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ABSTRACT

1. Ecosystem functioning relies heavily on belowground processes, which are largely regulated by plant fine-roots and their functional traits. However, our knowledge of fine-root trait distribution relies to date on local- and regional-scale studies with limited numbers of species, growth forms and environmental variation.

2. We compiled a worldwide fine-root trait dataset, featuring 1115 species from contrasting climatic areas, phylogeny and growth forms to test a series of hypotheses pertaining to the influence of plant functional types, soil and climate variables, and the degree of manipulation of plant growing conditions on species fine-root trait variation. Most particularly, we tested the competing hypotheses that fine-root traits typical of faster return on investment would be most strongly associated with conditions of limiting *versus* favourable soil resource availability. We accounted for both data source and species phylogenetic relatedness.

3. We demonstrate that (1) Climate conditions promoting soil fertility relate negatively to fine-root traits favouring fast soil resource acquisition, with a particularly strong positive effect of temperature on fine-root diameter and negative effect on specific root length (SRL), and a negative effect of rainfall on root nitrogen concentration; (2) Soil bulk density strongly influences species fine-root morphology, by favouring thicker, denser fine-roots; (3) Fine-roots from herbaceous species are on average finer and have higher SRL than those of woody species, and N₂-fixing capacity positively relates to root nitrogen; (4) Plants growing in pots have higher SRL than those grown in the field.

4. **Synthesis.** This study reveals both the large variation in fine-root traits encountered globally and the relevance of several key plant functional types and soil and climate variables for explaining a substantial part of this variation. Climate, particularly temperature, and plant functional types were the two strongest predictors of fine-root trait variation. High trait

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variation occurred at local scales, suggesting that wide-ranging belowground resource economics strategies are viable within most climatic areas and soil conditions.

Keywords: database; fine roots; functional biogeography; functional traits; N₂-fixation; phylogeny; plant growth form; plant resource economics; root function; soil properties

Introduction

Fine roots perform essential functions for plants including nutrient and water acquisition (Waisel *et al.* 2002) and influence a broad spectrum of ecological processes, from net primary production (Cadotte *et al.* 2009) to nutrient cycling (Freschet *et al.* 2013b; Hobbie 2015) and soil formation (Iversen 2010; Clemmensen *et al.* 2013; Bardgett *et al.* 2014). The influence of fine roots on these plant and ecosystem processes is largely mediated by their morphological, chemical and physiological traits (Bardgett *et al.* 2014). Similarly, differences in fine-root traits among species are thought to represent their evolutionary history and adaptations to a wide range of biotic and abiotic factors (Kembel & Cahill 2011; Comas *et al.* 2012).

As evidenced by a number of global syntheses on these topics, a considerable number of studies have explored the variation in ecosystem root biomass (e.g. Jackson *et al.* 1997), their vertical distribution in soils (Schenk & Jackson 2002), their fluctuations in productivity (Vogt *et al.* 1995) and turnover (Gill & Jackson 2000). Accounts of variation in morphological or chemical fine-root traits across ecosystems are also relatively common (e.g. Jackson *et al.* 1997; Iversen *et al.* 2015). However, to accurately determine the drivers of fine-root trait distribution, we need to focus most particularly on their variation at the level of species and plant individuals (e.g. Laughlin 2014; Violle *et al.* 2014), similar to what has been performed for leaf traits (e.g. Wright *et al.* 2005b; Maire *et al.* 2015). Current accounts of species fine-root trait variation are to date most often limited to the regional scale, focus either on woody

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or herbaceous species, and limit their scope to few drivers of trait variation (e.g. Kerkhoff *et al.* 2006; Salpagarova *et al.* 2014; Iversen *et al.* 2015). These studies nonetheless provide useful insights and hypotheses that could be tested globally on a more comprehensive dataset. For this purpose, we performed a global compilation of fine-root trait data including 1115 species from 55 published and unpublished studies that we refer to as the Rhizopolis database and explored the global variation in the four most commonly measured traits, fine-root nitrogen (N) concentration, mean diameter, tissue density and specific root length (SRL).

