "plant economics spectrum" in a subarctic flora. *Journal of Ecology* **98**: 362–373.

Freschet G, Pagès L, Iversen C, Comas L, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma J, *et al.* **2021a**. A starting guide to root ecology: Strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements. : 291.

Freschet GT, Roumet C. **2017**. Sampling roots to capture plant and soil functions. *Functional Ecology* **31**: 1506–1518.

Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald

B, Bardgett RD, De Deyn GB, Johnson D, Klimešová J, *et al.* 2021b. Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. *New Phytologist*: nph.17072.

Freschet GT, Valverde-Barrantes OJ, Tucker CM, Craine JM, McCormack ML, Violle C, Fort F, Blackwood CB, Urban-Mead KR, Iversen CM, *et al.* 2017. Climate, soil and plant functional types as drivers of global fine-root trait variation. *Journal of Ecology* **105**: 1182–1196.

Funk JL, Larson JE, Ames GM, Butterfield BJ, Cavender-Bares J, Firn J, Laughlin DC, Sutton-Grier AE, Williams L, Wright J. 2017. Revisiting the Holy Grail: Using plant functional traits to understand ecological processes: Plant functional traits. *Biological Reviews* **92**: 1156–1173.

Garavito NT, Newton AC, Golicher D, Oldfield S. 2015. The relative impact of climate change on the extinction risk of tree species in the montane tropical Andes. *PLOS ONE* **10**: e0131388.

Garnier E, Navas M-L, Grigulis K. 2016. *Plant functional diversity: Organism traits, community structure, and ecosystem properties.* Oxford, United Kingdom: Oxford University Press.

Gelman A, Goodrich B, Gabry J, Vehtari A. 2019. R-squared for Bayesian regression models. *The American Statistician* **73**: 307–309.

Girardin CAJ, Aragão LEOC, Malhi Y, Huaraca Huasco W, Metcalfe DB, Durand L, Mamani M, Silva-Espejo JE, Whittaker RJ. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles* **27**: 252–264.

Graefe S, Hertel D, Leuschner C. 2008. Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil* **313**: 155–166.

Graefe S, Hertel D, Leuschner C. 2010. N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests. *Acta Oecologica* **36**: 537–542.

Guisan A, Weiss SB, Weiss AD. 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology* **143**: 107–122.

Guo D, Xia M, Wei X, Chang W, Liu Y, Wang Z. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytologist* **180**: 673–683.

Hertel D, Leuschner C. 2011. Fine root mass and fine root production in tropical moist forests as dependent on soil, climate, and elevation. In: Bruijnzeel LA, Scatena

FN, Hamilton LS, eds. Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge: Cambridge University Press.

Hertel D, Leuschner C, Hölscher D. **2003**. Size and Structure of Fine Root Systems in Old-growth and Secondary Tropical Montane Forests (Costa Rica). *Biotropica* **35**: 143–153.

Hodge A. **2004**. The plastic plant: Root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.

Hogan JA, Valverde-Barrantes OJ, Ding Q, Xu H, Baraloto C. **2020**. Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China. *Annals of Forest Science* **77**: 79.

Hogan JA, Valverde-Barrantes OJ, Tang W, Ding Q, Xu H, Baraloto C. **2021**. Evidence of elemental homeostasis in fine root and leaf tissues of saplings across a fertility gradient in tropical montane forest in Hainan, China. *Plant and Soil* **460**: 625–646.

Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. **2011**. Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest: Root trait shifts along soil chronosequence. *Journal of Ecology* **99**: 954–963.

Homeier J. **2008**. The influence of topography on forest structure and regeneration dynamics in an Ecuadorian montane forest. In: Gradstein SR, Homeier J, Gansert D, eds. Biodiversity and Ecology Series. The Tropical Mountain Forest – Patterns and Processes in a Biodiversity Hotspot. Göttingen Centre for Biodiversity and Ecology, 97–107.

Homeier J, Breckle S-W, Günter S, Rollenbeck RT, Leuschner C. **2010**. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica* **42**: 140–148.

Homeier J, Hertel D, Camenzind T, Cumbicus NL, Maraun M, Martinson GO, Poma LN, Rillig MC, Sandmann D, Scheu S, *et al.* **2012**. Tropical Andean forests are highly susceptible to nutrient inputs—rapid effects of experimental N and P addition to an Ecuadorian montane forest. *PLOS ONE* **7**: e47128.

Homeier J, Leuschner C. **2021**. Factors controlling the productivity of tropical Andean forests: Climate and soil are more important than tree diversity. *Biogeosciences* **18**: 1525–1541.

Homeier J, Leuschner C, Bräuning A, Cumbicus NL, Hertel D, Martinson GO, Spannl S, Veldkamp E. **2013**. Effects of nutrient addition on the productivity of montane forests and implications for the carbon cycle. In: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W, eds. Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Berlin, Heidelberg: Springer Berlin Heidelberg, 315–329.

