

Size-dependent growth strategy and allometry, but not diversity, as major drivers of fine-root biomass and productivity across warm-temperate forest types

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Abstract

1. Fine roots play a pivotal role in terrestrial carbon and nutrient cycling. However, our knowledge on drivers of fine-root biomass (FRB) and productivity (FRP) focus on functional traits, biodiversity and abiotic factors, while less attention on allometric constraints, an indispensable driver of organism carbon partitioning. 2. We measured FRB (FRP) for 24 plots using 216 soil cores (ingrowth cores) from four forest types (birch, oak, larch and pine) on a warm-temperate mountain of north China, and investigated leaf, stem and fine-root functional traits, stand factors, diversity and soil fertility. We tested the allometric relationships among FRB, FRP, aboveground (leaf) biomass and functional traits, and examined how allometry, size-dependent growth strategies, the mass-ratio and complementary effects affected FRB and FRP directly and indirectly. 3. There is stable allometric relationship between FRP and FRB at both the soil-core and plot levels, and the former supported the predicted exponent for leaves ($=1$) of the metabolic scaling theory. Contrary to common observations, plot-scale FRB and FRP showed negative (or non-significant) relationships with aboveground (leaves) biomass. Instead, higher aboveground biomass led to more conservative growth strategies, which led to lower FRB, and thus lower FRP due to allometric constraints. Root traits (mass-ratio effect) showed the strongest direct effect on FRB, while diversity (complementary effect) and soil fertility revealed weak effects. FRP was strongly driven by allometry (FRB) and soil nitrogen, while functional traits and diversity affected FRP via FRB instead of directly. 4. Our results do not conflict with the positive correlations of FRB (FRP) with aboveground (leaf) biomass reported by large-scale studies, but together suggest changes of growth strategies with tree size vs. climate, which may affect aboveground-root relationship simultaneously. Thus, we suggest to carefully test allometric relationships to better understand how biodiversity, traits and stand factors affect fine-root dynamics.

Introduction

Fine roots, characterized by fast growing, short-lived and high turnover rates, account for about 3%~30% of stand biomass (Jackson et al. 1996, Jackson et al. 1997) and 33%~67% of annual primary productivity in forest ecosystems (Jackson et al. 1996, Brunner and Godbold 2007), play a pivotal role in ecosystem carbon and nutrients cycling (Gill and Jackson 2000). Many studies have examined the effects of stand factors, functional traits, biodiversity and abiotic factors on fine-root biomass and productivity (hereinafter FRB and FRP, respectively). Allometry is a basic and universal mechanism that control plant biomass and productivity (Brown et al. 2004, Chen et al. 2019), but have seldom been considered together with above-mentioned factors to evaluate their relative importance, which may hinder a more accurate understanding of fine-root dynamics.

It is widely known that there is a tight scaling relationship between aboveground productivity and biomass (Brown et al. 2004), and the Metabolic scaling theory (MST) predicts that the allometric exponent should be $3/4$ (Niklas and Enquist 2001, Enquist et al. 2007). However, whether this prediction can be generalized

to the FRP-FRB allometry is unclear, because fine roots are largely neglected by allometric studies (Chen et al. 2019). Fine roots are physiological active organs located at the terminal of plant vascular network, and turn over quickly. These key features are similar to leaves but differs markedly from woody organs (e.g. stem and coarse root), which may lead some (but clearly not all, see Guo et al. 2022) fine-root allometries to be similar to leaves (Chen et al. 2019, Deng et al. 2020). MST predicts that the allometric exponent between leaf productivity (gross photosynthesis) and biomass was 1 instead of 3/4 (Enquist et al. 2007), we tested whether this is true for fine roots.

Allometric theory and observational studies suggest there is a close isometric relationship between coarse roots and aboveground biomass (Enquist and Niklas 2002, Wang et al. 2008), but whether this is true for fine roots remains unclear. However, studies have found that stand factors, e.g. stand density and total basal area showed significant effects on FRB and FRP (Finér et al. 2011a, Förster et al. 2021). These factors are closely related to aboveground biomass (Sun et al. 2020, Miao et al. 2022) and thus their effects may reflect the allometric relationships between above- and below-ground organs. Previous study has pointed that increasing FRB can support higher aboveground biomass, reflecting a tight coupling between tree growth and root absorption (Farrar and Jones 2000). Finér et al. (2011a) did report FRB increased significantly with higher basal area (a surrogate of aboveground biomass) across a wide geographical region. On the contrary, other studies proposed FRB (FRP) to be more directly related with leaf than aboveground biomass (Chen et al. 2019). Here we tested the hypothesis that FRB (FRP) have positive allometric relationships with aboveground (leaf) biomass, and is more closely related with leaf biomass (Hypothesis 1).

Additionally, we can still derive another possible relationship between aboveground biomass and fine roots, based on recent findings on ecological strategies and allometry. MST states that body size (biomass) plays a central role in regulating organism structure and multiple functions, e.g. photosynthesis and growth (Enquist et al. 1999, Brown et al. 2004), and key traits for growth (e.g. specific leaf area) were found to change significantly with plant (organ) size, reflecting important shifts of ecological strategies across environmental gradients and taxa (Milla and Reich 2007, Niklas et al. 2007). When trees grow larger, a greater proportion of resource and energy is devoted to building and maintaining non-photosynthetic tissues for supports and defensive functions, which leads to more conservative growth strategies (Wright et al. 2004, Lin et al. 2022). Thus, stands (trees) with higher biomass and height generally have more conservative leaf and stem functional traits (Koch et al. 2004, Ryan et al. 2006). On the other hand, fine-root studies often found that lower FRB (FRP) are associated with more conservative root traits, e.g. lower specific root length and thicker root diameter (Ma et al. 2018, Förster et al. 2021). Taking these above- and below-ground findings together, it seems that increasing aboveground biomass will lead to lower FRB (FRP) through more conservative strategies (Hypothesis 2), which predicts a pattern converse to Hypothesis 1. We tested these two competing hypotheses by testing predictions of Hypothesis 2 as follows.

Prediction 2.1) both fine-root and leaf traits should reveal more conservative strategies with increasing tree size. Till now, the size-dependence of functional traits have been focused on leaf traits at organ scale (Niklas et al. 2007, Milla and Reich 2007), and allometric studies suggest the size-dependence of leaf traits follow a power scaling relationship with individual (organ) mass (Niklas et al. 2007), while fine roots and scaling relationships at community scale have received less attentions. Here, we tested whether it applied for the relationships of stand-scale leaf, stem and fine-root traits with aboveground biomass. Prediction 2.2) more conservative leaf and fine-root traits should lead to lower FRB and/or FRP. We assume that these relationships also follow a power scaling, and if true, it may provide new evidence of allometric control of fine roots via traits. Hypothesis 2 is also in line with the idea that above- and below-ground organs traits ought to be functionally coordinated (Reich 2014). However, leaf and stem traits do not seem to affect fine-root biomass dynamics directly, but instead are only correlated with FRB (FRP) due to their covariation with fine-root traits. If this is true, we expected that: Prediction 2.3) aboveground traits should reveal coordination with root traits during grow-strategies change with tree size, taxa and environment; and Prediction 2.4) aboveground traits should be less closely related with FRB (FRP) than root traits.

The Hypothesis 2 is further related with another long-lasting debate in ecology, i.e. the relative importance

of functional traits *vs.* biodiversity on ecosystem functions (van der Plas 2019). Overyielding for forest biomass or productivity in mixed-species forests has been demonstrated by a vast body of studies, which can be explained by the complementary effect that higher diversity increases niche complementarity among species and thus increasing community resource use (Sun et al. 2017, Barry et al. 2019, van der Plas 2019). But meanwhile, contrasted results of biodiversity effect also been reported (van der Plas 2019, Miao et al. 2022), which is also true for fine roots (Finér et al. 2017, Sun et al. 2017, van der Sande et al. 2017). Consequently, other scholars proposed the mass-ratio hypothesis, which states that ecosystem functions are mainly driven by the functional traits of dominant species in a community (Grime 1998). This hypothesis has received supports by many studies on aboveground biomass and productivity (Garnier et al. 2004, Miao et al. 2022), as well as findings that FRB and FRP had close relationships with root functional traits or species identity (Jacob et al. 2013, Finér et al. 2017). In this analysis, we also compare the relative effect of biodiversity (complementary effect) *vs.* functional traits (mass-ratio effect) on FRB (FRP).

Fine-root dynamics are also strongly affected by soil context (Hodge 2004). For instance, FRP across various terrestrial biomes increased with higher soil nitrogen and phosphorous concentrations at the global scale (Yuan and Chen 2012). These patterns are partly caused by that soil fertility directly affects root growth and biomass (Valverde-Barrantes et al. 2015), and can also be contributed by that functional traits, diversity and other biotic factors change remarkably with abiotic gradients (Joswig et al. 2022). Consequently, environmental (soil here) context should be considered when examining the effects of above-mentioned biotic factors on FRB and FRP.

In this study, we measured FRB and FRP for four typical forest types in warm-temperate forests of north China. We also investigated fine-root, leaf and stem traits, as well as various stand factors, diversity indices and soil properties. We aimed to: (1) test the above-mentioned potential mechanisms in affecting FRB and FRP, i.e., allometry (Hypothesis 1), size-dependent growth strategy (Hypothesis 2), complementary and mass-ratio effect; (2) examine how these mechanisms affect fine roots directly or indirectly, and what are their relative importance?

Material and methods

Study site and experimental design

The study site is located in the Mt. Baihua Reserve (39.84 °N, 115.57 °E) of Beijing, north China. The natural reserve lies in a warm temperate zone, with a subhumid continental monsoon climate. The mean annual temperature was 6~7 °C and the mean annual precipitation was 450~720 mm. The main soil type was brown soil, and the zonal forest type in the study area was warm-temperate deciduous broad-leaved forest, and forests here were dominant by secondary forests nowadays (Zhang et al. 2013).

In the summer of 2018, four typical broad- or needle-leaved forest types with similar altitude (around 1250 m a.s.l.) were selected (Table 1). (1) Oak forest, dominated by *Quercus mongolica*, with a proportion of total basal area more than 80%; (2) Birch forests, mainly composed of *Betula platyphylla*, mixed with a small amount of *Betula dahurica*; (3) Larch forest, dominated by *Larix principis-rupprechtii* and mixed with a few broadleaf species, such as *Quercus mongolica*; (4) Pine forest, with *Pinus tabulaeformis* as the absolute dominant species (relative basal area up to 95%). Six plots (20 × 30 m) were evenly set for each forest type as replicates, and totally 24 plots were established. Latitude, longitude, and elevation, as well as topography (slope and aspect) of each plot were recorded. Each plot was divided into 6 subplots (10 × 10 m), in which diameter at breast height (DBH) and height for all individual trees with DBH [?] 3 cm were measured. Tree height was measured using a VL400 instrument that measured height with ultrasound and laser (Haglof, Sweden).