The role of these four traits in plant functioning and resource economics (*sensu* Wright *et al.* 2004) has been relatively well described. Fine-roots with high N generally have higher metabolic activity and respiration (Reich *et al.* 2008; Roumet *et al.* 2016) but lower longevity (Tjoelker *et al.* 2005; Withington *et al.* 2006; McCormack *et al.* 2012), which is likely to be associated with higher rates of root proliferation and nutrient uptake (Bloom *et al.* 1992). Fine-roots with high diameter are able to penetrate denser soils, as they exert stronger root growth pressure (Matarechera *et al.* 1991), have higher longevity (McCormack *et al.* 2012) and can support more extensive mycorrhizal colonization (Comas *et al.* 2014) but show lower root proliferation rates (i.e. growth rate, *sensu* Eissenstat 1991; Chen *et al.* 2016). Fine-roots with high tissue density also show higher longevity, at least for non-woody species (Ryser 1996; Tjoelker *et al.* 2005), and are expected to be more resistant to belowground herbivory and drought (Fitter 1991; Wahl & Ryser 2000). Finally, larger SRL increases the efficiency of soil exploration or exploitation by fine roots at the cost of lower root longevity (Eissenstat *et al.* 2000; McCormack *et al.* 2012). As a consequence, higher SRL often implies a lower reliance on mycorrhizal association (Brundrett 2002; Chen *et al.* 2016) and faster turnover of root tissues (Bardgett *et al.* 2014). Our understanding of these four traits suggests that species with thin fine-roots and low tissue density as well as high fine-root N and SRL should generally be considered as having root strategies favouring *faster return on investment*, often

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associated with greater resource acquisition rates (*sensu* Eissenstat *et al.* 2000; Wright *et al.* 2004).

At the global scale we know that herbaceous species tend to have higher RNC than woody species (Kerkhoff *et al.* 2006). When compared among local flora, N₂-fixing species also appear to have higher fine-root N concentrations than non-fixing species (e.g. Tjoelker *et al.* 2005; Roumet *et al.* 2008). In addition, local-scale studies suggest that differences among growth forms could also be seen for morphological traits such as SRL and fine-root tissue density (e.g. Freschet *et al.* 2010; Laughlin *et al.* 2010), even within the herbaceous group (Roumet *et al.* 2008; Salpagarova *et al.* 2014).

Climatic and soil variables are often substantial drivers of both intra- and interspecific fine-root trait variation. Gu *et al.* (2014) observed for instance among 50 tropical and temperate tree species that tropical trees have on average thicker fine-roots with lower tissue density and higher SRL than temperate trees. Chen *et al.* (2013) observed the same pattern of decreasing fine-root diameter in 65 trees from sub-tropical to temperate areas but no difference in fine-root N. At the other side of the global temperature range, species from cold climates show relatively thinner fine-roots with higher SRL as compared to species of more temperate areas (Körner & Renhardt 1987). As shown for leaves, low temperatures are likely to positively affect fine-root N owing to the need for plants to offset the decreased rates of biochemical reactions at low temperature (Reich & Oleksyn 2004).

As the primary function of fine roots is the acquisition of soil resources such as water and nutrients, soil properties known to influence resource availability – e.g. pH, soil cation exchange capacity – are likely to be key determinants of global fine-root trait distribution. When considered at the global scale, variation in resource availability should also strongly depend on climate variables such as soil moisture and temperature, which positively influence microbial activity and nutrient cycling (Hakkenberg *et al.* 2008; Chapin *et al.* 2011;

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Maire *et al.* 2015). Overall, given the global positive association between aboveground traits representative of fast return on investment and resource availability (Ordoñez *et al.* 2009; Swenson *et al.* 2012; but see Moles *et al.* 2014; Maire *et al.* 2015), and acknowledging growing evidence for significant coordination between plant traits aboveground and fine-root traits (e.g. Freschet *et al.* 2013b; Reich 2014), one could expect that, in conditions of low soil fertility, plants would benefit more from having traits favouring resource conservation (e.g., high tissue density) rather than fast return on investment (e.g. high SRL and fine-root N). While several studies indeed found that low fertility was associated with high fine-root tissue density (e.g. Craine *et al.* 2001; Kramer-Walter *et al.* 2016), a positive trend was also observed between soil fertility and fine-root diameter (Kramer-Walter *et al.* 2016). Besides, global expectations for fine-root diameter remain uncertain as this trait relates negatively to SRL and positively to mycorrhizal colonization, both of which increase plant resource acquisition ability (Comas *et al.* 2014; Valverde-Barrantes *et al.* 2016). Additionally, both negative and positive relationships have been observed between SRL and drivers of soil fertility (e.g., Ryser & Eek 2000; Poot & Lambers 2003; Comas & Eissenstat 2004; Tjoelker *et al.* 2005) and between fine-root N and drivers of soil fertility (e.g. Hendricks *et al.* 2000; Yuan & Chen 2010).

