

Limited evidence of vertical root segregation in a subtropical forest

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Abstract

Vertical root segregation can be a key underpinning of species co-existence through below-ground niche partitioning but has rarely been tested in diverse forest communities. We randomly sampled > 4000 root samples from 625 0-30 cm soil profiles in a subtropical forest in China to determine the degree of vertical root segregation among 109 woody species and rooting plasticity in response to edaphic heterogeneity and root neighbours. Over 85% of species were predominantly distributed in the 0-10 cm soil zone, exhibiting low and inconsistent rooting plasticity in response to either edaphic heterogeneity or root neighbours. There was no evidence of vertical root segregation among co-occurring species. Contrastingly, the increase of one species' root abundance tended to increase, but not reduce other species' root abundance within soil zones. These findings suggest that interspecific differentiation of resource acquisition strategies might be more important than root segregation in mediating species co-existence in diverse forests.

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⁴Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada **Corresponding author:** Chengjin Chu (chuchjin@mail.sysu.edu.cn). Tel: (+86) 2084111541. Mailing address: Xingang Xi Road 135, Sun Yat-sen University, Guangzhou, 510275, China **Statement of authorship:** WL and CC conceived the project. WL synthesized the data and conducted the analyses with inputs from MN and JC. WL wrote the manuscript with input from CC, JC, YW and D.M.E. WL, RL and BL collected the root and soil data. **Data accessibility statement:** The data supporting the results will be archived in Dryad and the data DOI will be included once the manuscript is accepted.

Summary

Vertical root segregation can be a key underpinning of species co-existence through below-ground niche partitioning but has rarely been tested in diverse forest communities. We randomly sampled > 4000 root samples from 625 0-30 cm soil profiles in a subtropical forest in China to determine the degree of vertical root segregation among 109 woody species and rooting plasticity in response to edaphic heterogeneity and root neighbours. Over 85% of species were predominantly distributed in the 0-10 cm soil zone, exhibiting low and inconsistent rooting plasticity in response to either edaphic heterogeneity or root neighbours. There was no evidence of vertical root segregation among co-occurring species. Contrastingly, the increase of one species' root abundance tended to increase, but not reduce other species' root abundance within soil zones. These findings suggest that interspecific differentiation of resource acquisition strategies might be more important than root segregation in mediating species co-existence in diverse forests.

Introduction

Fine roots (<2 mm) are the most metabolically active part of root systems responsible for soil nutrient uptake, mycorrhizal symbiosis and interspecific interactions (Valverde-Barrantes *et al.* 2015; Eissenstat *et al.* 2015). In most ecosystems, fine roots are concentrated within the upper soil surface (e.g. 0-20 cm) where there are typically higher nutrient availability and lower physical impedance (Schenk & Jackson 2002). However, even within such a shallow profile, species may differ in their vertical relative root distributions, which is defined as the proportions of roots partitioned among soil zones (Herben *et al.* 2018; Zhou *et al.* 2020). Such difference may promote species co-existence through a more complete filling of below-ground space (Ma & Chen 2017) and complementary resource use among species (Blume-Werry *et al.* 2019). Nevertheless, very few studies have examined species-specific vertical root distributions in diverse forest communities, primarily due to the difficulty in identifying root materials to species. The lack of such information has hindered our understanding of rooting-depth mediated below-ground niche differentiation, root foraging strategies and species spatial distributions (Gale & Grigal 1987; Klimešová *et al.* 2016).

As root systems are highly plastic organs, vertical root distributions could express high phenotypic plasticity in response to external factors such as edaphic heterogeneity (Sainju & Good 1993; Case *et al.* 2020) and specific root neighbours (Zhang *et al.* 2019; Chen *et al.* 2020). Such adjustments may increase root nutrient uptake efficiency through optimizing root placement according to nutrient availability and neighbouring root identities (Mommer *et al.* 2012; Zhang *et al.* 2019). While effort is increasingly devoted to elucidating the mechanisms and consequences of root segregation (Holdo 2013; Kulmatiski *et al.* 2017), most studies are biased to artificial communities (Mahall & Callaway 1992; Belter & Cahill 2015; Zhang *et al.* 2019) or natural communities in arid and semi-arid regions, typically involving two species (Case *et al.* 2020; Chen *et al.* 2020; but see Valverde-Barrantes *et al.* 2015). As the direction and extent of rooting plasticity may be highly dependent on the number and identities of root neighbours, it remains uncertain if and to what extent relative root distributions would be affected by the presence of multiple interacting neighbours in complex forests. Such information is critical for the prediction of how the change of species composition and edaphic conditions may influence competitive interactions and root neighbourhood stability (Chen *et al.* 2018a, b).