Fine-root biomass sampling and processing

The “soil core method” was applied to determine FRB of each plot, a reliable method to estimate root biomass at community scale (Freschet et al. 2021). In August 2018, soil cores were extracted with soil augers (5 cm diameter) to a depth of 30 cm at nine evenly distributed locations per plot, and totally 216 soil cores were

sampled (9 cores x 24 plots). The extracted samples were put into zip-lock plastic bags immediately, and stored in cooling boxes filled with ice packs temporarily. Once all soil sampling was completed, samples were transported to the laboratory quickly and stored at -20 degC until further processing.

In the laboratory, soil core samples were first thawed and then rinsed with running water gently over a 0.2 mm sieve to separate the root from soil particles and other organic matter. Fine roots ([?] 1 mm in diameter, determined using vernier calipers) of arbor were separated manually using tweezers, and grouped into alive *vs* . dead roots. Alive roots were elastic, flexible, and free of decay; while dead roots were brown or black in color, rigid and inflexible, in various stages of decay (Freschet et al. 2021). After root traits measurements (see below), all fine-root samples were dried at 65 degC to a constant weight (at least 72 h), and weighted to obtain the dry mass data.

Fine-root productivity measurement

Here, the “ingrowth core method” was applied to estimate annual FRP, which has been widely used in studies worldwide (Freschet et al. 2021). After FRB sampling, the remaining coring holes were used to install ingrowth cores. The cylindrical ingrowth cores of 5 cm diameter and 35 cm length were made of high-density polyethylene net cylinder with a 2 mm mesh diameter, which allowed the regrowth of roots and the movement of soil macrofauna into the core. The ingrowth cores were installed into the holes down to 30 cm depth, with the top 5 cm of the ingrowth core sticking out of the ground to facilitate the subsequent harvest. Then, each core was filled with its native root-free soil and compacted to keep the root growth environment maintained as original as possible. After one year incubation, in August 2019, all ingrowth cores were retrieved and transported to the laboratory, and processed with the same protocol as the root biomass samples mentioned-above.

FRB was calculated as the dry mass of alive roots, and FRP was calculated as the dry mass of all fine roots (alive and dead roots) detected in the ingrowth core (Freschet et al. 2021). In this study, we calculated FRB and FRP at both the soil-core and plot scales down to 30 cm soil depth (Jackson et al. 1996) to test Hypothesis 1. Plot-scale FRB ($\text{g}\cdot\text{m}^{-2}$) and FRP ($\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$) were calculated as the mean dry mass of nine cores per m^2 of plot area.

Quantification of tree diversity

To test the effect of tree diversity (complementary effect) on FRB and FRP, we used species, functional and phylogenetic diversity metrics, which represent different facets of biodiversity (van der Plas 2019). For species diversity, we calculated species richness and Pielou’s evenness indices. For functional diversity, we first selected 14 species for traits sampling (including four dominant species and other common species), whose basal area together accounted for [?] 85% of total basal area in each plot. We measured four leaf and stem functional traits, which were closely related to plant life-history and growth strategies (Wright et al. 2004, Perez-Harguindeguy et al. 2013). For each species, three healthy individuals with medium DBH were randomly selected for sampling. We cut three twigs exposed to the sun from the upper canopy of each tree with a tree pruner, and then separated [?] 30 g healthy, complete leaves from the twigs for trait measurement. Fresh leaves were scanned using a CanoScan LiDE 100 scanner (Canon, Japan) *in situ*, then leaf area was calculated using the Image J software. Tree-ring cores were extracted for above-mentioned sampled trees, and we measured volume of the fresh wood cores using water-displacement method. In laboratory, all samples were oven-dried to constant weight for at least 72 h at 65 degC, and weighted to obtain dry mass (Perez-Harguindeguy et al. 2013). Specific leaf area (SLA, $\text{mm}^2\cdot\text{mg}^{-1}$) was calculated as leaf area divided by dry mass, and wood density ($\text{g}\cdot\text{m}^{-3}$) was calculated as the wood-core volume divided by its dry mass. For leaf chemistry, leaf carbon (Leaf C, $\text{mg}\cdot\text{g}^{-1}$) and nitrogen (Leaf N, $\text{mg}\cdot\text{g}^{-1}$) content were measured using an elemental analyzer (2400 Series II CHNS/O Analyzer, PerkinElmer, Boston, USA). Trait values were averaged across all sampled replicates for each species. Based on these traits data, we computed functional dispersion (FDis) index for each plot to quantify functional dissimilarity, using the “FD” R package (Laliberté and Legendre 2010). We chose FDis because it was more reasonable for communities with fewer species (when species richness = 1, FDis = 0). We also calculate Faith’s phylogenetic diversity (PD) index

to quantify phylogenetic diversity of community, using the V.PHYLOMAKER package of R developed by (Jin and Qian 2022).

Quantification of community-scale trait values for aboveground and root traits

To explore the effects of functional traits (growth strategy) on plot-scale FRB and FRP, i.e. to test the mass-ratio effect and the size-dependent growth strategy hypothesis (Hypothesis 2), we quantified community-scale trait values for each above- and below-ground functional trait. For leaf and stem traits, community-weighted mean (CWM) was calculated as the mean trait value weighted by species' relative basal area within each plot (Garnier et al. 2004). Furthermore, functional identity of dominant species for each plot, including leaf form (broad *vs* . needle-leaf) and leaf phenology (evergreen *vs* . deciduous) were also considered.

Fine-root traits were measured for each of the 216 root biomass samples before oven drying. Living fine roots separated from each soil core were spread homogeneously in a plastic tray and scanned at a resolution of 300 dpi using a scanner (Epson Perfection V700 Photo, Canada). Fine-root length, area, volume, as well as average diameter (RAD, mm) of each soil core were calculated through image analyzing, using the WinRhizo software (Regent Instruments Inc., Quebec, Canada, 2009). Based on these morphological parameters, we calculated specific root length (SRL, $\text{cm} \cdot \text{g}^{-1}$) and root tissue density ($\text{g} \cdot \text{cm}^{-3}$). SRL links the carbon cost of root proliferation to the overall benefit, and is widely used to characterize the efficiency of fine-root resource uptake. SRL was calculated as total fine-root length divided by root dry mass of each soil core. Root tissue density informed the carbon investment needed per unit increment of root volume, and was calculated as fine-root dry mass divided by root volume of each soil core (Freschet et al. 2021). Since we sampled enough (nine) soil cores evenly across each 20 x 30 m plot, community-scale value for each fine-root trait was calculated by averaging the nine samples within plot.

Aboveground biomass and stand factors

For each plot, we calculated aboveground and leaf biomass ($\text{t} \cdot \text{ha}^{-1}$) to test their allometric relationships with fine roots (Hypothesis 1) and the Hypothesis 2 of size-dependent growth strategy. Aboveground (leave) biomass for each tree were estimated from its DBH and height using the biomass equations provided by Fang et al. (2006) and Chen and Zhu (1989), and then summed to obtained plot biomass. Stem density ($\text{No} \cdot \text{ha}^{-1}$) and total basal area were also calculated because these stand factors may significantly affect fine roots (Finer et al. 2011a).

Measurements of soil properties

Soil properties, such as soil fertility and water are closed related to fine-root growth and spatial distribution, thus may affect FRB and FRP (Yuan and Chen 2012). We set up two soil profiles at two contrasting corners of each plot and collected soil samples at the depth of 0~10, 10~20, 20~30 cm. All soil samples were air dried for more than two weeks and sieved through a 2 mm sieve to remove stones, roots, and other residues. Soil water content (%) was determined by oven-drying soil samples at 105 degC for 48 h and weighing. Three indices closely related to soil fertility were quantified. Soil total nitrogen (Soil N, $\text{g} \cdot \text{kg}^{-1}$) and organic carbon ($\text{g} \cdot \text{kg}^{-1}$) were measured using the PerkinElmer 2400 elemental analyzer, and the inorganic carbon in soil samples were removed by acid fumigation before measurements. Soil total phosphorus (Soil P, $\text{g} \cdot \text{kg}^{-1}$) was measured by the alkali fusion-Mo-Sb Anti spectrophotometric method (Sparks et al. 2020). Finally, the measured values of each soil strata for the two profiles were averaged to represent the soil context of a plot.

Statistical analyses

In summary, we explained FRB and FRP with four groups of predictors. (1) Soil properties (soil water content, organic carbon concentration, soil N and soil P concentration); (2) Stand factors (total basal area, stand density, aboveground and leaf biomass); (3) Functional traits, including two categorical variables: leaf phenology (evergreen *vs* . deciduous) and leaf form (broad *vs* . needle-leaf), CWMs of wood density, SLA, Leaf C and N (CWM_{WD} , CWM_{SLA} , CWM_{LC} and CWM_{LN} , respectively), and community-scale fine root traits (RAD, SRL and root tissue density); (4) Different dimensions of tree diversity (species richness and evenness, FDis and PD).

Before data analyses, FRB, FRP, aboveground and leaf biomass, functional traits and stand factors were log-transformed to increase normality and homoscedasticity of residuals (He et al. 2009), and to test the possible allometric relationships among them; while other quantitative variables were standardized using the Z-Score method. One-way analysis of variance (ANOVA) and multiple comparisons were used to test the differences in FRB, FRP and other variables among forest types. Standard major axis regression was used to fit scaling relationships to test Hypotheses 1. To explore the drivers of FRB and FRP (to test Hypotheses 2), we first examined the bivariate relationships of FRB (FRP) with the four groups of predictors above-mentioned. Then, multiple regression model was used to evaluate the collective effect of all predictors, and used model selection based on Bayesian information criteria to drop variables to obtain the most parsimonious model. The variance inflation factor (VIF) was also calculated to exclude variables with $VIF > 3$ to avoid multicollinearity (Zuur et al. 2010). During model selection, root tissue density was excluded from the initial model for FRB due to its strong collinearity with FRB. Since our results showed FRB as a basic allometric constraint on FRP, but previous studies rarely considered this effect when explaining FRP, thus we analyzed two scenarios, i.e. including *vs.* excluding FRB in the initial model for FRP, so as to examine the differences. We applied hierarchical partitioning for the variables in the final models, implemented by the “rdacca.hp” package (Lai et al. 2022), to quantified their relative importance. We conducted 999 randomizations to test the significance of the predictors.

Finally, structural equation model (SEM), implemented by the “piecewiseSEM” package (Lefcheck 2016) was used to explore the hypothesized causal relationships concerning two Hypotheses. To simplify SEM structure and to avoid collinearity, we selected one strongest predictor from each group based on multivariate analyses. CWM_{LN} and RAD was selected for leaf and root trait, respectively, while species richness and soil N was used to represent diversity and soil fertility, respectively. Since our data did not supported Hypothesis 1, we examined the effect of aboveground biomass on both root and leaf traits, and the pathways of root trait on FRB and FRP, as well as the coordination between root and leaf traits to test Hypothesis 2. We also tested the allometric constraints of FRB on FRP, and the effect of diversity on FRB and FRP, as well as the effect of soil N on fine roots and the potential effect of leaf N on soil N. The Fisher’s C statistic was used to assess the SEM fits, and ap -value > 0.05 suggested that the model had adequately reproduced the hypothesized causal relationship (Duffy et al. 2016, Lefcheck 2016).