Soil bulk density is also likely to be an important driver of fine-root trait variation as it generally affects species fine-root diameter positively and SRL negatively (Clark *et al.* 2003). This is most likely because plants with higher fine-root diameter have greater root elongation performance in denser soils (Materchera *et al.* 1992), whereas the contrary may be true in less dense soils (Eissenstat *et al.* 2015).

Among the many studies measuring root trait variation, a large proportion is performed under controlled conditions, which can strongly affect plant traits (Mokany & Ash 2008; Poorter *et al.* 2016). It is therefore necessary to determine to what extent fine-root trait values

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measured in highly- or partly-controlled conditions (e.g. pots or common-gardens, respectively) differ from those in natural conditions (e.g. Cordlandwehr *et al.* 2013; Kazakou *et al.* 2014). In a recent synthesis of the impact of plant growing conditions on their functional characteristics, Poorter *et al.* (2016) showed that lab-grown plants had higher leaf N concentrations and different aboveground morphology, which suggest that similar changes may be observed belowground. The generally younger age of plants grown in pots (Poorter *et al.* 2016) may for instance result in higher SRL than observed in the field owing to less root secondary development (Pregitzer *et al.* 2002).

Following from our understanding of fine-root trait variation across plant functional types, soil and climate variables at local and regional scales, and experimental conditions we tested four main hypotheses. While doing so, we controlled for the effect of ‘study’ and species phylogeny.

- (1) Fine-root traits favouring higher rates of resource acquisition are likely to be most strongly associated with climate and soil variables favouring soil resource availability (such as high temperature and precipitation, and high pH and cation exchange capacity of soils), reflecting the trend globally observed for aboveground traits; or alternatively with conditions of low soil resource availability, as suggested by observations across regional gradients (e.g. Körner & Renhardt 1987; Kramer-Walter *et al.* 2016).
- (2) Soil bulk density will be associated with species of higher fine-root diameter and lower SRL.
- (3) Plant functional types summarize important differences in fine-root traits. Particularly, forb and graminoid species will tend to have fine-roots with a faster return on investment (high fine-root N and SRL, and low fine-root diameter and

tissue density) than woody species, and N₂-fixation capacity will positively influence fine-root N concentration.

(4) Plants growing in controlled conditions will display higher fine-root N and SRL as compared to plants growing in the field.

Materials and Methods

DATA COLLECTION

Data for the four fine-root traits used in this study were extracted from the Rhizopolis database. This database was compiled by the authors of this study from both published and unpublished datasets resulting from their own work and an independent literature survey (Table S1). This database is available as part of the Fine-Root Ecology Database (FRED; <http://roots.ornl.gov>; Iversen *et al.*, in press), released in March 2017. A dataset was considered suitable only when it contained at least two of the focal traits for at least three species grown in greenhouse, common garden, plantation or natural conditions. Root trait data obtained on seedlings (subjective cut-off of < 2 months for herbaceous and < 6 months for woody species) or in hydroponic conditions were excluded. Within each site, trait values from all replicates of a given species were averaged. When datasets included data from the same species in different natural sites, all observations were retained. This resulted in 55 datasets with 8714 root trait observations for a total of 1115 species from 597 genera in 135 families.

Taxonomic nomenclature was standardised using accepted names from The Plant List (<http://www.theplantlist.org/>). Taxon records for which the name was not fully resolved (e.g. *Aster* sp.) were given unique identifiers. With respect to plant functional types, species were sorted into four main growth forms (Graminoids, Forbs, Shrubs and Trees) and N₂-fixation ability (able/not able to fix atmospheric N₂), which were established based on the information

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provided in the TRY database (<https://www.try-db.org/TryWeb/Home.php>). In the case of species not referenced in TRY, information was retrieved from alternative sources (Tela Botanica 2015; USDA NRCS 2015).