Within soil zones, the degree of interspecific root segregation could be ultimately determined by their innate difference in root system architecture (Schenk & Jackson 2005) and rooting plasticity in response to edaphic heterogeneity or/and neighbour structure (Zhang *et al.* 2019; Case *et al.* 2020; Zhou *et al.* 2020). Despite the proposed mechanisms, the generalization of vertical root segregation in natural communities have not

been fully identified, with both apparent (Kesanakurti *et al.* 2011; Herben *et al.* 2018) and minor rooting differentiation observed (von Felten & Bernhard 2008; Hoekstra *et al.* 2015). Whether and how rooting differentiation mediates species co-existence remains a subject of intensive studies. Valverde-Barrantes *et al.* (2015) recently reported that root depths of temperate trees in the 0-60 cm soil zone were largely overlapped and exhibited low responsiveness to neighbours. However, root depths alone may fail to fully capture root niches, as species with similar root depths may differ considerably in their relative root distributions (Schmid & Kazda 2001; Bennett *et al.* 2002; Herben *et al.* 2018). It is thus unclear whether relative root distribution represents a root niche dimension independent of root depth that may contribute to vertical root segregation.

In this study, we collected > 4000 root segments from 625 soil samples within the 0-30 cm soil zone in a subtropical forest, China. From these samples, we quantified the relative root distributions of 53 woody species, modeled rooting plasticity of the 29 most common species as a function of soil heterogeneity and root neighbours and finally examined how individual roots of the identified 109 species were vertically placed. We used these data to test three hypotheses. First, we predicted high interspecific differentiation in relative root distributions, with some predominantly placing their roots in specific soil zones whereas some others being homogeneously distributed. Second, we predicted high rooting plasticity in response to either edaphic heterogeneity or/and root neighbours that may optimize root placement according to nutrient availability and neighbour root competition. Specifically, due to the potential pre-emptive utilization of soil resources by some proliferative species (Campbell *et al.* 1991), we predicted that the increase of one species' root abundance would reduce other species' root proliferation, resulting in pervasive negative correlations in relative root abundance among species pairs. Finally, depending on the differentiation in relative root distributions among species complementarily combined with high rooting plasticity, we predicted that heterospecific roots would be vertically segregated either simply by avoiding co-occurring or by avoiding placing similar relative root abundance in the same soil zones.

Materials and Methods

Site description

This study was conducted in the 50-ha Heishiding (HSD) Forest Dynamic Plot (23.455 °N, 111.908 °E; altitude: 435-698 m) in Guangdong province, China. This area belongs to subtropical monsoon climate, with a mean annual temperature of 19.6 °C and mean precipitation of 1740 mm. The plot has a rough terrain with the slope ranging from 7 ° to 75 °. The floristic composition of the plot is characteristic of evergreen broad-leaved forests with *Castanopsis carlesii* (Fagaceae), *Cryptocarya concinna* (Lauraceae) and *Altingia chinensis* (Altingiaceae) being the dominant canopy species.

Root excavating and identification

Root sampling was conducted in early summer from April to June in 2016 by randomly selecting 625 locations in the 50-ha plot as described in detail in Luo *et al.* (2020). In brief, at each location, three 300-cm³ soil cubes (5 × 6 × 10 cm) were sequentially extracted with a depth increment of 10 cm using a 5 × 6 × 40 cm steel spade. To further explore vertical root distributions in deeper soils, 12 cubes were sampled to a depth of 100 cm. An additional 300-cm³ soil cube of soil next to each root-sampling location was collected for further analyses of soil chemical and textural properties.

In the laboratory, each soil cube was soaked in water for *c.* 40 min and intact and all well-branched woody fine root segments ([?] 2 mm in diameter) with length [?] 10 cm were selected for further analysis. Root segments generally included 2-4 orders of roots (Valverde-Barrantes *et al.* 2015). For each soil cube, the selected root segments were further sorted into morphotypes based on root branching patterns, color, distinctive odor, diameter and the presence of nodules or latex (Luo *et al.* 2020). As reported in Luo *et al.* (2020), some root morphotypes could be confirmed to species based on their identifiable and conservative root characteristics. All other morphotypes were sequenced and compared with four DNA barcodes (*rbcLa*, *ITS2*, *matK* and *trnH-psb*) generated from leaf collections of 237 tree canopy species in the plot (Zhou 2014). Following these procedures, we identified *c.* 94% of the morphotypes that in combination contained 143 species. 109 species with occurrences [?] 5 cubes were selected for the present study.