All the statistical analyses were implemented in R studio (R version 3.5.1).

Results

Differences among forest types

Both FRB (85.3 *vs.* 53.6 $g \cdot m^{-2}$) and FRP (161.3 *vs.* 128.7 $g \cdot m^{-2} \cdot a^{-1}$) were significantly ($p < 0.05$) higher in broad-leaved (birch and oak) than in needle-leaved (larch and pine) stands, though FRP did not differed significantly when compared among the four forest types (Figs. 1a-b). Conversely, both aboveground and leaf biomass was significantly higher in needle-leaved than in broad-leaved stands (Figs. 1c-d). Broad-leaved forests showed more acquisitive strategy than needle-leaved stands in terms of both leaf and fine-root traits. For instance, CWM_{SLA} , CWM_{LN} and SRL were significantly higher, while CWM_{LC} and RAD were significantly lower in broad-leaved stands, compared with needle-leaved stands (Figs. 1e-h; Table 1).

For tree diversity, species and functional diversity differed significantly among forest types with species richness, Pielou’s evenness and FDis higher in larch and birch stands, while lower in oak and pine stands (Table 1).

Testing the scaling relationships

We tested allometric relationship between FRB and FRP at both the soil-core and plot scales (Fig. 2). The allometric exponents for soil-core samples across all plots (9 cores x 24 plots), and from broad-leaved and needle-leaved plots, had a 95% confidence interval (CI) including 1. However, when regressed with the plot-scale FRP and FRB data, the exponents for all plots and for broad-leaved and needle-leaved plots did not have a 95% CI including 1.

Contrary to Hypothesis 1, plot-scale FRB and FRP were negatively related to aboveground biomass, and the relationships were significant for all plots and also for some forest types (Figs. 3a-b). FRB and FRP revealed non-significant overall correlations with leaf biomass, because the relationships were positive for some forest types (e.g. larch) while negative for others (e.g. pine, Figs. 3c-d).

Relationships of FRB, FRP, aboveground and leaf biomass with functional traits

Consistent with Hypothesis 2, aboveground biomass showed close scaling relationships with root and leaf traits, e.g. positively correlated with CWM_{LC} and RAD, while negatively correlated with CWM_{LN} and SRL, though some relationships were not significant in some forest types (Fig. 4). However, leaf biomass only showed significant relationships with leaf traits, i.e., CWM_{SLA} , CWM_{LC} and CWM_{LN} , but generally not related with root traits we considered (Table S1).

FRB and FRP showed positive scaling relationship with SRL, CWM_{LN} , CWM_{SLA} and root tissue density, while negative relationship with RAD and CWM_{LC} (Table 2). However, FRB and FRP were not related with wood density and leaf phenology (deciduous *vs.* evergreen trees).

Relative importance of biotic and abiotic factors on FRB and FRP

Hierarchical partitioning analysis revealed that, for the variables retained in the model for FRB (Fig. 5a), RAD presented to be the strongest predictor (explaining 39.1% of variation), followed by species richness (14.5%). Other variables, however, were not significant in the permutation test. For FRP (Fig. 5b), aboveground biomass, soil N and FRB were the strongest predictors (21.4%, 20.0%, 16.4%, respectively). However, if the allometric constraint by FRB was not considered in the initial model, species richness entered the model and exhibited significant effects on FRP (Fig. 5c).

The SEM (Fig. 6) revealed a p -value of 0.087 which indicated good model fit, and 56% and 70% of variations in FRB and FRP were explained, respectively. For FRB, RAD had direct and negative effect, with a standardized path coefficient of -0.64. Species richness and soil N also showed weak positive effects on FRB at $P < 0.1$ level. Aboveground biomass decreased FRB indirectly via RAD (which exhibited a close negative covariation with CWM_{LN}), and also decreased CWM_{LN} directly. For FRP, soil N and FRB showed the strongest direct and positive effect (path coefficient = 0.50 and 0.45, respectively). Other pathways on FRP, however, were not significant.

Discussion

Allometric relationship between fine-root biomass and productivity

As mentioned in Introduction, to better understand how stand factors, functional traits and diversity affect fine roots, we first tested possible allometric relationships concerning FRB and FRP. Based on some functional similarities between leaves and fine roots (see Introduction), the FRP-FRB scaling exponent should conform to MST's prediction for leaves (=1). This was supported by our data at the soil-core (organ) scale, which is also true for both needle- and broad-leaved stands (Fig. 2a). However, Guo et al. (2022) found that multiple scaling relationships between fine-root area, volume, diameter and mass all conform to MST's predictions for tree woody organs instead of leaves. Their results and ours are not exclusive because they examined allometries among traits related to root morphology, while we examined the FRP-FRB allometry concerning root productivity. Fine roots have important structural differences from leaves, including a key difference that leaves are nearly two-dimensional while fine roots are three-dimensional objects similar to woody organs (Price and Enquist 2007), which can lead to markedly difference in morphological allometries (Guo et al. 2022). Thus, our results, together with Guo et al. (2022), suggest that fine roots may be "leaves underground" in terms of productivity-related allometries, but differ from leaves for morphology-related allometries.

We found that the FRP-FRB scaling exponent at plot (community) scale deviated from 1 (Fig. 2b). Different exponents among biological scales are also frequently reported for other scaling relationships, which is expected by allometric theories, because the scaling up from organ to community scale involves multiple

physiological and community processes (e.g. competition, see Enquist et al. 2003, Chen et al. 2019). The complicate mechanisms are still under exploration (e.g. Chen et al. 2019) and beyond the scope of this study. However, in a meta-analysis at global scale, Deng et al. (2020) reported an isometric scaling between community-scale FRP and FRB which hold true for various biomes from grasslands to tropical forests. Collectively, these results confirm there are tight allometric relationships between FRP and FRB from organ to community scale, and thus are indispensable when examining the drivers of fine-roots dynamics.

As we expected, in the SEM, the allometric constraint (FRB) presented to be a top direct modulator of FRP (Fig. 6). In a meta-analysis including 186 stands globally, Finer et al. (2011b) also found that FRB was the most important predictor of FRP at both the stand and individual scales, out of various abiotic and biotic predictors. In our multivariate models that consider the FRP–FRB allometry, diversity revealed no significant effect on FRP (Figs. 5b and 6). However, if we did not consider FRB when explaining FRP (a common practice in previous studies), stepwise regression obtained a result that diversity exhibited significant effect (Fig. 5c), implying that diversity effect reported in some studies may have been overestimated by containing the effect of FRP–FRB allometry.

Size-dependent growth strategy as a strong drive of FRB and FRP

The Hypothesis 1 that there is a positive scaling relationship of aboveground biomass with FRB (and thus with FRP *via* FRP-FRB allometry) was not supported, because both FRB and FRP showed negative scaling relationship with aboveground biomass (Figs. 3a-b). These negative relationships also persist within the broad- and needle-leaved (e.g. oak and pine) stands, and thus is not simply a result that broadleaf plots have lower aboveground biomass but higher FRB and FRP than needle-leaved ones (Fig. 1). Considering previous findings that both fine and coarse root biomass are positively scaled with aboveground biomass (Enquist and Niklas 2002, Wang et al. 2008, Chen et al. 2019), a possible explanation for our results is that FRB and FRP are more closely (and positively) related with leaf biomass than aboveground biomass (Vanninen and Makela 1999, Chen et al. 2019). However, we found that leaf biomass showed both positive and negative relationships with FRB and FRP, even within broad-leaved or needle-leaved stands (e.g. larch *vs.* pine, Figs. 3c-d). Thus, the other part of Hypothesis 1 was not supported either.

Consistent with the Prediction 2.1 of Hypothesis 2, stands with higher aboveground biomass revealed more conservative growth strategies (Fig. 4), as indicated by higher RAD and leaf C, lower SRL and leaf N (Wright et al. 2004, Reich 2014, Ma et al. 2018), suggesting that there is a trade-off between tree size and fast-growing (acquisitive) strategy. Notably, while this trade-off is partly due to needleleaf species have more conservative strategies than broadleaf ones (Reich et al. 1997), it is also evident within the needleleaf and broadleaf stands. This is because larger trees have much higher maintenance cost and transpiration need due to more aboveground and leaf biomass, and thus large trees had to invest more on persistence and stress tolerance rather than growth (Lin et al. 2022). We also found that root functional traits were less correlated with leaf than aboveground biomass (Table S1). Leaves have a much faster turnover rate than trunks, and thus leaf biomass is not a good indicator of tree size, as reflected by that biomass allocation to leaves is more insensitive to tree size than stem (Sun et al. 2020). Thus, the weaker relationships of root traits with leaf biomass may confirm tree size (aboveground biomass) as a key driver of ecological strategies concerning root growth.

Consistent with the Prediction 2.2, stands with faster-growing strategy (e.g. lower RAD and higher leaf N) had higher FRB and FRP (Table 2), thus the Hypothesis 2 was well supported. The above results together suggest that higher aboveground biomass leads to more conservative strategy (irrespective of needleleaf or broadleaf stands) and thus results in lower FRB, which in turn lead to lower FRP due to allometric constraints, and these hypothesized pathways were well visualized by the SEM (Fig. 6). Noted that other mechanisms may also contribute to the negative relationships of aboveground biomass with FRB and FRP observed here. Fine roots are closely affected by mycorrhizal fungi (Ma et al. 2018), and the four dominant species examined here are all associated with ectomycorrhizal (EcM) fungi (Steidinger et al. 2019). Our results that needleleaf stands showed higher RAD while lower SRL than broadleaf ones (Fig. 1) suggest stronger association with EcM fungi for needleleaf stands (Bergmann et al. 2020), consistent with the fact

that coniferous species rely more heavily on EcM fungi (Fernandez and Kennedy 2016). However, RAD and SRL changed markedly with aboveground biomass for all plots and also within the larch stands (Fig. 4). This may suggest that larger trees rely more on EcM fungi to absorb soil nutrients more efficiently to support their great biomass, which also means lower needs for their own fine roots (thus may lead to lower FRP observed here). Thus, the effects of tree size and mycorrhizal fungi on root growth strategies may be not exclusive but instead working together. However, this is only a hypothesis and still wait to be tested with soil fungi data in future analyses.