Plant growth conditions were categorized as in ‘pot’ (indoors or outdoors), in ‘common garden’ (outdoors plantations), or in ‘field’ conditions (natural conditions), in order to differentiate between different degrees of climate and soil manipulation. In addition, we recorded how the fine-root sampling pool was defined in each study. Four root sampling categories were most commonly employed: roots ≤ 2 mm in diameter, roots ≤ 1 mm in diameter, first-order roots and the first-three-order roots (i.e., functional approach; McCormack *et al.* 2015). In this study, we only considered the root sampling category ≤ 2 mm (74% of observations) because other sampling categories showed strongly unbalanced distribution across climatic areas, growth forms and N₂-fixation capacity. This root sampling category represents those parts of the roots with resource acquisition functions, although the validity of this assumption is likely to vary across species. While recent studies (e.g., McCormack *et al.* 2015) have advocated the use of more refined root sampling schemes, fine-roots ≤ 2 mm form the bulk of fine-root trait data available at present and show similar patterns to roots of the first-three-orders only (Freschet & Roumet, in press). In this context, fine-root diameter represents the mean diameter of the fine-root pool involved in the acquisition of soil resources. It is only slightly biased by the use of a ≤ 2 mm cut-off limit because within this category fine-roots close to 2mm in diameter represent only a small proportion of the total length of fine-roots over which fine-root diameter is averaged.

Owing to gaps in locally-measured climate data, we used climate data available from the Worldclim database (Hijmans *et al.* 2005) to represent common-garden and field observations. Climate variables retrieved were mean annual temperature (MAT) and mean annual precipitation (MAP) averaged over the period 1960-1990. Climate data resolution was

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1 km², and discrepancies between local climate data and the Worldclim database were observed for high elevation sites where abrupt variation in altitude may not be accurately accounted for by the 1 km² grid. To limit this bias, whenever high discrepancies were recorded, local climate data rather than global data were retained.

Across all studies, little common information was available regarding edaphic characterization. Common-garden and field observations were therefore linked to soil properties as found in the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC 2012) based on their geographic coordinates. We assumed that soils of common-garden studies were representative of that of the local area, if not otherwise stated in the published articles. The main topsoil (0-30 cm depth) properties retrieved included soil pH, cation exchange capacity, organic carbon content, clay fraction and bulk density. Only soil pH, cation exchange capacity and bulk density were kept in subsequent analyses because of strong correlations among variables in the retrieved soil data – cation exchange capacity was strongly correlated to soil organic carbon content ($R^2 = 0.72$) and bulk density strongly correlated with soil clay content ($R^2 = 0.67$) – in order to avoid issues of collinearity. Soil data were obtained from gridded datasets of 1 km², which we acknowledge can lead to biased representation of these variables in locations with wide ranges in climate and soil conditions, such as mountainous areas.

ROOT DATA COVERAGE

The database covers most of the range of mean annual temperature–rainfall space in which higher plants are found, as well as the major climatic areas of the world. However, some large geographic regions are not represented, such as Siberia, the Middle East, North and Central Africa, and Central America (Fig. 1). The majority of species originate from the temperate area (48% of observations), followed by cold (21%), arid (16%) and tropical areas

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(15%). With respect to species counts across broad phylogenetic clades, the representativeness of the dataset is reasonably good. Eudicots (56% of this dataset, compared to ~66% of the world's species) and monocots (37% vs ~26%) account for the largest number of species of vascular plants, followed by magnoliids (3.6% vs ~3.4%) and gymnosperms (2.6% vs ~0.3%), whereas pteridophytes are under-represented (1.1% vs ~4.3%). The four main growth forms are all well represented in the dataset, with forbs (37% of observations in this dataset, compared to ~34% of species in the TRY database) and graminoids (35% vs ~24%) being the two groups most represented, followed by trees (15% vs ~24%) and shrubs (12% vs ~18%). The group of N₂-fixers is also well represented with over 8% of observations. Finally, 69% of data were obtained on plants growing in natural conditions against 10% in common-garden and 21% in pots.

PHYLOGENY CONSTRUCTION

A phylogenetic tree was constructed (Fig. S1) using the comprehensive Angiosperm species-level phylogeny from Zanne *et al.* (2014), as updated by Qian & Yin (2015). This time-calibrated tree includes nearly all families of extant seed plants: species placement relied on seven gene regions, with orders and families constrained by the APG III (2009). We used S.PhyloMaker (Qian & Jin 2015) to generate a phylogeny containing species from the Rhizopolis database from this megaphylogeny. More than 98% of species represented by at least one of the four focal traits (N, diameter, tissue density, SRL) could be included in the resulting phylogenetic tree. Where species or genera were not represented in the larger tree, they were added as uninformative (e.g. basal) polytomies. The final tree was ultrametric with time-calibrated branches (Fig. S1).