Soil variables

Thirty-two soil variables were measured for each sampling location, including a number of macro- and micronutrients and variables associated with soil textural properties (Table S1). Details about soil variables measurements are described in Table S2. Preliminary analysis showed that most micronutrients, excepting for soil copper (Cu), had weak associations with fine root trait plasticity and biomass accumulation. Consequently, we selected 13 soil variables previously identified in the literature (Kesanakurti *et al.* 2011; Valverde-Barrantes *et al.* 2015a; Luo *et al.* 2020) to frequently influence root growth and trait variation for the present study, including soil pH, electrical conductivity, total organic carbon, total nitrogen, total phosphorus, total potassium, hydrolysable nitrogen, available phosphorus, available potassium, sand content, silt content, clay content and available Cu.

Quantification of species-level root-placement patterns and relative root distributions

Species root-placement patterns were categorized into seven types based on their occurrences in the 0-30 cm soil zone (Fig. 1). These included roots that occurred only in the 0-10 cm soil zone (type 1), 10-20 cm soil zone (type 2), 20-30 cm soil zone (type 3), throughout the 0-20 cm soil zone (type 4), throughout the 0-30 cm soil zone (type 5), throughout the 10-30 cm soil zone (type 6) and roots that occurred both in the 0-10 and 20-30 cm soil zone (type 7). For a soil cube, individual species' root-placement pattern was assigned with one of the seven possible rooting types (Fig. 1). Relative root distributions were determined as the relative root abundance in the 0-10, 10-20 and 20-30 cm soil zones, with zones without roots assigned a score of 0%. Root abundance was indicated by species fine root length because root length is likely a better indicator of foraging effort than root mass. As individual root segments could not be accurately traced to specific parental trees, we focused on species-level relative root distribution for the 109 species with occurrences [?] 5 cubes. Each 30-cm deep soil cube represents a root neighbourhood with three soil zones.

Statistical analysis

Testing the differentiation of relative root distributions among species

To increase statistical power, the comparisons of relative root distributions were focused on the 53 most common species with occurrences [?] 15 cubes. For a given species, we calculated the averaged value of relative root abundance in each soil zone of that species and tested whether soil zone significantly influenced the means of relative root abundance using a one-way Welch's ANOVA. Pairwise comparisons of the means of relative root abundance among soil zones was performed using the Games-Howell Post-Hoc Test. Finally, we categorized the 53 species into different groups based on their relative root distributions using clustering analysis.

Testing rooting plasticity in response to edaphic heterogeneity and root neighbours

The plasticity of relative root distributions in response to edaphic heterogeneity and root neighbours was evaluated for each species with separate redundancy analysis (RDA). As it is required in an RDA analysis the number of observations of the response variable should be greater than that of explanatory variables to avoid overfitting (Legendre *et al.* 2013), we focused on the 29 most common species with occurrences [?] 30 cubes. This maximized the number of root neighbours that could be included in the RDA analysis, giving the minimum observations of 30 in the relative root distribution for the focal species.

For each species, relative root abundance (%) in the 0-10 cm soil zone was treated as the response variable. Additionally, two predictor variable matrices were created, one of which described the presence-absence of the remaining 28 species within the 0-30 cm soil zone and the other described edaphic conditions regarding the 13 selected soil variables. We then performed a global analysis to test the importance of each factor in the matrix separately (ter Braak *et al.* 2012). When the global analysis was significant, a step-wise RDA was performed to select the parsimonious subsets of competitor species and soil factors as explanatory variables (Blanchet *et al.* 2008). Lastly, we performed a variance partitioning to determine the relative importance of soil variables and root neighbours on rooting plasticity as described in Peres-Neto *et al.* (2006).

To examine whether the increase of one species' root abundance would reduce neighbours' root abundance, we performed a pairwise correlation of relative root abundance between a focal species and each of the remaining 28 species. Finally, to examine whether species relative root distributions would be influenced by heterospecific root crowdedness, we used a correlation analysis to examine the relationship between the focal species relative root distributions and both heterospecific root richness and total root length in root neighbourhoods.

Testing vertical root segregation in root neighbourhoods

Vertical root segregation was tested in two complementary ways using all the identified root morphotypes (i.e. a specific species composed of several root segments) belonging to 109 species sampled from 604 root neighbourhoods. First, we tested whether species were vertically segregated simply by exhibiting different root-placement patterns (i.e. root depth) within the 0-30 cm soil zones (Fig. 1a, 1c). Second, we sequentially tested whether species were vertically segregated by avoiding placing similar relative root abundance within the 0-10, 10-20 and 20-30 cm soil zone, respectively (Fig. 1b, 1d).