Another noteworthy point is that our results were obtained in stands with similar climate but contrasting fast *vs.* slow growth strategies. Across large climate gradient of mid- to high-latitudes, forests under a harsher climate generally have lower FRB and FRP (Wang et al. 2018), and composed of species with more conservative growth strategy (Wright et al. 2004, Joswig et al. 2022), and stronger EcM fungi dependence (Steidinger et al. 2019) and further, aboveground biomass can also decrease significantly (Wang et al. 2006, Wang et al. 2008). In this situation, higher aboveground biomass is related to a faster-growing strategy (as driven by climate), which explain why some broad-scale studies found positive relationship between aboveground biomass and FRB (Finer et al. 2011a), or between leaf biomass and FRB (Chen et al. 2019). Thus, our results are consistent with these broad-scale studies in that fast-growing strategy both leads to higher FRB and FRP; however, in our study the change towards slow-growing strategy with increasing tree size is more important. Consequently, the relationships between fine roots and aboveground biomass should be control by both mechanisms (climate- and size-dependent growth strategies), and our results suggest that in broad-scale studies the latter mechanism may still work but was masked by the strong converse effect of climate, which deserves future tests.

Relative importance of mass-ratio vs. complementary effect on FRB and FRP

In natural communities, the effect of biodiversity on ecosystem functions has long been debated, as positive, neutral and even negative diversity effects have been reported for both aboveground (van der Plas 2019) and fine-root biomass and productivity (Finer et al. 2017, Sun et al. 2017, van der Sande et al. 2017). Here we found positive direct effect of species richness on FRB but not FRP, and the effect on FRB was only marginally significant (Fig. 6), which weakly supported the complementary effect. Instead, root trait presented much stronger effect on FRB than diversity (Fig. 5), thus strongly supported mass-ratio effect, consistent with previous findings (Jacob et al. 2013, Finer et al. 2017). For instance, Finer et al. (2017) found that the proportion of conifers, instead of diversity, explained more variations in FRB across six major European forest types. Additionally, we found that FRB was negatively related to RAD, while positively related to SRL (Table 2). This suggests that higher root biomass in this area is not the result of long-term accumulation of ‘thicker roots’ (characterized by slower growth, longer lifespan), but rather a result of massive proliferation of ‘thinner roots’ (with high absorption capacity and physiological activity) which leads to higher root density in soil space. Conversely, Valverde-Barrantes et al. (2015) reported that FRB of temperate deciduous forests in USA was negatively correlated with SRL. Thus, the relationship between FRB and root traits may be not fixed, but instead depend on the foraging strategies of specific species and soil context (van der Sande et al. 2017). As we expected, soil N showed the strongest positive effect on FRP (Fig.6), implying strong nitrogen limitation in study area (Du et al. 2020).

The mass-ratio effect is also supported by our result that more conservative leaf traits are associated with lower FRB and FRP (Table 2, Fig. 6), suggesting a future possibility to estimate FRB and FRP based on aboveground traits and biomass (considering the great difficulty in measuring fine roots). Similarly, van der Sande et al. (2017) found that the CWM of leaf C/N had a significant negative relationship with FRB. These correlations between leaf traits and FRB (FRP) can not mean that aboveground traits affect fine roots directly, but rather reflect that above- and below-ground organs are functionally coordinated. This idea was supported by our finding of strong coordination between leaf N and RAD (Fig. 6, supporting Prediction 2.3), and that aboveground traits were less closely related with FRB (FRP) than root traits (Table 2, supporting Prediction 2.4). Fine roots are under a very different environment (in soil) from leaves, and thus it natural that their growth strategies should differ somehow (Weemstra et al. 2016), as indicated

by that plants allocate N and P differently to leaves and roots (Tang et al. 2018). Meanwhile, various soil fungi have complex interactions with fine-roots traits which strongly affects FRB (FRP), but should not affect leaf traits directly (Ma et al. 2018, Bergmann et al. 2020). Thus, further understanding the scaling relationships between leaf and root traits, and their scaling with aboveground and fine-root biomass and productivity, may be a premier to estimate FRB and FRP from aboveground organs.

Conclusions

In this analysis, through testing potential allometric constraints on FRB and FRP, we found the size-dependent growth strategies as an important driver of fine-root dynamics at a local scale, which may work together with the climate-dependent growth strategies in driving broad-scale FRB and FRP patterns. If both mechanisms are verified in the future, they should have wide applications for estimating FRB (FRP) more accurately from aboveground organs so as to better understand global and local forest carbon sinks (Chen et al. 2019). Our results also showed that incorporating allometric relationships help to better understand how mass ratio, complementarity, and stand factors affect fine-root dynamics: tree size decrease FRB through leading to a more conservative strategy, and FRB affects FRP by allometric constraints, while biodiversity and root traits may mainly affect FRP *via* FRB instead of directly.

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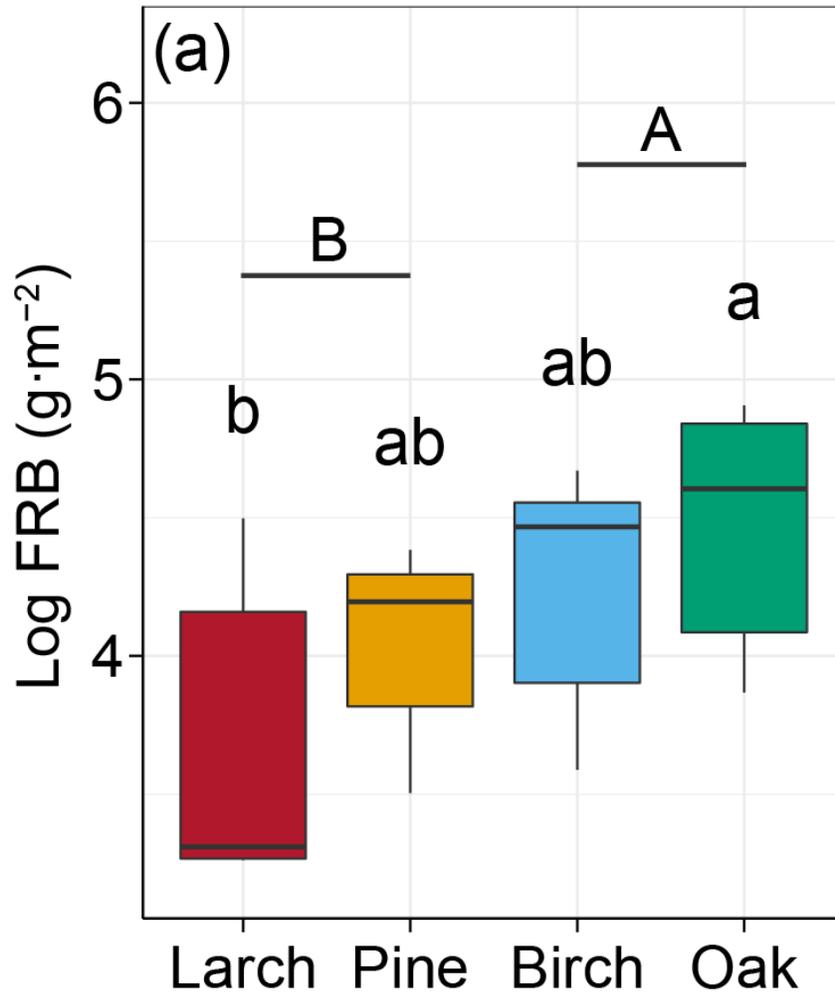
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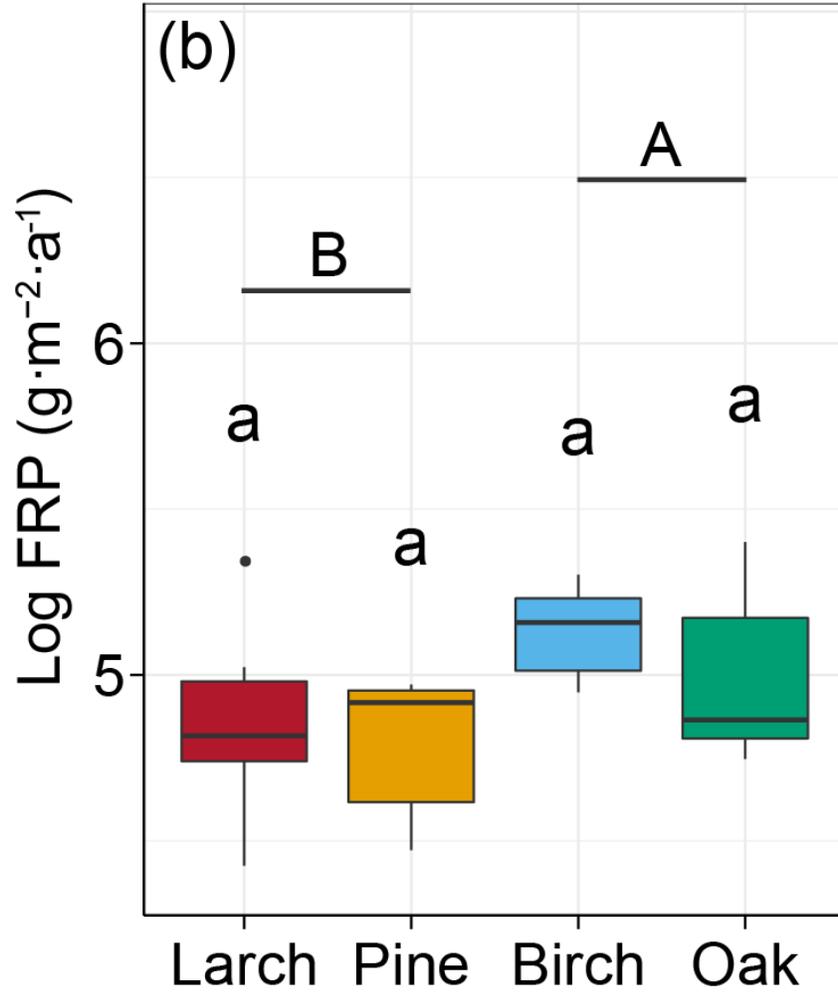
Table 1: Community characteristics of four forest types sampled from the warm temperate forest on Mt. Baihua, North China. For each forest type, the mean value (+ standard error) was reported for each stand parameter. Different letters within each column indicate significant differences ($p < 0.05$). In the last row, the values in brackets refer to the species' percentage in total basal area.