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DATA ANALYSIS

As the data in these analyses represented 55 studies conducted using different methods and for different purposes, we treated ‘study’ as a random effect. For each trait, we used a random-effect model with ‘study’ as random factor to calculate a best linear unbiased predictor (BLUP) of the mean trait value (and standard error) for each species. The BLUPs were calculated with mixed linear model (lmer() in ‘lme4’ package; Bates et al. 2015); these were used as the species’ mean trait values in the subsequent analyses.

Recent papers have highlighted the importance of phylogenetic corrections for meta-analyses and similar comparative analyses (Chamberlain *et al.* 2012), as phylogenetic relatedness can represent a significance source of non-independence between observations. We tested for phylogenetic signal (Pagel’s λ) in the values of each of the four root traits (phylosig function in ‘phytools’ package; Revell 2012). Values of Pagel’s λ close to zero indicate phylogenetic independence, whereas values approaching 1 indicate an increasing similarity among closely related taxa (Münkemüller *et al.* 2012). All four traits had λ values significantly different from zero, suggesting significant phylogenetic signal in trait distribution and justifying the inclusion of phylogeny as part of the error structure in our models.

Given the lack of within-species variation for most traits in the dataset and to avoid overfitting, we were unable to fit a general linear mixed model with phylogeny as a random effect (e.g. Ives & Helmus 2011). Instead, for each trait separately, we chose to fit a general least squares model in which the correlation structure was a phylogenetic tree reflecting the relatedness among species (using gls function from ‘nlme’ package; Pinheiro *et al.* 2015). These models recognize the shared evolutionary history and therefore non-zero error covariances among data points, and so they transform the data to reflect this. Linear regression is then applied to the transformed data (Stone *et al.* 2011).

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For the first set of phylogenetic generalized least-square models, we included as fixed effects *plant growth conditions*, *climatic area*, *plant growth form* and *N₂-fixation capacity*.

For comparison, we also constructed matching general least-square models that did not include the phylogenetic correction. This allowed us to consider how the phylogenetic correction altered the effect of fixed variables on root traits. For each model, we present the least square mean contribution of significant fixed effects, and also performed post-hoc Tukey tests to assess the significance of the differences among the levels of the fixed effects. We calculated the variance explained by the model using type III sums of squares and conservatively partitioned it among fixed factors by calculating the variance explained gained by adding the focal factor after other factors were already included in the model. In a second step, we repeated the same approach (accounting for species phylogeny) on a subset of our data excluding observations from plants grown indoors or in pot, in order to test the effect of global climate and soil variables. This time, we included as fixed effects *plant growth form*, *MAT*, *MAP*, *soil pH*, *cation exchange capacity* and *bulk density* in our models for all four traits. Data for all four root variables were log-transformed prior to all analyses, and we determined that model assumptions were met for each model.

The interaction effects between *MAT* and *MAP* and between *soil pH* and *cation exchange capacity* on root traits were also included in the second step of our analyses, but are not presented here as they were consistently found to be non-significant for all four traits. For both steps, no differences were observed between shrubs and trees and observations for these categories were pooled. All analyses were conducted using R version 3.2.3.

Results

Large trait variation was observed for all four traits globally, with roughly 10-, 20-, 20- and 300-fold differences in mean fine-root diameter, N, tissue density and SRL, respectively

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(using 95% confidence interval range; Fig. 2). As a point of comparison, the 20-fold difference in fine-root N (from 1.7 to 39.3 mg g⁻¹) was twice this of its aboveground analogue, leaf N, in a dataset of comparable size and geographical spread (10-fold difference, from 6.3 to 58.7 mg g⁻¹; Freschet *et al.* 2011). Large trait variation also occurred within local flora, with up to 4-, 9-, 10- and 50-fold differences in mean fine-root diameter, N, tissue density and SRL, respectively (Fig. 2), as well as within climatic areas, plant growth forms, N₂-fixation ability, and plant growth conditions (see Fig. 3).