As each root morphotype was assigned a specific rooting type (Fig. 1) that was treated as a categorical functional trait, we constructed a trait dendrogram depicting the pairwise functional distance of all the identified and coded morphotypes based on a Gower Distance and determined the mean pairwise functional distances (MPD) of root neighbourhoods (Gower 1971; Laliberte *et al.* 2014; Swenson 2014). We then constructed 999 null communities for each root neighbourhood, from which the mean and the standard deviations of the 999 simulated MPDs were determined using the picante package (Kembel *et al.* 2010). Null communities were constructed by randomizing the pairwise functional distances of the coded morphotypes by shuffling the tip names of the trait dendrogram, keeping species occurrences constant. Finally, we determined the standardized effect size of the functional MPD (SESMPD) to quantify the functional similarity of co-occurring species based on their root-placement patterns following the equation:

$$\text{SESMPD} = \frac{(\text{MPD}_{\text{obs}} - \text{mean}(\text{MPD}_{\text{null}}))}{\text{sd}(\text{MPD}_{\text{null}})},$$

where MPD_{obs} represents the observed MPD. The $\text{mean}(\text{MPD}_{\text{null}})$ and $\text{sd}(\text{MPD}_{\text{null}})$ represent the mean and the standard deviations of the 999 simulated MPDs, respectively. Root neighbourhoods with a positive SESMPD indicated functional overdispersion (i.e. vertical root segregation) with values greater than 1.96 indicating significant segregation, whereas root neighbourhoods with a negative SESMPD indicated functional clustering (i.e. vertical root aggregation) with values below -1.96 indicating significant root aggregation (e.g. Swenson 2014). The absolute value of SESMPD indicated the magnitude of the difference between the observed and the simulated MPD. Similarly, we quantified root segregation based on species relative root distributions simply by replacing the root-placement-pattern-based trait dendrogram with a trait dendrogram constructed based on species relative root distribution. In addition to using MPD, we also used the standard deviation and variance of relative root distributions to evaluate the similarity of root depths among co-occurring species. For a specific soil zone, we constructed a trait dendrogram based on species relative root abundance in the soil zone.

Under the prediction of vertical root segregation, either by way of avoiding co-occurring or placing similar relative root abundance within the same soil zone, we would expect pervasive functional overdispersion in root neighbourhoods, which could be supported by the following two observations. First, there existed a higher proportion of root neighbourhoods that exhibited functional overdispersion than clustering. Second, and more importantly, that the difference between the observed and simulated MPD, measured as the mean of the SESMPD, was significantly higher than the expectation of zero when using a two-tail Student's *t* test (Yang *et al.* 2014).

All statistical analyses were performed in the R 3.6.0 statistical software (R Development Core Team, 2019).

Results

Differentiation of relative root distributions among species

At the root neighbourhood level, root species richness per sampling unit (5x6 cm) in the 0-10, 10-20 and 20-30 cm soil zone was 4.15, 2.73 and 2.18, respectively (Figs. 2a, S1a) and decreased to approximately one below 40 cm (Fig. 2a). Root abundance also decreased sharply as increasing soil depths with over 65% of roots concentrating within the 0-30 cm soil zone (Figs. 2b, S1b).

In support of our hypothesis, although most species were found in the 0-10 cm soil zone (Figs. 3a, S2), species differed in their relative root distributions that could broadly be categorized into five groups (Table S3; Fig. 3b). Specifically, for over 50% of species, root abundance was the highest in the 0-10 cm soil zone and had similar root abundances in 10-20 and 20-30 cm soil zone (group A). For 21% of species, root abundance was the highest in the 0-10 cm soil zone and decreased significantly toward the deeper zones (group B). 11% of species were homogeneously distributed throughout the 0-30 cm soil zone (group C; Fig. 3b). An additional 18.8% of species similarly had the highest fraction of roots in the 0-10 cm soil zone with their root abundance exhibiting inconsistent patterns among the deeper two zones (group D). For some species, root abundance in the 20-30 cm zone was significantly higher than the 10-20 cm zone or that root abundance was similar among the uppermost two zones. One species' roots were concentrated in the 10-20 cm soil zone (*Xanthophyllum hainanense*, group E).

Vertical root segregation in root neighbourhoods

Our hypothesis that individual species in root neighbourhoods would be vertically segregated was generally not supported. Although there were higher proportions of root neighbourhoods where heterospecific roots tended to avoid co-occurring (Fig. 4a) or avoid placing similar root abundance in the same soil zone (Table 1; Fig. 4b-d) than that tended to co-occur, the proportions of root neighbourhoods that either exhibited significant root segregation or aggregation were very low and did not differ substantially (Table 1). Furthermore, the mean of the standardized effect size of the four parameters measuring rooting similarity did not differ significantly from zero (Fig. 4), indicating that the diversity of root-placement patterns in the observed communities did not differ significantly from that of randomly simulated distributions. Moreover, in contrast to our prediction, when only roots that occurred throughout the 0-30 cm soil zone were included in the analysis, we found a higher proportion of root neighbourhoods that exhibited root aggregation (54%-76%) than that exhibited root segregation (24%-47%; Table S4). Such aggregated patterns were significant in the 20-30 cm soil zone when rooting similarity was evaluated based on the variance of co-occurring species' relative root distribution (Table S4), suggesting that species have similar root abundance in the 20-30 cm soil zone.