Homeier J, Seeler T, Pierick K, Leuschner C. **2021**. Leaf trait variation in species-rich tropical Andean forests. *Scientific Reports* **11**: 9993.

Homeier J, Werner FA, Gradstein SR, Breckle S-W, Richter M. **2008**. Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. Ecological Studies. Gradients in a Tropical Mountain Ecosystem of Ecuador. Berlin, Heidelberg: Springer.

Huasco WH, Riutta T, Girardin CAJ, Pacha FH, Vilca BLP, Moore S, Rifai SW, Aguila-Pasquel J del, Murakami AA, Freitag R, *et al.* **2021**. Fine root dynamics across pantropical rainforest ecosystems. *Global Change Biology* **27**: 3657–3680.

Hu Y, Pan X, Yang X, Liu G, Liu X, Song Y, Zhang M, Cui L, Dong M. **2019**. Is there coordination of leaf and fine root traits at local scales? A test in temperate forest swamps. *Ecology and Evolution* **9**: 8714–8723.

Inman-Narahari F, Ostertag R, Asner GP, Cordell S, Hubbell SP, Sack L. **2014**. Trade-offs in seedling growth and survival within and across tropical forest microhabitats. *Ecology and Evolution* **4**: 3755–3767.

Iversen CM. **2010**. Digging deeper: Fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. *New Phytologist*: 346–357.

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet GT, Kattge J, Roumet C, Stover DB, Soudzilovskaia NA, Valverde-Barrantes OJ, *et al.* **2017**. A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist* **215**: 15–26.

Jackson RB, Mooney HA, Schulze E-D. **1997**. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* **94**: 7362–7366.

Jia S, Wang Z, Li X, Zhang X, Mclaughlin NB. **2011**. Effect of nitrogen fertilizer, root branch order and temperature on respiration and tissue N concentration of fine roots in Larix gmelinii and Fraxinus mandshurica. *Tree Physiology* **31**: 718–726.

Jin Y, Qian H. **2019**. V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography* **42**: 1353–1359.

Jones MM, Szyska B, Kessler M. **2011**. Microhabitat partitioning promotes plant diversity in a tropical montane forest: Microhabitats and tropical montane ferns. *Global Ecology and Biogeography* **20**: 558–569.

Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L, Coomes DA. **2018**. Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* **21**: 989–1000.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. **2010**. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**: 1463–1464.

Kong D, Ma C, Zhang Q, Li L, Chen X, Zeng H, Guo D. **2014**. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**: 863–872.

Kong DL, Wang JJ, Kardol P, Wu HF, Zeng H, Deng XB, Deng Y. **2016**. Economic strategies of plant absorptive roots vary with root diameter. *Biogeosciences* **13**: 415–424.

Kramer-Walter KR, Bellingham PJ, Millar TR, Smissen RD, Richardson SJ, Laughlin DC. **2016**. Root traits are multidimensional: Specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**: 1299–1310.

Kreuzwieser J, Gessler A. **2010**. Global climate change and tree nutrition: Influence of water availability. *Tree Physiology* **30**: 1221–1234.

Kruschke JK. **2011**. *Doing Bayesian data analysis: A tutorial with R and BUGS.* Amsterdam: Elsevier.

Kübler D, Hildebrandt P, Günter S, Stimm B, Weber M, Mosandl R, Muñoz J, Cabrera O, Zeilinger J, Silva B. **2016**. Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest. *Erdkunde* **70**: 19–47.

Kumordzi BB, Aubin I, Cardou F, Shipley B, Violle C, Johnstone J, Anand M, Arsenault A, Bell FW, Bergeron Y, *et al.* **2019**. Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants (E Dorrepaal, Ed.). *Functional Ecology* **33**: 1771–1784.

Laliberté E. **2017**. Below-ground frontiers in trait-based plant ecology. *New Phytologist* **213**: 1597–1603.

Laliberté E, Legendre P. **2010**. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**: 299–305.

Laliberté E, Legendre P, Shipley B. **2014**. *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology.*

Laughlin DC. **2014**. The intrinsic dimensionality of plant traits and its relevance to community assembly (S Wilson, Ed.). *Journal of Ecology* **102**: 186–193.

Laughlin DC, Lusk CH, Bellingham PJ, Burslem DFRP, Simpson AH, Kramer-Walter KR. **2017**. Intraspecific trait variation can weaken interspecific trait correlations when assessing the whole-plant economic spectrum. *Ecology and Evolution* **7**: 8936–8949.

Laughlin DC, Mommer L, Sabatini FM, Bruelheide H, Kuyper TW, McCormack ML, Bergmann J, Freschet GT, Guerrero-Ramírez NR, Iversen CM, *et al.* **2021**. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution* **5**: 1123–1134.