SOIL AND CLIMATIC VARIABLES

The climatic area from which plants originate was the most important factor associated with trait variation for fine-root N, diameter and SRL (Table 1). Before correcting for the influence of species' evolutionary history on their distribution across climatic areas, it accounted for 12, 16, 8 and 18% of the variation in fine-root N, diameter, tissue density and SRL, respectively (Table S2). Nevertheless, owing to the non-random distribution of species among climatic areas, accounting for phylogenetic relatedness resulted in a lower explained trait variation for three traits out of four (7, 34, 2 and 12% of the variation in fine-root N, diameter, tissue density and SRL, respectively; Table 1). Generally, species from tropical areas showed the lowest fine-root N and SRL and highest fine-root diameter, and species from cold climates showed particularly thin fine-roots and high SRL (Fig. 4). Because climatic area is a relatively coarse index of climate variation, we explored further the specific effects of selected soil and climate variables.

Focusing on the subset of our data collected from outdoor conditions, there was no single climatic or soil variable that consistently explained the majority of variation in all four fine-root traits (Table 2). Instead, the variation in each trait was related to a different set of variables. Focusing first on climate, mean annual temperature was negatively related to fine-

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root N and SRL (2% and 17% explained variation, respectively) and positively related to fine-root diameter and tissue density (29% and 2% explained variation, respectively) (Table 2). Mean annual precipitation was associated with decreasing fine-root N and diameter (10% and 1% explained variation, respectively) and showed no relationship with fine-root tissue density and SRL (Table 2).

Regarding soil variables, cation exchange capacity showed a strong positive relationship with fine-root tissue density (13% explained variation; Table 2), whereas fine-root N and SRL showed no trend and fine-root diameter instead related negatively to soil cation exchange capacity (1% explained variation). Soil pH was negatively related to fine-root N and tissue density (4% and 3% explained variation, respectively), while fine-root diameter and SRL showed no trend (Table 2). Finally, thicker, denser fine-roots with lower SRL were found at higher soil bulk density (Table 2).

PLANT FUNCTIONAL TYPES

Plant growth form explained a substantial portion of trait variation (6, 18, 4 and 6% of the variation in fine-root N, diameter, tissue density and SRL, respectively; Table S2), but here again, accounting for phylogenetic structure substantially reduced its predictive value (2, 13 and 2% of the variation in fine-root N, tissue density and SRL, respectively, and non-significant for fine-root diameter; Table 1). This occurred because of the overlap between growth form classification and phylogenetic clades. For instance, the graminoid group includes almost all herbaceous monocots, whereas the forb group includes all herbaceous eudicots. The retained significant effect of plant growth form after phylogenetic correction for fine-root N, tissue density and SRL indicates that this classification remains useful independent of the monocot/eudicot dichotomy. Two important trends consistently emerged with and without phylogenetic correction. First, in contrast to our expectations, graminoids

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stood out with generally lower fine-root N, and tissue density than forbs, shrubs and trees (Fig. 4). Second, woody species showed lower SRL than forbs and graminoids owing to higher tissue density. Shrubs and trees did not show any substantial or significant differences in any of our models.

Plant N₂-fixation capacity was positively but weakly related to fine-root N (2% explained variance) and negatively to SRL (1% explained variance; Table S2). Once corrected by phylogenetic relatedness these weak trends disappeared (Table 1), mostly because of the constrained distribution of N₂-fixers to the Fabaceae family (96% of N₂-fixers in this dataset; Fig. S1).

PLANT GROWTH CONDITIONS

According to the phylogenetically corrected models, plant growing conditions were significantly, but only moderately associated to changes in two root traits, tissue density and SRL. Supporting our expectations, SRL of plants grown in pots was higher than those of plants grown in common-gardens or in the field (Table 1; Fig. 4). While this trend held for both phylogenetically-corrected and non-corrected analyses (Table 1), there was clear evidence that part of the trend observed in the non-corrected analyses was driven by a high proportion of pot studies focussing on herbaceous species (91% of studies) which generally had high SRL (Fig. 3; Fig. S1). Finally, plants growing in the field showed lower fine-root tissue density than those grown in common-garden (Table 1; Fig. 4).