Rooting plasticity in response to edaphic heterogeneity and root neighbours

Our hypothesis that relative root distribution would express high plasticity in response to edaphic heterogeneity or/and root neighbours was not fully supported. For the 29 most common species, we only found two species' relative root abundance in the 0-10 cm zone to be influenced by the presence of the remaining 28 species in the 0-30 cm soil zone (Fig. S3). When interspecific root interactions were examined by correlating pairwise species' relative root abundance of the 29 species in the 0-10, 10-20 and 20-30 cm soil zone, there were 7.6%, 4.9 %, and 7.1% of species pairs that exhibited a significant correlation, respectively (Fig. 5). However, contrary to our prediction, excepting for some negative correlations observed in the 0-10 cm soil zone (Fig. 5a), all the correlations were positive (Fig. 5b, 5c), suggesting that, if such interactions were direct, the increase of one species' root abundance tends to increase, but not overwhelm other species' root abundance (Fig. 5). Again, contrary to our hypothesis, species' relative root abundance in the 0-10 cm zone was neither affected by heterospecific root richness (Fig. S4) nor by root abundance (i.e. total root length) in the 0-30 cm soil zone (Table S5).

When heterospecific root richness and abundance were quantified only for the 0-10 cm soil zone, only two of the six most common species exhibited significant rooting plasticity in response to neighbours with contrasting responses. While *Schima superba* tended to place fewer roots in the 0-10 cm soil zone with increased heterospecific root richness (Table S6), *Altingia chinensis* placed more roots in the 0-10 cm soil zone with increased heterospecific root abundance (Table S7), suggesting a relatively minor and inconsistent effect of

heterospecific root crowdedness on the focal species relative root abundance. Similarly, there were only four of 29 species whose relative root abundance exhibited significant plasticity in response to edaphic heterogeneity (Fig. S3). For all the four species, relative root abundance in the 0-10 cm soil zone was negatively correlated with soil nutrient availability, suggesting increased root proliferation in nutrient-poor soil patches.

Discussion

Root neighbourhood level and species-level relative root distribution

Examination of relative root distributions revealed the concentration of fine roots in the 0-10 cm soil zone in our experimental subtropical forest. Both root richness and abundance were largely reduced below 40 cm (Fig. 2). Similarly, individual species' root abundance declined sharply and became variable in the deeper zones, presumably due to higher edaphic heterogeneity (Fig. S5). Consequently, although we examined root distributions only within the 0-30 cm soil zone, this allowed the examination of *c.* 70% of fine roots' placement patterns and interspecific interactions across the 0-100 cm soil profile (Fig. 2b).

Our study partially supported the differentiation of relative root distributions among species. Although a majority of species had the highest root abundance in the 0-10 cm soil zone, some canopy trees predominantly placed their roots in the 10-20 cm soil zone or were homogeneously distributed throughout the 0-30 cm soil zone (Fig. 3b). These findings expand prior studies indicating similar root depths of coexisting temperate trees (Valverde-Barrantes *et al.* 2015), raising the possibility of interspecific vertical root segregation through differentiation in relative root distributions (Schmid & Kazda 2001; Herben *et al.* 2018).

Plasticity of relative root distribution in response to root neighbours and edaphic heterogeneity