Lavorel S. **2013**. Plant functional effects on ecosystem services. *Journal of Ecology* **101**: 4–8.

Lavorel S, Garnier E. **2002**. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.

Leps J, De Bello F, Lavorel S, Berman S. **2006**. Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia* **78**: 481–501.

Leuschner C, Moser G, Bertsch C, Röderstein M, Hertel D. **2007**. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology* **8**: 219–230.

Leuschner C, Wiens M, Harteveld M, Hertel D, Tjitrosemito S. **2006**. Patterns of fine root mass and distribution along a disturbance gradient in a tropical montane forest, central Sulawesi (Indonesia). *Plant and Soil* **283**: 163–174.

Leuschner C, Zach A, Moser G, Homeier J, Graefe S, Hertel D, Wittich B, Soethe N, Iost S, Röderstein M, *et al.* **2013**. The carbon balance of tropical mountain forests along an altitudinal transect. In: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W, eds. Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Berlin, Heidelberg: Springer Berlin Heidelberg, 117–139.

Liang M, Liu X, Parker IM, Johnson D, Zheng Y, Luo S, Gilbert GS, Yu S. **2019**. Soil microbes drive phylogenetic diversity-productivity relationships in a subtropical forest. *Science Advances* **5**: eaax5088.

Liese R, Alings K, Meier IC. **2017**. Root branching is a leading root trait of the plant economics spectrum in temperate trees. *Frontiers in Plant Science* **8**.

Link RM. **2018**. Calculation of the topographical position index, slope and aspect for the MATRIX plots (Loja/Zamora province, Southern Ecuador).

Lippok D, Beck SG, Renison D, Hensen I, Apaza AE, Schleuning M. **2014**. Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. *Journal of Vegetation Science* **25**: 724–733.

Liu B, Li H, Zhu B, Koide RT, Eissenstat DM, Guo D. **2015**. Complementarity in nutrient foraging strategies of absorptive fine roots and arbuscular mycorrhizal fungi across 14 coexisting subtropical tree species. *New Phytologist* **208**: 125–136.

Liu C, Xiang W, Zou L, Lei P, Zeng Y, Ouyang S, Deng X, Fang X, Liu Z, Peng C. **2019**. Variation in the functional traits of fine roots is linked to phylogenetics in the common tree species of Chinese subtropical forests. *Plant and Soil* **436**: 347–364.

Liu J, Yunhong T, Slik JWF. **2014**. Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. *Forest Ecology and Management* **330**: 75–81.

López-Angulo J, Swenson NG, Cavieres LA, Escudero A. **2018**. Interactions between abiotic gradients determine functional and phylogenetic diversity patterns in Mediterranean-type climate mountains in the Andes. *Journal of Vegetation Science* **29**: 245–254.

Luebert F, Weigend M. **2014**. Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* **2**.

Lugli LF, Andersen KM, Aragão LEOC, Cordeiro AL, Cunha HFV, Fuchslueger L, Meir P, Mercado LM, Oblitas E, Quesada CA, *et al.* **2019**. Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil* **450**: 49–63.

Luo W, Lan R, Chen D, Zhang B, Xi N, Li Y, Fang S, Valverde-Barrantes OJ, Eissenstat DM, Chu C, *et al.* **2021**. Limiting similarity shapes the functional and phylogenetic structure of root neighborhoods in a subtropical forest. *New Phytologist* **229**: 1078–1090.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. **2018**. Evolutionary history resolves global organization of root functional traits. *Nature* **555**: 94–97.

Makita N, Hirano Y, Dannoura M, Kominami Y, Mizoguchi T, Ishii H, Kanazawa Y. **2009**. Fine root morphological traits determine variation in root respiration of Quercus serrata. *Tree Physiology* **29**: 579–585.

Malizia A, Blundo C, Carilla J, Osinaga Acosta O, Cuesta F, Duque A, Aguirre N, Aguirre Z, Ataroff M, Baez S, *et al.* 2020. Elevation and latitude drives structure and tree species composition in Andean forests: Results from a large-scale plot network. *PLOS ONE* **15**: e0231553.

Marañón T, Navarro-Fernández CM, Gil-Martínez M, Domínguez MT, Madejón P, Villar R. **2020**. Variation in morphological and chemical traits of Mediterranean tree roots: Linkage with leaf traits and soil conditions. *Plant and Soil* **449**: 389–403.

Martin RE, Asner GP, Bentley LP, Shenkin A, Salinas N, Huaypar KQ, Pillco MM, Ccori Álvarez FD, Enquist BJ, Diaz S, *et al.* 2020. Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Frontiers in Plant Science* **10**.