Discussion

Previous studies have shown that interspecific differences in aboveground plant traits are primarily a reflection of their evolutionary history and adaptations to a wide range of biotic and abiotic factors (Wright *et al.* 2005b; Cornwell *et al.* 2014). Using a large and novel

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dataset, we demonstrate that primarily climate (mean annual temperature and precipitation) and to a lesser extent plant functional types (i.e., growth form and N₂-fixation ability) and soil variables (pH, cation exchange capacity, bulk density) account for the global variation in four key fine-root traits. Similar to previous aboveground observations, our results show high root trait variation at local scales among co-occurring species (Wright *et al.* 2004; Freschet *et al.* 2010) despite local environmental constraints.

CLIMATE AND SOIL CONDITIONS ARE THE MAIN DRIVERS OF ROOT TRAIT VARIATION AT GLOBAL SCALES

Three of the four studied fine-root traits (fine-root N, diameter and SRL) show strong variation among climatic areas. Most particularly, species from cold areas are characterized by the highest SRL and thinnest fine-roots, a suite of root traits known to favour resource acquisition, and species from tropical areas display relatively conservative fine-root traits (thick fine-roots with low SRL and N). These results obtained at the global scale confirm and extend the patterns observed at finer scales, such as in studies comparing root traits of alpine herbaceous species from different altitudes (Körner & Renhardt 1987) and from temperate *versus* tropical or subtropical woody species (Chen *et al.* 2013; Gu *et al.* 2014). Our study further demonstrate that contrasting climatic and soil variables relate to changes in distinct fine-root traits. Specifically, we observe that temperature has a strong effect on traits related to root thickness (diameter and SRL), whereas precipitations mostly influence fine-root N and soil properties (cation exchange capacity and bulk density) strongly affect fine-root tissue density. The relationship between both temperature and precipitation and root traits is likely due to the predominant role of climate in regulating soil processes, particularly nutrient and water availability. While temperature and precipitation regimes can in some instances be partly disconnected from the actual soil conditions (Moles *et al.* 2014), they still generally

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strongly relate to organic matter turnover rates and water and nutrient cycling (e.g. Chapin *et al.* 2011).

Overall, temperature has the strongest link to fine-root trait variation, particularly fine-root diameter and SRL and to a lesser extent fine-root N and tissue density. The production of thin roots is generally associated with faster root elongation rates (Eissenstat *et al.* 2015) and higher potential to proliferate in nutrient patches (Hodge 2004). Further, high SRL roots have cost-efficient morphological structure for soil exploration or exploitation that implies faster return on investment strategies (Eissenstat *et al.* 2000). This should be particularly useful in colder environments where root nutrient absorption rates are lower (Chapin 1974) and where strong seasonality and soil freezing could lead to heterogeneous and intermittent soil microbial activity and nutrient availability (Bardgett *et al.* 2005; Chen *et al.* 2013). High SRL has also been considered as an alternative to mycorrhizal colonisation in arctic and alpine regions where non-mycorrhizal species are more widespread and root mycorrhizal colonization levels are highly variable (Gardes & Dahlberg 1996; Comas *et al.* 2012). Finally, this trend appears consistent with the greater proportion of biomass generally allocated to roots in colder habitats (Reich *et al.* 2014; Iversen *et al.* 2015). The relatively weak negative relationship between temperature and fine-root N suggests that the decreased rates of biochemical reactions at low temperature (Reich & Oleksyn 2004) are not strongly compensated by increases in fine-root N that would support higher potential respiration rate and metabolic activity (Reich *et al.* 2008; Bardgett *et al.* 2014).

Rainfall is the main driver of fine-root N but has little or no effect on other fine-root traits. At high rainfall fine-roots appear able to perform at low levels of N in their tissues, whereas species from environments with lower rainfall tend to maintain higher fine-root N. High rainfall is generally associated with readily available soil N, but also high potential N losses via denitrification, leaching and runoff (Chapin *et al.* 2011). Therefore, plants growing

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in high rainfall conditions may benefit more from investing in dense networks of roots and/or mycorrhizal hyphae to capture available sources of N prior to leaching rather than from investing in high root metabolism and specific nutrient uptake rates (i.e. high fine-root N; Bloom *et al.* 1992; Reich *et al.* 2008). In contrast, environments with low rainfall generally have fluctuating soil moisture conditions and slower organic matter cycling. Here, investments in high N fine-roots and therefore fine-root metabolism (e.g., Liu *et al.* 2010) could represent a more efficient strategy to compete with microbial communities during pulses of nutrient and water availability (Schimel & Bennett 2004; Liu *et al.* 2016). Although not reflected in our global analysis, local evidence that xeric environments favour thinner roots with higher SRL (Espeleta & Donovan 2002; Metcalfe *et al.* 2008) suggests nonetheless that morphological adaptations can also be observed locally in response to water shortage. Similarly, at extremely low rainfall conditions, root drought-avoidance strategies (ephemeral, high N, high SRL fine-roots) can coexist with perennial roots (Salguero-Gómez & Casper 2011; Liu *et al.* 2016).