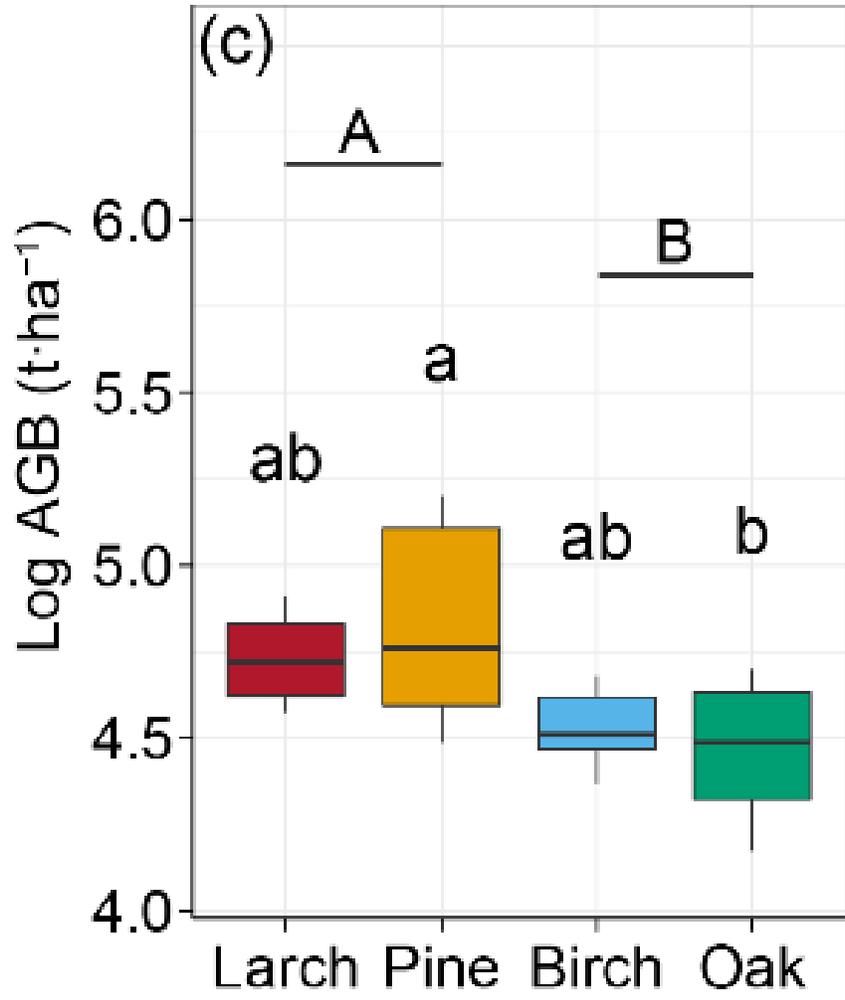
Forest type	Larch forest	Pine forest	Birch forest	Oak forest
Soil nitrogen ($\text{g}\cdot\text{kg}^{-1}$)	1.9±0.0a	1.6±0.6a	2.2±0.5a	1.7±0.8a
Fine-root biomass ($\text{g}\cdot\text{m}^{-2}$)	46.8±31.2	60.3±19.0	75.9±29.7	94.7±38.6
Fine-root productivity ($\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$)	134.1±42.9	123.3±26.2	170.6±24.1	151.9±44.6
Aboveground biomass ($\text{t}\cdot\text{ha}^{-1}$)	114.2±15.7	130.2±40.9	93.3±11.0	88.6±18.0
Leaf biomass ($\text{t}\cdot\text{ha}^{-1}$)	4.3±0.6	17.8±4.9	6.0±1.8	4.8±0.5
Specific root length ($\text{m}\cdot\text{g}^{-1}$)	13.6±2.0	14.3±1.3	17.3±2.2	15.5±4.3
Species richness	7±3ab	4±3b	9±1a	6±2ab
Pieolu's evenness	0.70±0.05a	0.29±0.26b	0.79±0.06a	0.49±0.24ab
Functional dispersion	0.19±0.06a	0.04±0.05b	0.11±0.04ab	0.07±0.07b
Phylogenetic diversity	111.2±230.5a	1088.1±192.3a	982.5±305.2a	693.9±348.4a
Species composition	<i>Larix principis-rupprechtii</i> (69%) <i>Quercus mongolica</i> (23%)	<i>Pinus tabuliformis</i> (95%)	<i>Betula platyphylla</i> (54%) <i>Betula dahurica</i> (17%)	<i>Quercus mongolica</i> (82%)

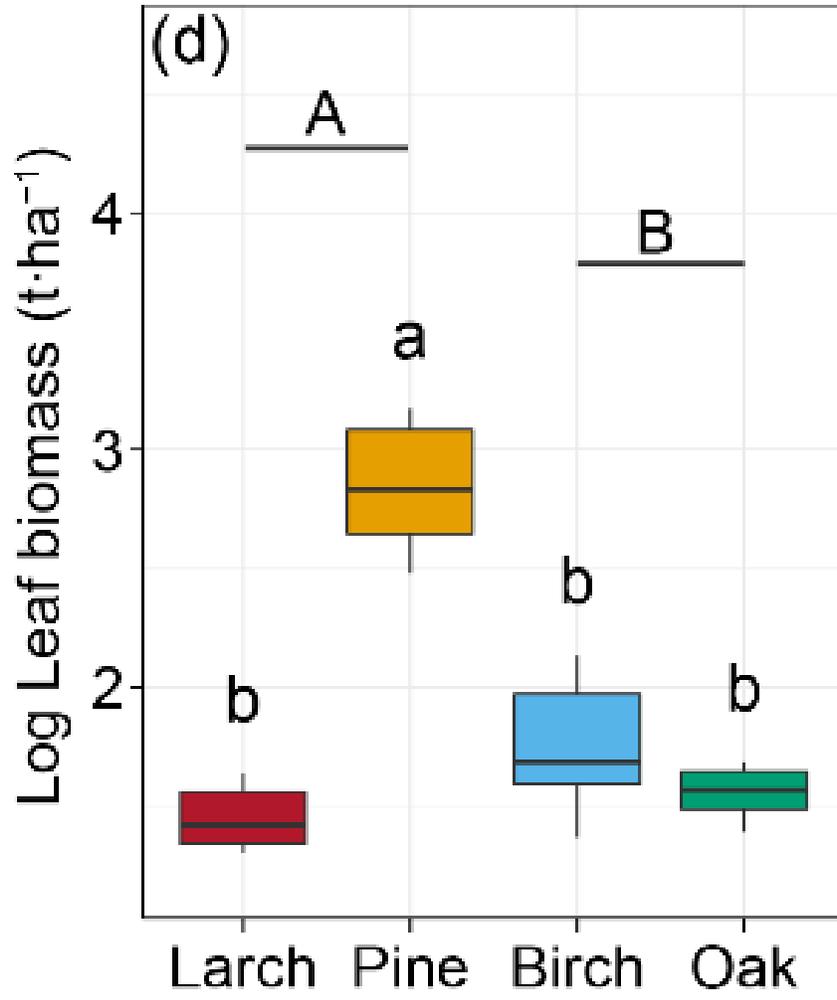
Fig. 1 : Comparison of plot-level fine-root biomass and productivity (a~b), aboveground and leaf biomass (c~d), and some leaf and root traits (e~h). Different lowercase letters indicate significant difference among

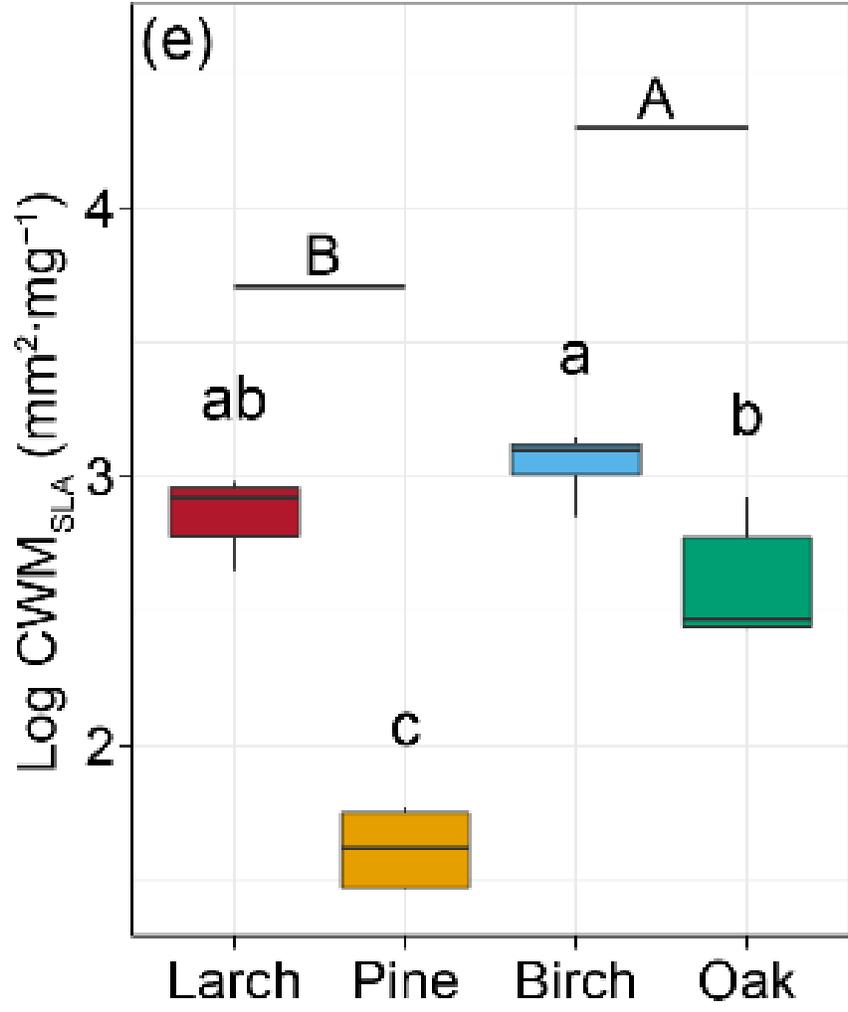
the four forest types, while capital letters indicate difference between needle-leaved (larch and pine) and broad-leaved stands (birch and oak) at $p < 0.05$. FRB, fine-root biomass; FRP, fine-root productivity; AGB, aboveground biomass; CWM, community-weighted mean; SLA, specific leaf area; LN, leaf nitrogen concentration; LC, leaf carbon concentration; RAD, root average diameter.