Mason NWH, de Bello F. **2013**. Functional diversity: A tool for answering challenging ecological questions (B Wilson, Ed.). *Journal of Vegetation Science* **24**: 777–780.

Mason NWH, Mouillot D, Lee WG, Wilson JB. **2005**. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* **111**: 112–118.

Mason NWH, Richardson SJ, Peltzer DA, Bello F de, Wardle DA, Allen RB. **2012**. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology* **100**: 678–689.

Mathez-Stiefel S-L, Peralvo M, Báez S, Rist S, Buytaert W, Cuesta F, Fadrique B, Feeley KJ, Groth AAP, Homeier J, *et al.* 2017. Research priorities for the conservation and sustainable governance of Andean forest landscapes. *Mountain Research and Development* **37**: 323–339.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. **2013**. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*: 823–831.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB, *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505–518.

McCormack ML, Guo D, Iversen CM, Chen W, Eissenstat DM, Fernandez CW, Li L, Ma C, Ma Z, Poorter H, *et al.* 2017. Building a better foundation: Improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* **215**: 27–37.

McCormack ML, Iversen CM. **2019**. Physical and Functional Constraints on Viable Belowground Acquisition Strategies. *Frontiers in Plant Science* **10**: 1215.

McGill BJ, Enquist BJ, Weiher E, Westoby M. **2006**. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**: 178–185.

Messier J, Lechowicz MJ, McGill BJ, Violle C, Enquist BJ. **2017**. Interspecific integration of trait dimensions at local scales: The plant phenotype as an integrated network. *Journal of Ecology* **105**: 1775–1790.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C. **2011**. Global Biodiversity Conservation: The Critical Role of Hotspots. In: Zachos FE, Habel JC, eds. Biodiversity Hotspots. Berlin, Heidelberg: Springer Berlin Heidelberg, 3–22.

Mokany K, Roxburgh SH. **2010**. The importance of spatial scale for trait-abundance relations. *Oikos* **119**: 1504–1514.

Mommer L, Kirkegaard J, van Ruijven J. **2016**. Root–root interactions: Towards a rhizosphere framework. *Trends in Plant Science* **21**: 209–217.

Morueta-Holme N, Engemann K, Sandoval-Acuña P, Jonas JD, Segnitz RM, Svenning J-C. **2015**. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. *Proceedings of the National Academy of Sciences* **112**: 12741–12745.

Moser G, Leuschner C, Hertel D, Graefe S, Soethe N, Iost S. **2011**. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment. *Global Change Biology* **17**: 2211–2226.

Moser G, Leuschner C, Röderstein M, Graefe S, Soethe N, Hertel D. **2010**. Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity* **3**: 151–164.

Mouchet MA, Villéger S, Mason NWH, Mouillot D. **2010**. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* **24**: 867–876.

Muscarella R, Kolyaie S, Morton DC, Zimmerman JK, Uriarte M. **2019**. Effects of topography on tropical forest structure depend on climate context. *Journal of Ecology*.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. **2000**. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

Nakagawa S, Schielzeth H. **2013**. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**:

133–142.

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Lõhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A, *et al.* 2007. Specific root length as an indicator of environmental change. *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* **141**: 426–442.

Paine CET, Baraloto C, Díaz S. **2015**. Optimal strategies for sampling functional traits in species-rich forests. *Functional Ecology* **29**: 1325–1331.

Pakeman RJ. **2011**. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology* **99**: 1143–1151.

Paradiso E, Jevon F, Matthes J. **2019**. Fine root respiration is more strongly correlated with root traits than tree species identity. *Ecosphere* **10**: e02944.

Paulick S, Dislich C, Homeier J, Fischer R, Huth A. **2017**. The carbon fluxes in different successional stages: Modelling the dynamics of tropical montane forests in South Ecuador. *Forest Ecosystems* **4**: 5.

Pérez-Escobar OA, Zizka A, Bermúdez MA, Meseguer AS, Condamine FL, Hoorn C, Hooghiemstra H, Pu Y, Bogarín D, Boschman LM, *et al.* 2022. The Andes through time: Evolution and distribution of Andean floras. *Trends in Plant Science* **0**.

Pérez-Ramos IM, Roumet C, Cruz P, Blanchard A, Autran P, Garnier E. **2012**. Evidence for a “plant community economics spectrum” driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology* **100**: 1315–1327.

Peters T, Drobnik T, Meyer H, Rankl M, Richter M, Rollenbeck R, Thies B, Bendix J. **2013**. Environmental changes affecting the Andes of Ecuador. In: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W, eds. Ecological Studies. Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Berlin, Heidelberg: Springer Berlin Heidelberg, 19–29.

Petter G, Wagner K, Wanek W, Sánchez Delgado EJ, Zotz G, Cabral JS, Kreft H. **2016**. Functional leaf traits of vascular epiphytes: Vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Functional Ecology* **30**: 188–198.

