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

Kerstin Pierick1, Christoph Leuschner1,2 and Jürgen Homeier1,2

1Plant Ecology and Ecosystems Research, University of Goettingen, Untere Karstspüle 2, Göttingen 37073, Germany; 2Centre for Biodiversity and Sustainable Land Use, University of Goettingen, Büsingen 1, Göttingen 37077, Germany

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 favourable soil conditions due to environmental filtering. We provide evidence of a high degree of phylogenetic conservatism in fine root traits.

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; Chavez et al., 2009; Diaz 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 (WRIT et al., 2004), the RES predicts a growth-survival trade-off for fine roots, in which root form and function are optimised 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...
Research that can offset the selective pressure on certain root functional 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 scarcity 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; Ford & 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; Muscarella et al., 2019; Blanchard 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; Simova 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 (Buttfield & 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 hypothesised 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.

Materials and Methods

Study area

The study was conducted in the montane forests of the Reserva San Francisco in southern Ecuador (Province Zamora-Chinchipe; Supporting information Fig. S1a). The study area is located in the Río San Francisco valley on the eastern slopes of the Andean mountain range Cordillera Real at around 2000 m asl, 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 hygic 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 et al., 2008, 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).

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. S1b; Table S1). The slope position of the plots was characterised 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 neighbourhood within a radius of 200 m (Link, 2018). Negative values indicated lower slope positions, positive values upper slope positions, and values around zero characterised 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 centred around 0. Plot elevation varied only slightly between 1913 m and 2089 m asl and was independent of TPI.

In each plot, we randomly selected 10 trees with a diameter at breast height (dbh) of ≥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 Prunus spinosa 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 ≥ 10 cm, average: 44%, Table S2). The full species list is given in the Table S3.

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 ≤ 2 mm) were reached. Even though the arbitrarily chosen diameter threshold of 2 mm has recently been criticised 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 ≤ 2 mm produce only marginally different results to measurements on the first three root orders. An analysis based on root orders is much more labour 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 analytical 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 d. In the following step, the roots were washed and dead material was discarded. Then the roots were placed in a water-filled Plexiglas™ 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 (Régent 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 ($N_{\text{root}}$) was analysed using a C : N elemental analyser (Vario EL III; Elementar, Hanau, Germany) at the Department of Plant Ecology, University of Göttingen, Germany.

Statistical analyses

**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. S2). Furthermore, we conducted a principal components analysis (PCA) with these parameters and inspected the correlation coefficients of the first two axes with TPI (Fig. S3). 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. S4.

**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 10 000 iterations. A detailed description of the method is given in Methods S1.

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 centred 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 $d_{\text{root}}$, SRL, RTD, RBI and $N_{\text{root}}$ 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.

**Results**

**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. S3a). 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 (Figs S2, S3b).

**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 $N_{\text{root}}$ 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 (Figs 1, 2; Table S4). However, only small proportions of the variance (11.0% and 12.4% for RBI and $N_{\text{root}}$, respectively, and less than 10% for $d_{\text{root}}$ 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 of variation of all fine root traits (ranging from 40.2% for RBI and SRL to 79.9% for $N_{\text{root}}$). 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% ($N_{\text{root}}$) (Fig. 3). The combined random intercepts for phylogenetically dependent and independent species effects as fitted by the five models are displayed for all studied species in Fig. S5.

**Phylogenetic PCA**

The phylogenetic PCA for the five fine root traits showed no clear one-dimensional spectrum. RBI and $d_{\text{root}}$ were mostly associated
with the first axis (which accounted for 45% of variation), whereas RTD, SRL and Nroot 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 droot, and lower SRL and Nroot (Fig. 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. 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. S6), it should be interpreted with care.

Discussion

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 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., 2015a; 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.

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 Nroot to decrease, from the lower
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 et al., 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 fertilisation experiment in the montane forests of the study region revealed a general co-limitation of tree growth by plant macronutrients (N, P, Ca, K, Mg) is a major factor differing variables suggested that variation in the availability of all five macronutrients (N, P, Ca, K, Mg) is a major factor differentiating between lower slope and upper slope positions. The results of a fertilisation 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; Carate-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 favourable to less favourable 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 down-slope and up-slope 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 (Bruner 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., 2015a; Kramer-Walter et al., 2016; Weemstra et al., 2016). Root diameter, branching and SRL can be interpreted as one dimension and RTD and Nroot as a second dimension, which both seem to be related to the topographic gradient.

**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; Mascarell et al., 2019), Liu et al. (2014) observed, in agreement with this study, a higher functional diversity at the lower slopes in a tropical rainforest. 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 rainforest. 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 metres 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.