Our hypothesis that relative root distribution would exhibit high plasticity in response to edaphic heterogeneity and root neighbours was not fully supported. For most species, relative root distribution was neither affected by edaphic heterogeneity nor by the presence of specific root neighbours (Fig. S3), suggesting that neighbourhood species composition is not a good predictor of a focal species' root depth. Likewise, most species' relative root distributions were unaffected by heterospecific root richness or abundance (Tables S5-S7; Figs. S3, S4), as observed in temperate forests and mountain grasslands (Valverde-Barrantes *et al.* 2015; Herben *et al.* 2018). Similarly, Cahill (2003) reported that grassland species did not exhibit substantial changes in root-shoot ratios with increasing below-ground competition, suggesting that increased heterospecific root mass may not necessarily be indicative of higher competitive pressure exerted on the focal species. However, these findings contrasted with previous studies reporting apparent neighbour-induced rooting plasticity (e.g. Cahill *et al.* 2010; Belter & Cahill 2015; Zhang *et al.* 2019). An explanation for the discrepancy might be that, in contrast to greenhouse experiments that have usually involved two species (Cahill *et al.* 2010; Belter & Cahill 2015), individual species in natural communities experience high niche overlap and diffuse competition. Specifically, in competitive neighbourhoods composed of multiple species, the addition or removal of a single neighbour may not have a significant effect on the competition experienced by the target plant (Dyer & Rice 1997). Another reason might be that in species-rich communities, species exhibit varied rooting plasticity, both directionally and magnitudinally, in response to different neighbours, resulting in overall neutral adjustments of root depth (Litav 1967; Brisson & Reynolds 1994; Caldwell *et al.* 1996; Schenk *et al.* 1999).

Root proliferation usually decreases as increasing heterospecific root abundance, presumably due to intensified competitive pressure and stronger chemical inhibitive effects (Brisson & Reynolds 1994). However, we found that the increase of one species' root abundance did not reduce other species' root abundance (Fig. 5). Instead, the pervasive positive associations of species pairs suggest concurrent root proliferation of co-occurring species into the same soil zones (Fig. 5b, 5c; Belter & Cahill 2015). Nevertheless, based on the positive association among two species, we could not conclude that such species can mutually and directly facilitate their root growth, as such correlations could simply result from the collinearity of species root abundance with other unaccounted-for factors. For instance, similar responses of root proliferation to limiting nutrients or soil microbes may lead to the co-occurrence of the paired species (Rog *et al.* 2020).

These uncertainties highlight the need for further manipulative experiments examining the direct and indirect paths of which root-to-root interactions play to better understand below-ground processes in complex forest communities (Belter & Cahill 2015; Zhanget al. 2019).

At the species level, the variation of relative root abundance in the 0-10 cm soil zone was high (CV: 38%-144%), suggesting that, in addition to the possible effects of edaphic heterogeneity and root neighbours, other factors also contribute to such variations. For instance, as root segments were randomly sampled, those sampled on the margin of the root system could be relatively shallowly placed, giving that root abundance generally declines with increasing distance from the parental tree stem (Jones *et al.* 2011). Such spatial arrangement of root systems could cause additional rooting variations independent of soil heterogeneity and root neighbours. However, prior studies also indicated that root-placement patterns were mainly affected by localized edaphic conditions, as root systems are modular, and each meristem can generate a potentially flexible and plastic root branches (Waiselet al. 2002). Nevertheless, the change of whole-plant root system arrangements still represents adaptive plasticity in response to root neighbours or soil conditions (Casper *et al.* 2003). Collectively, although there were substantial variations in relative root distribution left unexplained that could be attributable to tree ontogenetic stages or soil microbial interactions, our study suggests the relatively minor effect of interspecific interactions on a focal species' root distribution.

Limited evidence of vertical root segregation in root neighbourhoods

Our hypothesis that the differentiation in relative root distribution among species, complementarily combined with substantial rooting plasticity in response to edaphic conditions and neighbours, would ultimately result in vertical root segregation was not supported (Fig. 4). By contrast, the low differentiation of relative root distribution (Fig. 3), the neutral effect of root-to-root interactions on species rooting plasticity (Figs. 5, S3) and the random-to-aggregated root-placement patterns (Fig. 4; Table S4) suggest similar topsoil foraging of heterospecific roots. The generally random root-placement pattern observed here was similar to that reported in grasslands (Franket al. 2010) and greenhouse experiments (Litav 1967; Semchenkoet al . 2007). These findings were consistent with the 'symmetric root proliferation' hypothesis in that heterospecific roots can access and proliferate into the same soil patch (Valverde-Barrantes *et al.* 2015). Potential explanations for the lack of strong root segregation are elaborated below.

First, the differentiation of relative root distribution maybe not high enough to allow species to exhibit distinctive root depths specialized into specific soil zones. For instance, among the 53 species, only one species had roots concentrating within the 10-20 cm soil zone, and no species were concentrated in the 20-30 cm soil zone (Fig. 3b). Although some species may have higher root abundance in the deeper zones, based on neighbourhood- and species-level relative root distributions, we think it unlikely. The accumulation of $c. 70\%$ of fine roots in the 0-30 cm soil zone (Fig. 2b) and the co-occurrence of multiple species in the deeper zones (Fig. S5) suggest fairly shallow and homogeneous fine root distributions in the plot. Additionally, as revealed by the Post-Hoc comparison of species relative root abundance in the 10-20 cm soil zone, there were only seven of 2703 possible combinations of species pairs that exhibited significant rooting difference and all were found between *X. hainanense* and the other seven species, further suggesting minor interspecific differences in root depth. Moreover, although *X. hainanense* had distinctive root depth, most of its individuals were aggregated into the valley of the plot, rather than being widely distributed that would otherwise increase the diversity of root-placement patterns in root neighbourhoods. By contrast, the two most common species (*Pinus massoniana* and *Altingia chinensis*) were widely distributed across the plot, sharing similar rooting patterns with multiple co-occurring species (i.e. concentrating in the 0-10 cm soil zone; Fig. 3b), potentially resulting in spatial root aggregation.