Pierick K, Leuschner C, Homeier J. **2021**. Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. *New Phytologist* **230**: 129–138.

Poorter L, Bongers F. **2006**. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**: 1733–1743.

Porazinska DL, Bardgett RD, Blaauw MB, Hunt HW, Parsons AN, Seastedt TR, Wall DH. **2003**. Relationships at the Aboveground–Belowground Interface: Plants, Soil Biota, and Soil Processes. *Ecological Monographs* **73**: 377–395.

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL. **2002**. Fine root architecture of nine North American trees. *Ecological Monographs* **72**: 293–309.

Purschke O, Schmid BC, Sykes MT, Poschlod P, Michalski SG, Durka W, Kühn I, Winter M, Prentice HC. **2013**. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: Insights into assembly processes. *Journal of Ecology* **101**: 857–866.

R Core Team. **2020**. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

R Core Team. **2021**. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, Rasmussen CMØ, Richardson K, Rosing MT, Whittaker RJ, *et al.* **2019a**. Building mountain biodiversity: Geological and evolutionary processes. *Science* **365**: 1114–1119.

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J. **2019b**. Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* **365**: 1108–1113.

Reich PB. **2014**. The world-wide "fast–slow" plant economics spectrum: A traits manifesto. *Journal of Ecology* **102**: 275–301.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. **2003**. The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences* **164**: S143–S164.

Revell LJ. **2012**. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.

Rewald B, Ephrath JE, Rachmilevitch S. **2011**. A root is a root is a root? Water uptake rates of Citrus root orders: Water flux by root orders. *Plant, Cell & Environment* **34**: 33–42.

Rewald B, Rechenmacher A, Godbold DL. **2014**. It's complicated: Intraroot system variability of respiration and morphological traits in four deciduous tree species. *PLANT PHYSIOLOGY* **166**: 736–745.

Richter M. **2008**. Tropical mountain forests – distribution and general features. In: Gradstein SR, Homeier J, Gansert D, eds. Biodiversity and Ecology Series. The Tropical Mountain Forest – Patterns and Processes in a Biodiversity Hotspot. Göttingen: Göttingen Centre for Biodiversity and Ecology, 7–24.

Richter M, Beck E, Rollenbeck RT, Bendix J. **2013**. The study area. In: Bendix J, Beck E, Bräuning A, Makeschin F, Mosandl R, Scheu S, Wilcke W, eds. Ecological Studies. Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador. Berlin, Heidelberg: Springer.

Rillig MC, Aguilar-Trigueros CA, Bergmann J, Verbruggen E, Veresoglou SD, Lehmann A. **2015**. Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytologist* **205**: 1385–1388.

Robinson W. **1950**. Ecological Correlations and the Behavior of Individuals. *American Sociological Review* **15**: 351–357.

Röderstein M, Hertel D, Leuschner C. **2005**. Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology* **21**: 483–492.

Rollenbeck RT, Bendix J, Fabian P. **2011**. Spatial and temporal dynamics of atmospheric water and nutrient inputs in tropical mountain forests of southern Ecuador. In: Bruijnzeel LA, Scatena FN, Hamilton LS, eds. Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge: Cambridge University Press.

Rossi LMW, Mao Z, Merino-Martín L, Roumet C, Fort F, Taugourdeau O, Boukcim H, Fourtier S, Del Rey-Granado M, Chevallier T, *et al.* **2020**. Pathways to persistence: Plant root traits alter carbon accumulation in different soil carbon pools. *Plant and Soil*.

Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N, Vrignon-Brenas S, Cao K, Stokes A. **2016**. Root structure–function relationships in 74 species: Evidence of a root economics spectrum related to carbon economy. *New Phytologist* **210**: 815–826.

Saar L, de Bello F, Pärtel M, Helm A. **2017**. Trait assembly in grasslands depends on habitat history and spatial scale. *Oecologia* **184**: 1–12.

Salinas N, Cosio EG, Silman M, Meir P, Nottingham AT, Roman-Cuesta RM, Malhi Y. **2021**. Editorial: Tropical montane forests in a changing environment. *Frontiers in Plant Science* **12**.

Schellenberger Costa D, Gerschlauer F, Pabst H, Kühnel A, Huwe B, Kiese R, Kuzyakov Y, Kleyer M. **2017**. Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. *Journal of Vegetation Science* **28**: 684–695.

Schleuning M, Neuschulz EL, Albrecht J, Bender IMA, Bowler DE, Dehling DM, Fritz SA, Hof C, Mueller T, Nowak L, *et al.* 2020. Trait-Based Assessments of Climate-Change Impacts on Interacting Species. *Trends in Ecology & Evolution* **35**: 319–328.

Schleuter D, Daufresne M, Massol F, Argillier C. **2010**. A user's guide to functional diversity indices. *Ecological Monographs* **80**: 469–484.