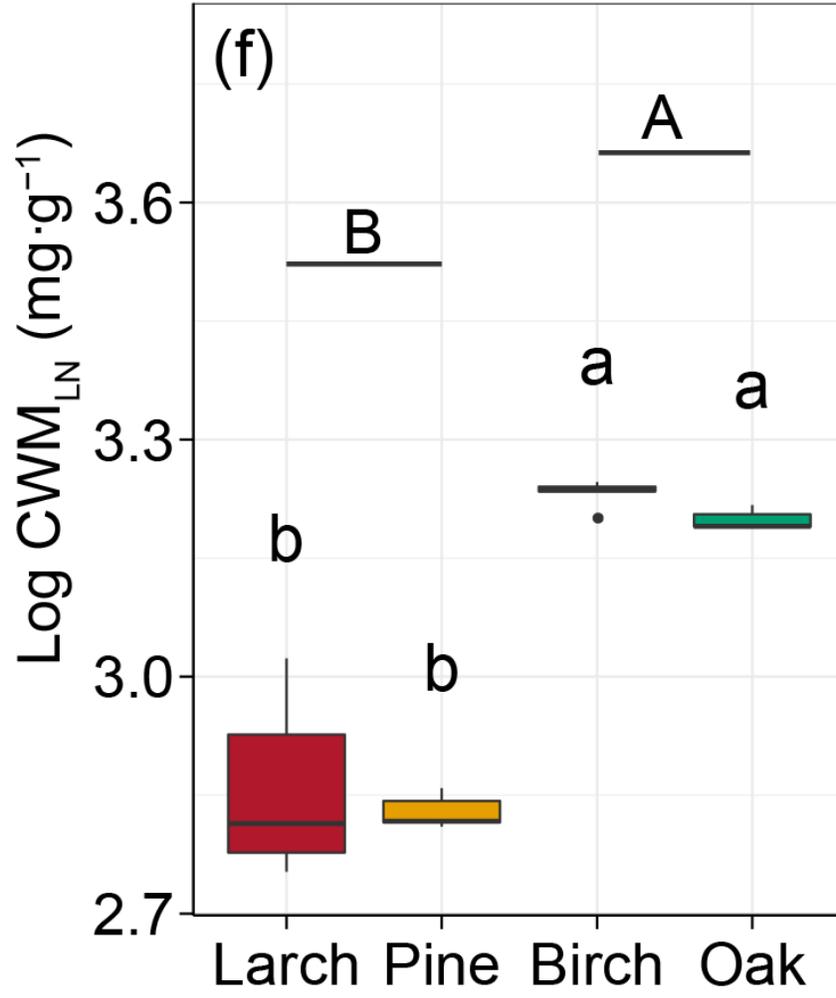


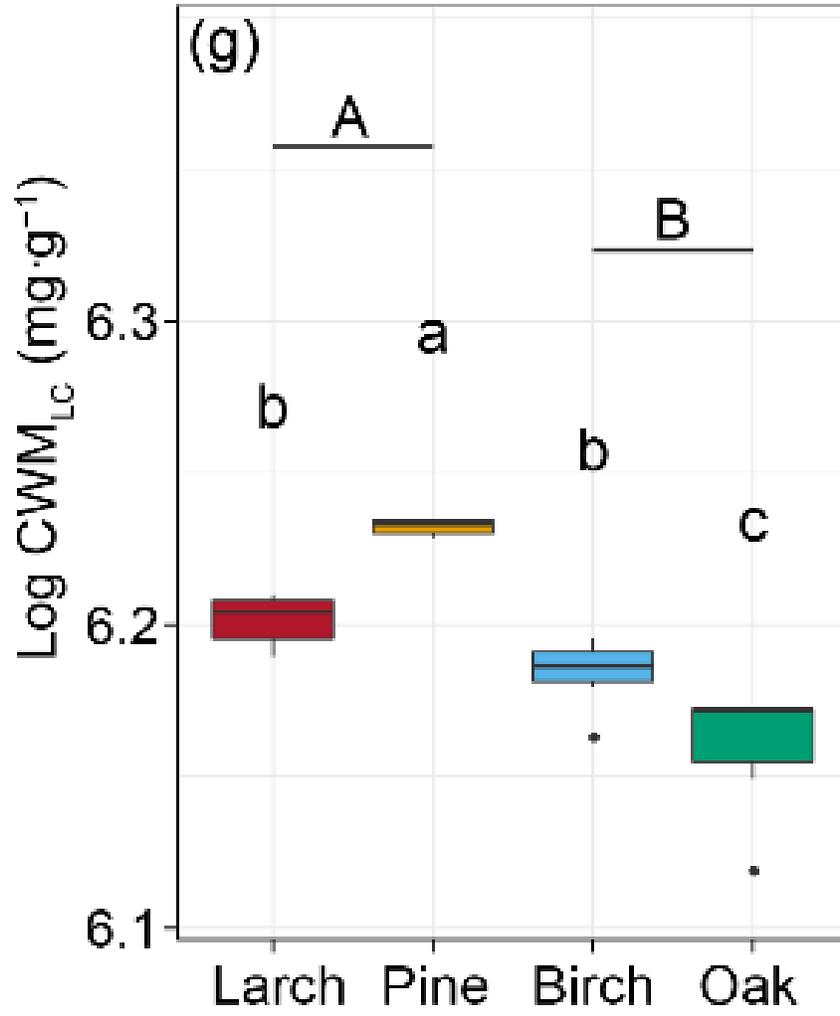












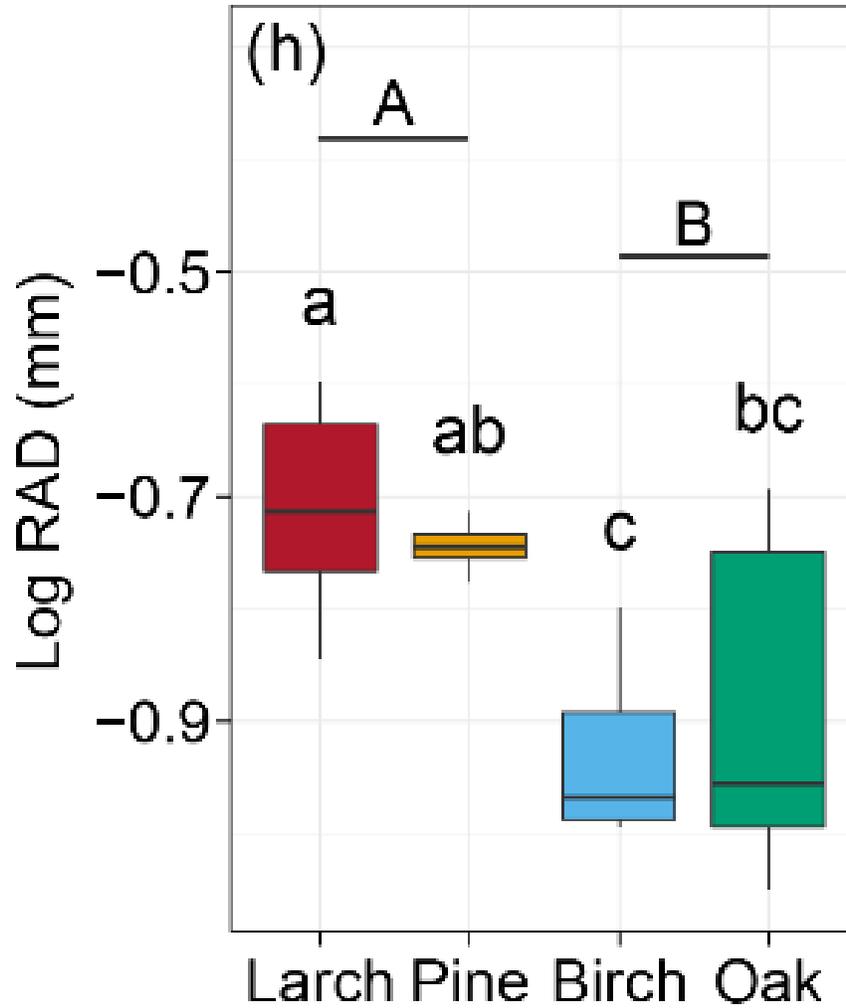


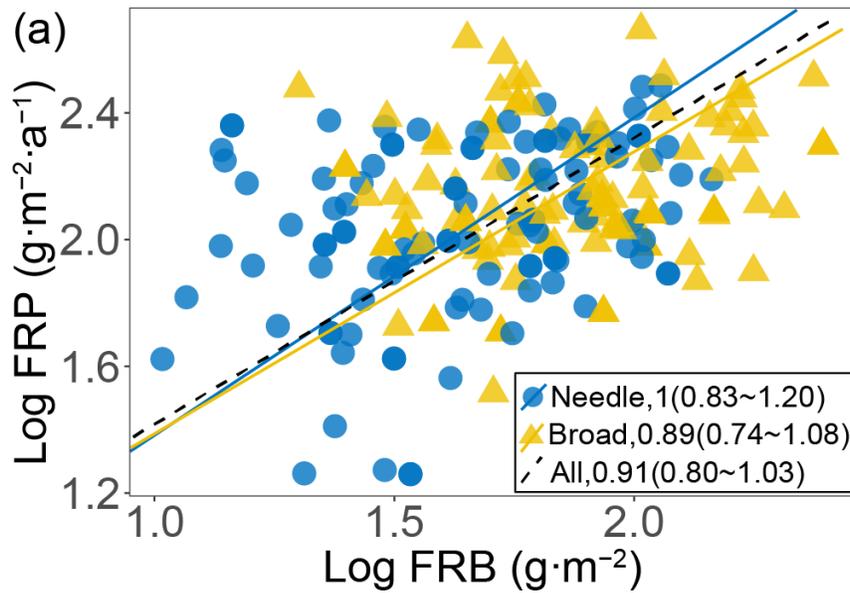
Table 2: The R^2 of each abiotic and biotic factors in explaining fine-root biomass and productivity for the 24 plots across forest types. Stand factor and functional trait variables were log-transformed. “-” denotes negative relationships while others were positive ones (except for the two categorical variables).

	Variable	log FRB	log FRP
Soil properties	Soil water content	-0.01	0.03
	Soil organic carbon concentration	0.01	0.47***
	Soil nitrogen concentration	0.00	0.35**
	Soil phosphorus concentration	-0.17*	-0.01
Stand factors	Total basal area	-0.03	-0.45***
	Stand density	0.07	0.26*
	Aboveground biomass	-0.12'	-0.52***
	Leaf biomass	-0.00	-0.09
Functional traits	Leaf form	0.22*	0.20*
	Leaf phenology	0.00	0.11
	CWMSLA	0.00	0.25*

	Variable	log FRB	log FRP
	CWM _{LC}	-0.13'	-0.22*
	CWM _{LN}	0.14'	0.20*
	CWM _{WD}	-0.00	-0.00
	Root average diameter	-0.45***	-0.31**
	Specific root length	0.15'	0.20*
	Root tissue density	0.52***	0.12'
Tree diversity	Species richness	0.18*	0.36**
	Pielou's evenness	0.03	0.34**
	Functional dispersion	-0.05	0.06
	Phylogenetic diversity	0.02	0.01

Abbreviations: FRB, fine-root biomass; FRP, fine-root productivity. CWM, community-weighted mean; SLA, specific leaf area; LC, leaf carbon concentration; LN, leaf nitrogen concentration; WD, wood density. Significant level: ', $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Fig. 2 : Allometric relationships between fine-root biomass (FRB) and productivity (FRP) at the soil-core (a) and plot (b) scales, fitted for needle-leaved (blue dots) and broad-leaved (yellow triangles) plots separately and for all data together (dashed line). Regressions lines were significant at $P < 0.1$, with slope and 95% confidence interval (in brackets) presented in figure legend.