Second, the symmetric root competition may also explain the lack of vertical root segregation. It is proposed that a dominant species with large root biomass does not get disproportionate fitness advantages, as an increase of neighbours' root biomass, even minor, may similarly exert competitive pressure on the dominant species' fitness (Cahill & Casper 2000; Demalach *et al.* 2016). The underlying mechanism may be that species competitive abilities cannot be ranked along a hierarchy in which only a single species gains competitive dominance (Gilpin 1975; Buss 1980). Instead, in an intransitive competitive network, when for example

species A is superior to species B, and B superior to C, it is more likely that C is superior to A ($A > B$; $B > C$; $C > A$; Buss, 1980). The correlations of species root biomass also imply that both facilitative and inhibitive interactions exist among species (Fig. 5a). Such an intransitive competitive network may prevent the predominance of a single species in root neighbourhoods (Laird & Schamp 2006).

Third, as found in our recent study in the same plot and elsewhere (Weemstra *et al.* 2016; Luo *et al.* 2020), the multidimensional nature of roots may also explain the prevalence of symmetric root proliferation. This suggests that species with different trait syndromes may exhibit comparable competitiveness under similar edaphic conditions. For instance, although thin roots with larger specific root surface area appear to be more competitive in nutrient foraging, due to their higher mycorrhizal colonization rates, thick roots may have larger hyphae surface area than thin roots. As a result, for a given amount of carbon for mycorrhizal root construction, thick and thin roots could have comparable absorptive areas and thus foraging capacities (Kong *et al.* 2014). This also helps explain the widespread co-existence of species with contrasting root morphologies and mycorrhizal types in temperate forests (Chen *et al.* 2018b; Valverde-Barrantes *et al.* 2018). Lastly, it is noteworthy that optional mechanisms rather than vertical root segregation also help to promote species co-existence. For instance, despite the similar root abundance partitioned into a specific soil zone, species may differ in the amount of biomass allocated to thin roots that may cause differentiation of root functional traits among species (Mommer *et al.* 2011). Such alternative strategies may confer a similar competitive advantage in response to edaphic heterogeneity and neighbour root competition.

Conclusions

Our results found that over 85% of species predominantly placed their fine roots in the 0-10 cm soil zone, resulting in the accumulation of *c.* 70% of fine root abundance in the 0-30 cm soil zone in our experimental subtropical forest. The low differentiation in relative root distribution among species, the neutral effect of root neighbours on species relative root distributions and the random-to-aggregated root-placement patterns suggest similar topsoil foraging among heterospecific roots and the adoption of alternative resource acquisition strategies that promotes species co-existence.

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Table 1 Testing interspecific vertical root segregation either based on root-placement patterns (MPD_{placement}) throughout the 0–30 cm soil zone or relative root abundance (MPD_{abundance}) in the 0–10 (P1), 10–20 (P2) and 20–30 cm (P3) soil zones using three different parameters. The similarity in relative root abundance of co-occurring species was evaluated with mean pairwise distances (MPD), standard deviation (SD) and variance (Variance) of species relative root abundance. Values indicate the proportions of root neighbourhoods with root segregation (Sepa.), significant segregation (Sig-S.), aggregation (Aggr.) and significant aggregation (Sig-A.). The mean of the standardized effect size of the corresponding parameter was compared with the null expectation of zero to examine whether it was significantly differed from zero across the entire study site.