Schmitt S, Hérault B, Ducouret É, Baranger A, Tysklind N, Heuertz M, Marcon É, Cazal SO, Derroire G. **2020**. Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. *Oikos* **129**: 1521–1530.

See CR, McCormack ML, Hobbie SE, Flores-Moreno H, Silver WL, Kennedy PG. **2019**. Global patterns in fine root decomposition: Climate, chemistry, mycorrhizal association and woodiness. *Ecology Letters* **22**: 946–953.

Shao X, Wang L, Zhang Q, Liu Y, Yang X. **2019**. Future direction of searching for root economics spectrum: Focusing on the fibrous roots 'absorptive unit'. *Ecosphere* **10**: e02716.

Shen Y, Gilbert GS, Li W, Fang M, Lu H, Yu S. **2019**. Linking aboveground traits to root traits and local environment: Implications of the plant economics spectrum. *Frontiers in Plant Science* **10**: 1412.

Shipley B, De Bello F, Cornelissen JHC, Laliberté E, Laughlin DC, Reich PB. **2016**. Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* **180**: 923–931.

Sierra Cornejo N, Hertel D, Becker JN, Hemp A, Leuschner C. **2020**. Biomass, morphology, and dynamics of the fine root system across a 3,000-m elevation gradient on Mt. Kilimanjaro. *Frontiers in Plant Science* **11**: 13.

Šímová I, Violle C, Kraft NJB, Storch D, Svenning J-C, Boyle B, Donoghue JC, Jørgensen P, McGill BJ, Morueta-Holme N, *et al.* 2015. Shifts in trait means and variances in North American tree assemblages: Species richness patterns are loosely related to the functional space. *Ecography* **38**: 649–658.

Soethe N, Lehmann J, Engels C. **2007**. Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. *Journal of Tropical Ecology* **23**: 319–328.

Soethe N, Wilcke W, Homeier J, Lehmann J, Engels C. **2008**. Plant growth along the altitudinal gradient — role of plant nutritional status, fine root activity, and soil properties. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. Ecological Studies. Gradients in a Tropical Mountain Ecosystem of Ecuador. Berlin, Heidelberg: Springer Berlin Heidelberg, 259–266.

Soh MCK, Mitchell NJ, Ridley AR, Butler CW, Puan CL, Peh KS-H. **2019**. Impacts of habitat degradation on tropical montane biodiversity and ecosystem services: A systematic map for identifying future research priorities. *Frontiers in Forests and Global Change* **2**.

Spasojevic MJ, Grace JB, Harrison S, Damschen EI. **2014**. Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *Journal of Ecology* **102**: 447–455.

Spitzer CM, Lindahl B, Wardle DA, Sundqvist MK, Gundale MJ, Fanin N, Kardol P. **2021**. Root trait–microbial relationships across tundra plant species. *New Phytologist* **229**: 1508–1520.

Spracklen DV, Righelato R. **2014**. Tropical montane forests are a larger than expected global carbon store. *Biogeosciences* **11**: 2741–2754.

St. Martin P, Mallik AU. **2021**. Soil chemistry drives below ground traits in an alternate successional pathway from forest to heath. *Oecologia* **195**: 469–478.

Stark J, Lehman R, Crawford L, Enquist BJ, Blonder B. **2017**. Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. *Oikos* **126**: 1650–1659.

Stock SC, Koester M, Boy J, Godoy R, Nájera F, Matus F, Merino C, Abdallah K, Leuschner C, Spielvogel S, *et al.* **2021**. Plant carbon investment in fine roots and arbuscular mycorrhizal fungi: A cross-biome study on nutrient acquisition strategies. *Science of The Total Environment* **781**: 146748.

Subramanian SV, Jones K, Kaddour A, Krieger N. **2009**. Revisiting Robinson: The perils of individualistic and ecologic fallacy. *International Journal of Epidemiology* **38**: 342–360.

Suding KN, Lavorel S, Chapin Iii FS, Cornelissen JHC, Díaz S, Garnier E, Goldberg D, Hooper DU, Jackson ST, Navas M-L. **2008**. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125–1140.

Sun L, Ataka M, Han M, Han Y, Gan D, Xu T, Guo Y, Zhu B. **2021**. Root exudation as a major competitive fine-root functional trait of 18 coexisting species in a subtropical forest. *New Phytologist* **229**: 259–271.

Swenson NG. **2013**. The assembly of tropical tree communities - the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography* **36**: 264–276.

Swenson NG, Anglada-Cordero P, Barone JA. **2011**. Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society B: Biological Sciences* **278**: 877–884.

Swenson NG, Weiser MD. **2010**. Plant geography upon the basis of functional traits: An example from eastern North American trees. *Ecology* **91**: 2234–2241.