Acknowledgements

We thank the Heinrich-Böll-Stiftung (P135312) and Deutsche Forschungsgemeinschaft (DFG; Ho3296-4, Ho3296-6, Le762-17) for funding, the Ministerio de Ambiente del Ecuador for granting the research permit (0014-ICFAUNA-DRLCH- VS-MAE), NCI for giving us access to the San Francisco reserve, Roman M. Link for statistical advice, helpful discussions and proofreading and three anonymous referees for their comments. Open access funding enabled and organized by Projekt DEAL.

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.

ORCID

Jürgen Homeier https://orcid.org/0000-0001-5676-3267
Kerstin Pierick https://orcid.org/0000-0002-1313-4601

References

Adams TS, McCormack ML, Eisenstat 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.
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.
Asfaw M, Cao M, Zhang G, Gu 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, Tupayachi R, Anderson CB, Sinca F, Carranza-Jimenez J, Bardgett RD, Mommer L, De Vries FT. 2014. Bendix J, Rollenbeck R, Richter M, Fabian P, Emck P. 2008. 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, Eisenstat 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.
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: 463–478.
Diaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16: 646–655.
Diaz S, Katte J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirsh C, Colin Prentice I et al. 2016. The global spectrum of plant form and function. Nature 529: 167–171.
Diaz S, Lavorel S, de Bello F, Quetier F, Grigulis K, Robson TM. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences, USA 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.
Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marqués JR, 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.
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. Journal of Ecology 108: 1565–1577.
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 Logtenstijn RSP, Aerts R. 2010. Evidence of the ‘plant economics spectrum’ in a subarctic flora. Journal of Ecology 98: 362–373.
Freschet GT, Roumet C. 2017. Sampling roots to capture plant and soil functions. Functional Ecology 31: 1506–1518.
Gelman A, Goodrich B, Gabry J, Vehtari A. 2019. R-squared for Bayesian regression models. *American Statistician* 73: 307–309.

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

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.

Hömeier J, Bredkle 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.

Hömeier J, Hertel D, Camenzind T, Cumbicus NL, Mazaun M, Martinson GO, Poma LN, Rillig MC, Sandmann D, Scheck 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.

Hömeier J, Werner FA, Gradstein R, Bredkle SW, Richter M. 2008. Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBFS. Gradients in a tropical mountain ecosystem of ecuador. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. *Gradients in a tropical mountain ecosystem of Ecuador*. Berlin, Germany: Springer, 87–100.

Iversen CM. 2010. Digging deeper: Fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. *New Phytologist* 146: 357–357.

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, USA* 94: 7362–7366.

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

Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips GO, Poma LN, Rillig MC, Sandmann D, Scheu S et al. 2019. Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* 21: 989–1000.

Kembl SW, Cowan PD, Helmsaari 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.

Kembl SW, Cowan PD, Helmsaari 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.

Kerswill PM, Qie L, Coomes DA. 2018. Evidence for a ‘plant community economics spectrum’ driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology* 108: 145–159.

Laliberté E, Prieto M, Villar R. 2018. Plant structure-function relationships in 74 woody communities: Are they aligned along the root economics spectrum? *Plant and Soil* 424: 35–49.

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

Lugli LF, Andersen KM, Arajogho LEOC, Condeiro AL, Cunha HFV, Fuchslueger L, Meir P, Mercado LM, Ollifos 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.

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eisenstat 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.

Mason NWH, Richardson SJ, Peltzer DA, de Bello F, 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.

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

Míguez-Ramos JM, Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N, Vrignon-Brenes S, Komi Y, Winter M, Prentice HC. 2013. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology* 99: 1143–1151.

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

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* 108: 145–159.

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.

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

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

Paulick S, Dislich C, Hömeier 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: 59–63.

Pérez-Ramos JM, 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.

Purschke O, Schmid BC, Sykes MT, Poschled 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.

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

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

de la Riva EG, Marañón T, Pérez-Ramos JM, 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: 35–49.

Roumet C, Birouste M, Picon-Cochard C, Ghemst M, Osman N, Vrignon-Brenes S, Cao K-F, 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.

Sha 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’. *Escophere* 10: e02716.

Sierra Cornejo N, Hertel D, Becker JN, Hemp A, Leuschner C. 2020. Biomass, morphology and dynamics of the fine root system across a 3000-m elevation gradient on Mt Kilimanjaro. *Frontiers in Plant Science* 11: 13.
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. 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.

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.

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.

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 A. 2001. Topographic position and landforms analysis. Poster presentation, ESRI user conference, July 2001, San Diego, CA.

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.

Westoby M, Falster DS, Moles AT, Vesk PA, Wright JJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33: 125–159.

Withington JM, Reich PB, Oleksyn J, Eisenstat 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: N₂O + NO flux of tropical montane forests. Global Biogeochemical Cycles 25: GB4009.