Parameter	Soil zone	Sepa. (%)	Aggr. (%)	Sig-S. (%)	Sig-A. (%)	Mean	P
MPD _{placement}	P1-P3	62	38	0.50	1.49	-0.04	0.30
MPD _{abundance}	P1	61	39	0.83	1.65	0.03	0.38
	P2	52	48	0.66	1.82	-0.02	0.56
	P3	48	52	1.65	0.82	-0.01	0.79
	P1	61	39	1.98	1.32	0.04	0.35
SD	P2	54	46	0.83	1.65	-0.02	0.57
	P3	49	51	2.31	0.66	-0.01	0.77
	P1	54	46	1.82	1.65	0.02	0.58
Variance	P2	48	52	0.99	1.82	-0.04	0.37
	P3	44	56	2.31	0.83	-0.02	0.60

Figure legends

Figure 1 Schematic diagram showing vertical root-placement patterns of individual species within the 0–30 cm soil zone. Each number in the box indicates a unique species with the solid black lines indicating species-specific roots. For each soil cube, species root-placement patterns were assigned with one of the seven possible rooting types based on their root depths. In the scenario of vertical root aggregation, species with similar root-placement patterns (a) or relative root distributions (b) are more likely to co-occur. In the scenario of vertical root segregation, species with different root-placement patterns (c) or relative root distributions (d) are more likely to co-occur. The width of the shapes in panel (b) and (d) is proportional

to the species' relative root abundance.

Figure 2 Root species richness (a) and relative root abundance (b) along the 0-100 cm soil profile. Different letters indicate significant difference among soil zones.

Figure 3 Relative root distributions for the 53 most common species within the 0-30 cm soil zone. Panel (a) shows the frequencies of species occurrences in the 0-10, 10-20 and 20-30 cm soil zones. Panel (b) shows the frequency distribution of species relative root abundance in the 0-10 cm soil zone. Species with asterisks suggest that soil zone had a significant effect on their relative root distributions, based on which the 53 species were grouped into five groups. Group A, relative root abundance in the 0-10 cm soil zone was significantly higher than the deeper two zones, while the deeper two showed no significant difference; Group B, relative root abundance in the 0-10 cm zone was the highest and it decreased significantly toward the deeper zones; Group C, relative root abundance did not differ significantly among soil zones; Group D, relative root abundance was the highest in the 0-10 cm soil zone while for some species, relative root abundance in the 20-30 cm zone was higher than the 10-20 cm zone; Group E, relative root abundance was the highest in the 10-20 soil zone; ns, nonsignificant. * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$.

Figure 4 Vertical root segregation evaluated based on root-placement patterns (a) within the 0-30 cm soil zone and relative root distributions (b-d) in the 0-10 cm soil zone. The similarity in relative root abundance of co-occurring species was evaluated with mean pairwise functional distances (MPD; b), standard deviation (SD; c) and variance (Variance; d). The histograms illustrate the frequency distribution of the standardized effect size of the corresponding parameters across 604 root neighbourhoods. In panel (a), a positive value indicates that co-occurring species in the 0-30 cm soil zone tended to avoid co-occurring in the same soil zone, whereas a negative value indicates that co-occurring species were more likely to co-occur in the same soil zone than expected. In panels (b)-(d), a positive value indicates that co-occurring species tended to avoid placing similar relative root abundance in the 0-10 cm soil zone, whereas a negative value indicates that co-occurring species tended to place more similar relative root abundance than expected in the 0-10 cm soil zone. The dashed red line in each panel indicates the mean value of the standardized effect size of the corresponding parameters.

Figure 5 Pairwise correlations of relative root abundance for the 29 most common species in the 0-10 (a), 10-20 (b) and 20-30 cm (c) soil zone. Black solid lines link two species with significant positive correlations, whereas blue dashed lines link two species with significant negative correlations. The size of the lines is proportional to the strength of the correlations.

Supporting Information

Figure S1 Root richness per cube (a) and relative root distributions (mean \pm SE) (b) for the 613 0-30 cm soil cubes.

Figure S2 Proportions of each rooting type (i.e. Fig. 1 in the main text) of the 53 most common species.

Figure S3 Multivariate variance partitioning for four individual species' relative root distributions.

Figure S4 The effect of heterospecific root richness in the 0-30 cm soil zone on the six most common species' relative root abundance (mean \pm SE) in the 0-10 cm soil zone.

Figure S5 Species-specific root distributions for the seven most common species with occurrences [?] 3 cubes throughout the 0-100 cm soil zone.

Table S1 Summary of the 32 soil variables measured.

Table S2 The details of measurements of soil variables.

Table S3 The comparison of relative root abundance among soil zones for the 53 most common species.

Table S4 Testing vertical root segregation based on species relative root abundance in the 0-10 (P1), 10-20 (P2) and 20-30 cm (P3) soil zone using three different parameters.

Table S5 The relationship between relative root abundance of the six most common species in the 0-10 cm soil zone and heterospecific root abundance in the 0-30 cm soil zone.

Table S6 The relationships between relative root abundance of the six most common species in the 0-10 cm soil zone and heterospecific root richness in the 0-30 cm soil zone.

Table S7 The relationship between relative root abundance of the six most common species in the 0-10 cm soil zone and heterospecific root abundance in the 0-10 cm soil zone.

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