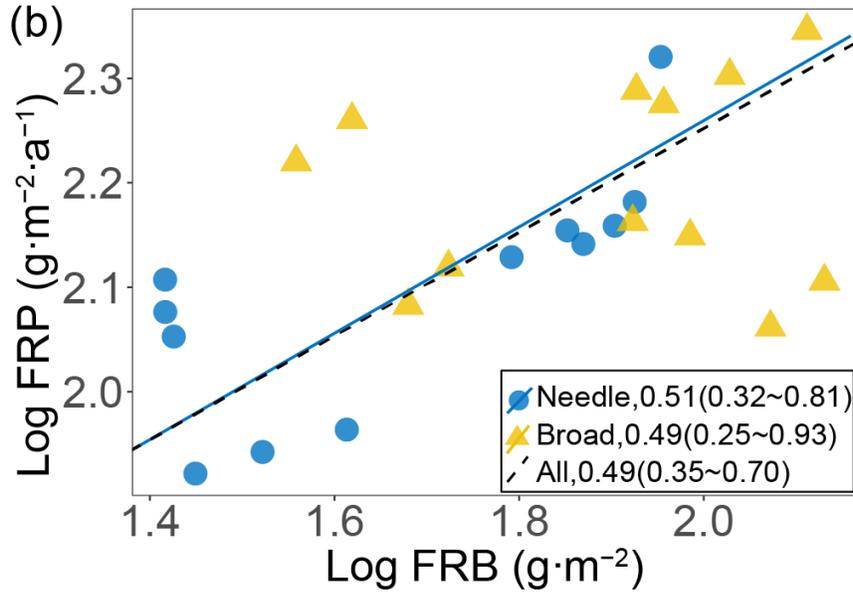
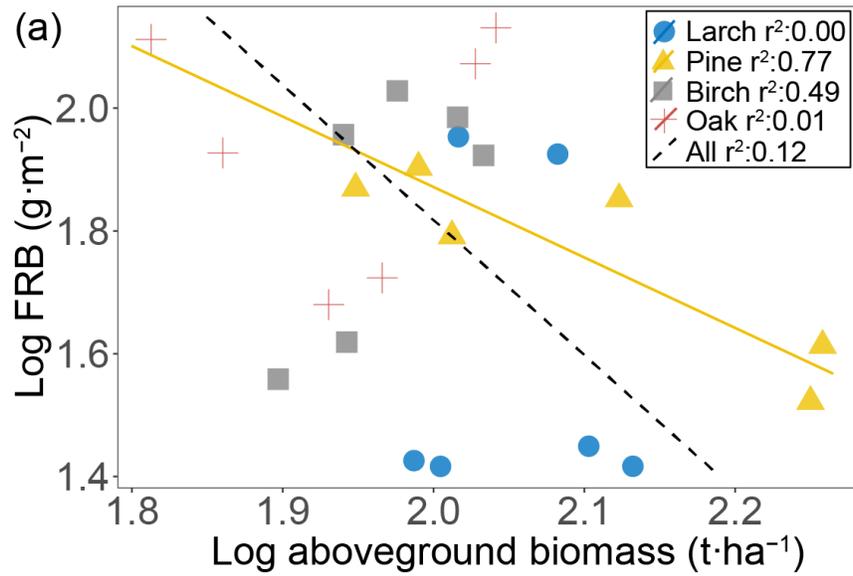
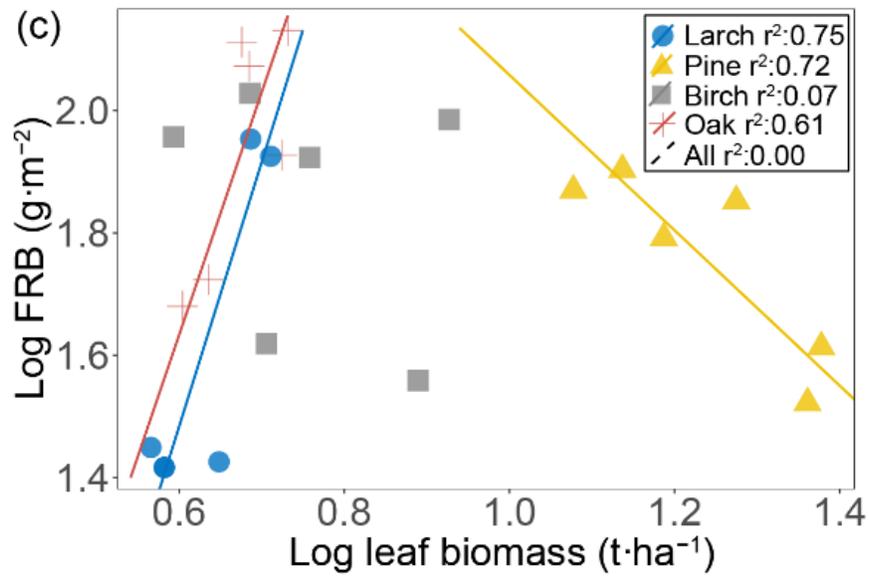
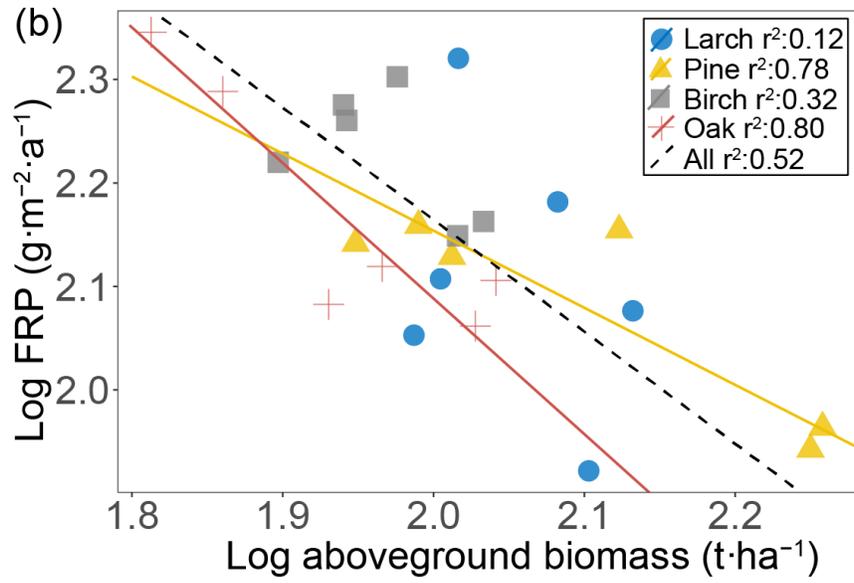


Fig. 3 : Relationships of plot-scale fine root biomass (FRB) and productivity (FRP) with aboveground and leaf biomass, fitted for all plots together (dashed line) and for the four forest types. Regressions lines were drawn for relationships significant at $P < 0.1$.





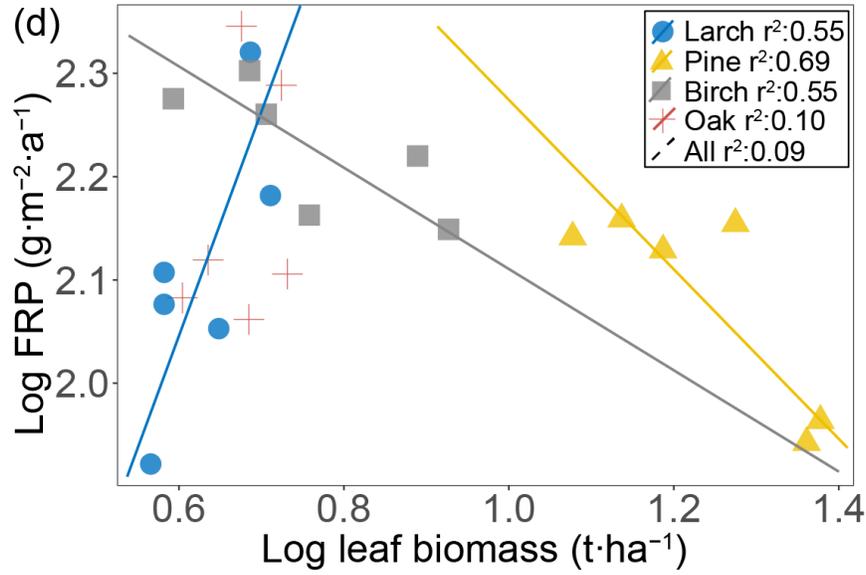
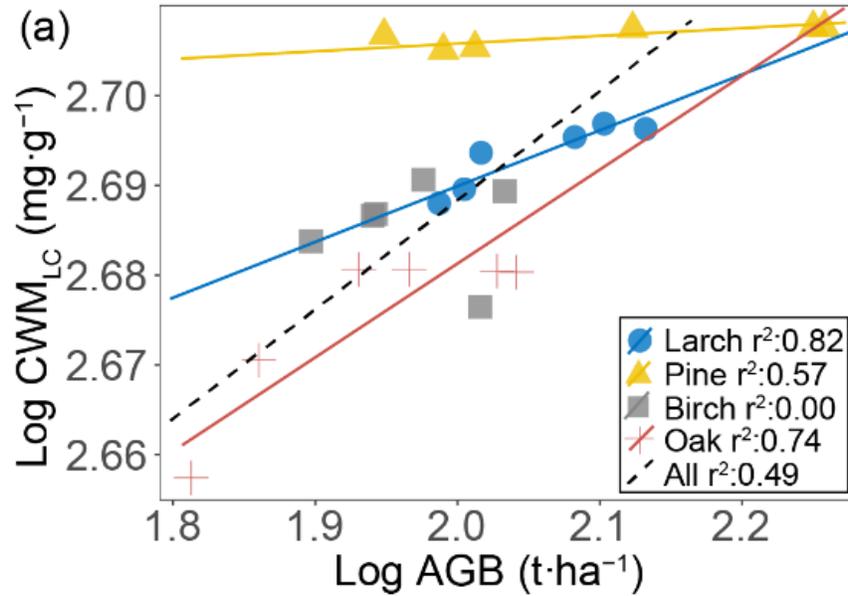
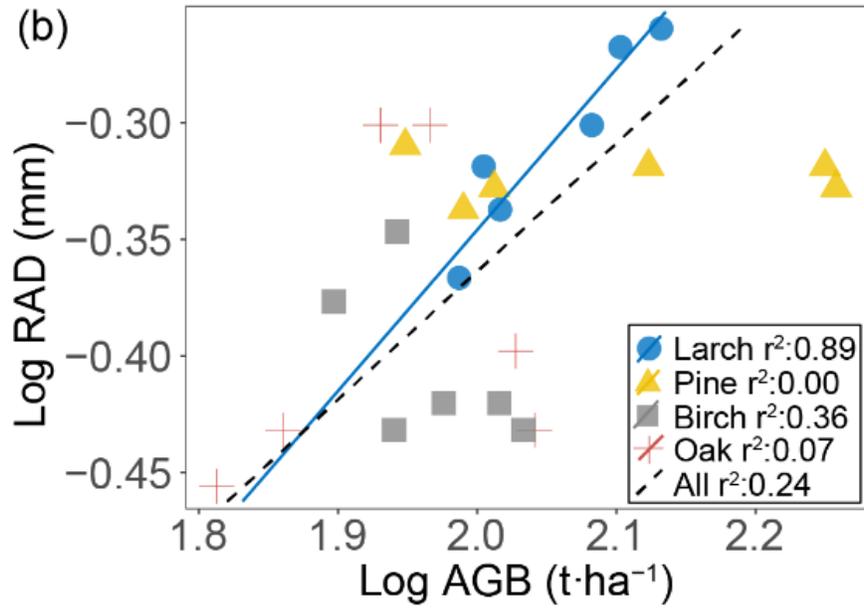


Fig. 4: Relationships of plot aboveground biomass with some leaf and fine-root functional traits at community level, fitted for all plots (dashed line) and for each forest type. Regression lines represent significant relationships at $p < 0.1$. AGB, aboveground biomass; CWM, community-weighted mean; LC, leaf carbon concentration; LN, leaf nitrogen concentration; RAD, root average diameter; SRL, specific root length.