Takyu M, Aiba S-I, Kitayama K. **2003**. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* **134**: 397–404.

Tanner EVJ, Vitousek PM, Cuevas E. **1998**. Experimental investigation of nutrient limitation of forest growth of wet tropical mountains. **79**: 13.

Tapia-Armijos MF, Homeier J, Draper Munt D. **2017**. Spatio-temporal analysis of the human footprint in South Ecuador: Influence of human pressure on ecosystems and effectiveness of protected areas. *Applied Geography* **78**: 22–32.

Tapia-Armijos MF, Homeier J, Espinosa CI, Leuschner C, Cruz M de la. **2015**. Deforestation and Forest Fragmentation in South Ecuador since the 1970s – Losing a Hotspot of Biodiversity. *PLOS ONE* **10**: e0133701.

Tautenhahn S, Grün-Wenzel C, Jung M, Higgins S, Römermann C. **2019**. On the relevance of intraspecific trait variability—A synthesis of 56 dry grassland sites across Europe. *Flora* **254**: 161–172.

Tiede Y, Schlautmann J, Donoso DA, Wallis CIB, Bendix J, Brandl R, Farwig N. **2017**. Ants as indicators of environmental change and ecosystem processes. *Ecological Indicators* **83**: 527–537.

Tilman D. **1988**. *Plant Strategies and the Dynamics and Structure of Plant Communities. (MPB-26), Volume 26*. Princeton University Press.

Tito R, Vasconcelos HL, Feeley KJ. **2020**. Mountain ecosystems as natural laboratories for climate change experiments. *Frontiers in Forests and Global Change* **3**.

Tjoelker MG, Craine JM, Wedin D, Reich PB, Tilman D. **2005**. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* **167**: 493–508.

Trocha LK, Bu B, Zadworny M. **2017**. The interactive impact of root branch order and soil genetic horizon on root respiration and nitrogen concentration. *Tree Physiology* **37**: 1055–1068.

Ulrich W, Zaplata MK, Winter S, Fischer A. **2017**. Spatial distribution of functional traits indicates small scale habitat filtering during early plant succession.

Perspectives in Plant Ecology, Evolution and Systematics **28**: 58–66.

Umaña MN, Arellano G, Swenson NG, Zambrano J. **2021**. Tree Seedling Trait Optimization and Growth in Response to Local-Scale Soil and Light Variability. *The Bulletin of the Ecological Society of America* **102**.

Ushio M, Fujiki Y, Hidaka A, Kitayama K. **2015**. Linkage of root physiology and morphology as an adaptation to soil phosphorus impoverishment in tropical montane forests. *Functional Ecology* **29**: 1235–1245.

Valverde-Barrantes OJ, Freschet GT, Roumet C, Blackwood CB. **2017**. A worldview of root traits: The influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist* **215**: 1562–1573.

Valverde-Barrantes OJ, Smemo KA, Blackwood CB. **2015a**. Fine root morphology is phylogenetically structured, but nitrogen is related to the plant economics spectrum in temperate trees. *Functional Ecology* **29**: 796–807.

Valverde-Barrantes OJ, Smemo KA, Feinstein LM, Kershner MW, Blackwood CB. **2013**. The distribution of below-ground traits is explained by intrinsic species differences and intraspecific plasticity in response to root neighbours (D Guo, Ed.). *Journal of Ecology* **101**: 933–942.

Valverde-Barrantes OJ, Smemo KA, Feinstein LM, Kershner MW, Blackwood CB. **2015b**. Aggregated and complementary: Symmetric proliferation, overyielding, and mass effects explain fine-root biomass in soil patches in a diverse temperate deciduous forest landscape. *New Phytologist* **205**: 731–742.

van de Pol M, Wright J. **2009**. A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour* **77**: 753–758.

Vehtari A, Gelman A, Gabry J. **2017**. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**: 1413–1432.

Vehtari A, Gelman A, Simpson D, Carpenter B, Bürkner P-C. **2021**. Rank-normalization, folding, and localization: An improved $\widehat{R}$ for assessing convergence of MCMC. *Bayesian Analysis* **16**.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. **2007**. Let the concept of trait be functional! *Oikos* **116**: 882–892.

Visser MD, Bruijning M, Wright SJ, Muller-Landau HC, Jongejans E, Comita LS, de Kroon H. **2016**. Functional traits as predictors of vital rates across the life cycle of tropical trees. *Functional Ecology* **30**: 168–180.

Vleminckx J, Fortunel C, Valverde-Barrantes O, Timothy Paine CE, Engel J, Petronelli P, Dourdain AK, Guevara J, Béroujon S, Baraloto C. **2021**.

Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species. *Oikos* **130**: 1139–1208.