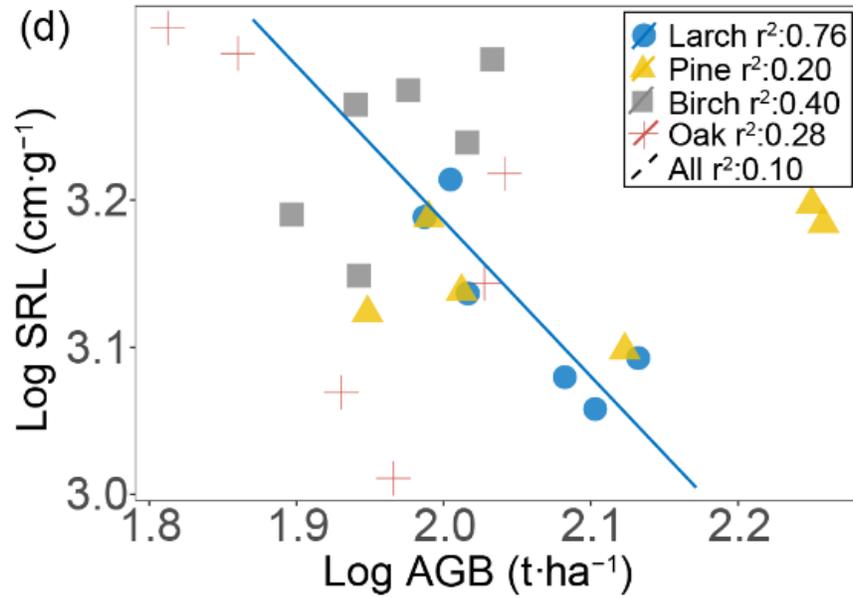
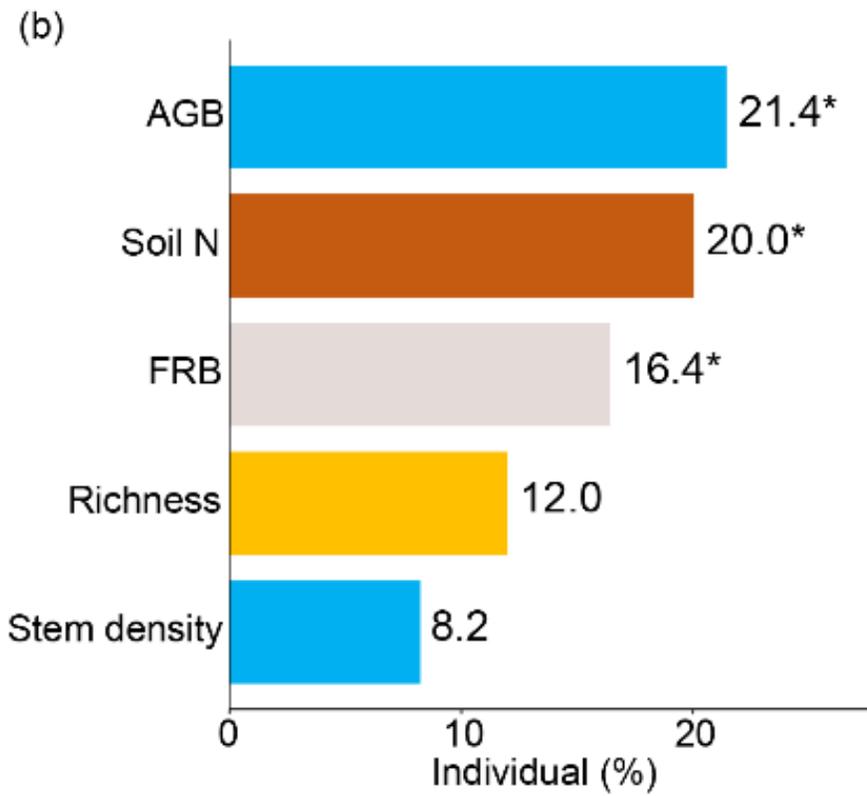
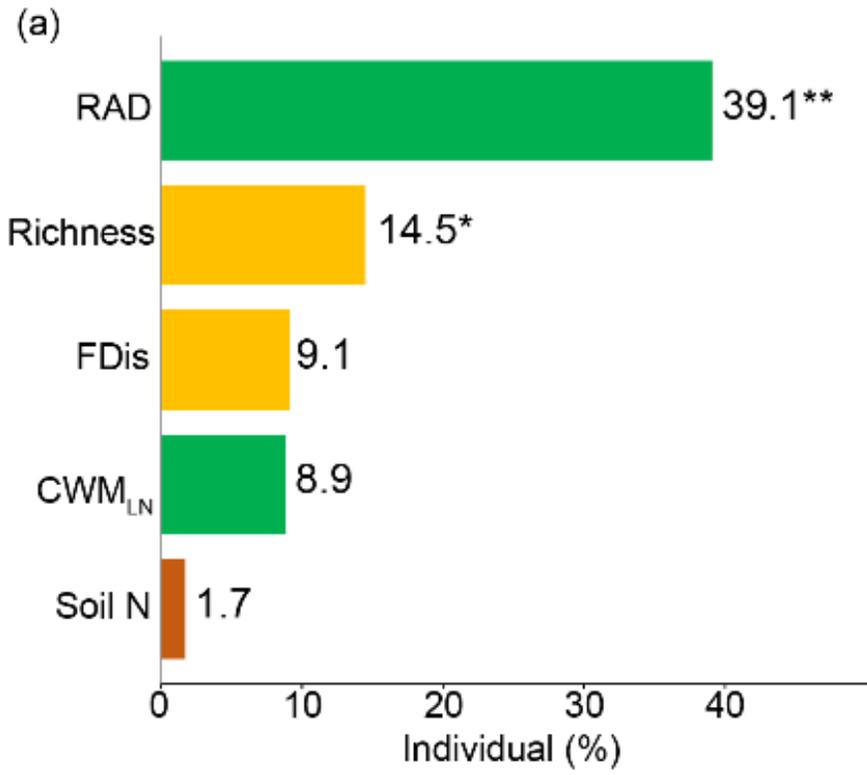


Fig. 5 : Hierarchical partitioning for the relative importance of variables retained in the final models for explaining fine-root biomass (a) and productivity. To explain root productivity, we analyzed two scenarios (see Methods): fine-root biomass (FRB) was included (b) or not included (c) in the initial multivariate model. Variable importance was calculated as the percentage of variance explained. Abbreviations: Soil N, soil nitrogen concentration; RAD, root average diameter; Richness, species richness; FDis, functional dispersion; CWM_{LN}, community-weighted mean of leaf nitrogen concentration. AGB, aboveground biomass. *, the variable was significant in the test based on 999 randomizations.



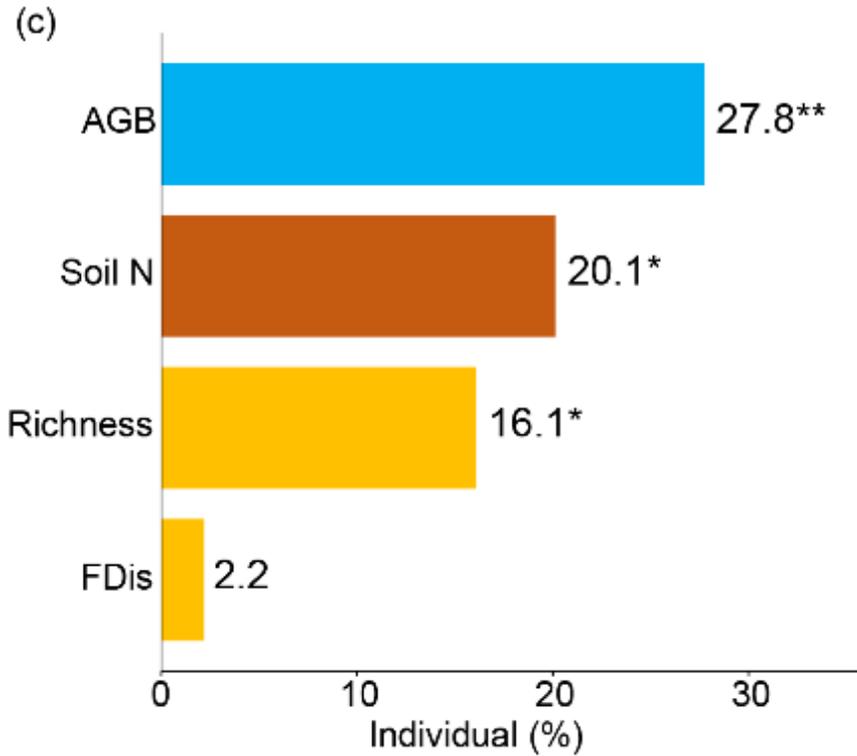


Fig. 6: Structural equation model (SEM) for the effects of aboveground biomass (AGB), functional traits, allometry, soil fertility and diversity on plot-scale fine-root biomass (FRB) and productivity (FRP). The results of model fitting are indicated at the bottom of the figure (df, degrees of freedom; a p -value > 0.05 indicates good model fit). Blue arrows for positive pathways, and red arrows for negative ones, while gray bidirectional arrow for covariations. The numeric values next to the arrows and arrow width represent standardized path coefficients ($^{\circ}$, $P < 0.1$; * , $P < 0.05$; ** , $P < 0.01$). The R^2 for each component model is given near the box of the response variable. Abbreviations: RAD, root average diameter; CWM_{LN} , community-weighted mean of leaf nitrogen concentration; Richness, species richness; Soil N, soil nitrogen concentration.