Wang Y, Li Z, Wang Z, Gu J. **2019**. Functional trait plasticity but not coordination differs in absorptive and transport fine roots in response to soil depth. *Forests* **11**: 42.

Wang R, Wang Q, Zhao N, Xu Z, Zhu X, Jiao C, Yu G, He N. **2018**. Different phylogenetic and environmental controls of first-order root morphological and nutrient traits: Evidence of multidimensional root traits. *Functional Ecology* **32**: 29–39.

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Putten WH van der, Wall DH. **2004**. Ecological Linkages Between Aboveground and Belowground Biota. *Science*.

Warren JM, Hanson PJ, Iversen CM, Kumar J, Walker AP, Wullschleger SD. **2015**. Root structural and functional dynamics in terrestrial biosphere models - evaluation and recommendations. *New Phytologist* **205**: 59–78.

Weemstra M, Freschet GT, Stokes A, Roumet C. **2020**. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. *Functional Ecology* **35**: 342–356.

Weemstra M, Mommer L, Visser EJW, Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ. **2016**. Towards a multidimensional root trait framework: A tree root review. *New Phytologist* **211**: 1159–1169.

Weigelt A, Mommer L, Andraczek K, Iversen CM, Bergmann J, Bruelheide H, Fan Y, Freschet GT, Guerrero-Ramírez NR, Kattge J, *et al.* **2021**. An integrated framework of plant form and function: The belowground perspective. *New Phytologist* **232**: 42–59.

Weintraub SR, Taylor PG, Porder S, Cleveland CC, Asner GP, Townsend AR. **2015**. Topographic controls on soil nitrogen availability in a lowland tropical forest. *Ecology* **96**: 1561–1574.

Weiss AD. **2001**. Topographic Position and Landforms Analysis.

Wen Z, Li H, Shen Q, Tang X, Xiong C, Li H, Pang J, Ryan MH, Lambers H, Shen J. **2019**. Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *New Phytologist* **223**: 882–895.

Werner FA, Homeier J. **2015**. Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. *Functional Ecology* **29**: 430–440.

Westerband AC, Funk JL, Barton KE. **2021**. Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. *Annals of Botany* **127**: 397–410.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. **2002**. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics* **33**: 125–159.

Westoby M, Wright IJ. **2006**. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* **21**: 261–268.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, *et al.* **2019**. Welcome to the tidyverse. *Journal of Open Source Software* **4**: 1686.

Wilcke W, Boy J, Goller R, Fleischbein K, Valarezo C, Zech W. **2011**. Effect of topography on soil fertility and water flow in an Ecuadorian lower montane forest. In: Bruijnzeel LA, Scatena FN, Hamilton LS, eds. Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge: Cambridge University Press.

Wilcke W, Oelmann Y, Schmitt A, Valarezo C, Zech W, Homeier J. **2008a**. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. *Journal of Plant Nutrition and Soil Science* **171**: 220–230.

Wilcke W, Yasin S, Schmitt A, Valarezo C, Zech W. **2008b**. Soils along the altitudinal transect and in catchments. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. Ecological Studies. Gradients in a Tropical Mountain Ecosystem of Ecuador. Berlin, Heidelberg: Springer.

Williams A, Langridge H, Straathof AL, Muhamadali H, Hollywood KA, Goodacre R, Vries FT. **2021**. Root functional traits explain root exudation rate and composition across a range of grassland species (T Walker, Ed.). *Journal of Ecology*: 1365–2745.13630.

Withington JM, Reich PB, Oleksyn J, Eissenstat DM. **2006**. Comparisons of Structure and Life Span in Roots and Leaves Among Temperate Trees. *Ecological Monographs* **76**: 381–397.

Wolf K, Veldkamp E, Homeier J, Martinson GO. **2011**. Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. *Global Biogeochemical Cycles* **25**: n/a–n/a.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, *et al.* **2004**. The worldwide leaf economics spectrum. *Nature* **428**: 821.

Xia M, Valverde-Barrantes OJ, Suseela V, Blackwood CB, Tharayil N.

2021. Coordination between compound-specific chemistry and morphology in plant roots aligns with ancestral mycorrhizal association in woody angiosperms. *New Phytologist*: nph.17561.

Yaffar D, Defrenne CE, Cabugao KG, Kivlin SN, Childs J, Carvajal N, Norby RJ. **2021**. Trade-Offs in Phosphorus Acquisition Strategies of Five Common Tree Species in a Tropical Forest of Puerto Rico. *Frontiers in Forests and Global Change* **4**.

Yahara H, Tanikawa N, Okamoto M, Makita N. **2019**. Characterizing fine-root traits by species phylogeny and microbial symbiosis in 11 co-existing woody species. *Oecologia* **191**: 983–993.

Zadworny M, McCormack ML, Mucha J, Reich PB, Oleksyn J. **2016**. Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. *New Phytologist* **212**: 389–399.