While soil properties strongly affect fine-root tissue density, they have surprisingly modest influence on fine-root N, diameter and SRL. The strong positive influence of cation exchange capacity – a measure of soil capacity to retain cations (e.g. NH_4^+ , K^+ , Ca^{2+}) that positively influences root access to these nutrients – on fine-root tissue density suggests that species have longer root lifespan and more resource-conservative root strategies in more fertile conditions (Ryser 1996; Tjoelker *et al.* 2005). However, this is not supported by other trait variation with cation exchange capacity. The increasing fine-root N observed with decreasing soil pH also suggests that limited nutrient availability for plants favours species with high metabolism (Roumet *et al.* 2016). Indeed, across the pH range observed in our dataset (from 4.5 to 7.8), decreasing pH implies lower nutrient mobility in soil solution. However, again, this trend was relatively weak and not paralleled with consistent variation in

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fine-root diameter, tissue density and SRL. Overall, the lack of consistent relationships between soil properties and root traits related to thickness could result from the multidimensionality of roots (Weemstra *et al.* 2016) – aimed at acquiring water and different nutrients with contrasting mobility in soil – and the variable reliance of different plant species on symbiotic associations for resource acquisition (Comas *et al.* 2014; Valverde-Barrantes *et al.* 2016).

The positive effect of soil bulk density, which is a function of the mineral and organic composition of soil and its degree of compaction, on fine-root diameter is consistent with expectations of stronger radial root growth in conditions of root growth impedance (Goodman & Ennos 1999; Clark *et al.* 2003). Further, species with thicker fine-roots are generally better adapted to denser soils because of their higher penetration strengths (Materechera *et al.* 1992). Additionally, soil bulk density is strongly positively related to fine-root tissue density, which could relate to the thicker cell walls of roots growing under high soil density that are necessary to support higher root turgor pressure (Bengough *et al.* 2006). As a result, SRL is also found to be lower in denser soils, likely owing to the combined effect of increased fine-root diameter, higher tissue density and lower elongation rates (Bengough *et al.* 2011).

Overall, the generally weaker relationship between fine-root traits and soil variables as compared to climate variables and the inconsistent responses observed across traits for cation exchange capacity and pH must be considered with caution. Indeed, the highly heterogeneous nature of soil properties and their abrupt variations at multiple spatial scales are only coarsely represented by the large-scale estimates of soil variables available for this global analysis.

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GLOBAL FINE-ROOT TRENDS AMONG PLANT FUNCTIONAL TYPES

Graminoids, forbs and woody species are considered ecologically useful functional groups because they summarize major functional differences among plant species, at least for aboveground plant parts (Lavorel *et al.* 1997). This has however only partly been tested belowground as most studies on fine-root traits are based within either grassland or forest ecosystems and few have explored the variation in fine-root traits across both herbaceous and woody species. Our study reveals major global differences among plant functional types, and challenges findings from other global and regional studies.

With regard to fine-root morphology, the significantly lower SRL and higher tissue density of woody species found here imply higher construction costs, higher lifespan and slower nutrient acquisition rates (McCormack *et al.* 2012; Liu *et al.* 2016) as compared to fine-roots of herbaceous species (forbs and graminoids). Woody plants generally have extensive long-lived root systems from which fine-roots extend to access to large soil volumes. In contrast, herbaceous fine-root systems should grow denser fine-root networks to explore the soil. In this context, herbaceous species may have, on average, favoured strategies of fast return on investments, which implies faster root growth and greater plasticity and turnover, in order to either explore large soil volumes at lower cost or to more quickly respond to spatial and temporal heterogeneity in nutrient and moisture supply.

Among non-woody plants, the even lower fine-root tissue density of graminoid species as compared to those of forbs is generally consistent with the absence of secondary growth generally observed in graminoids (Kutschera 1960; Craine *et al.* 2001; Roumet *et al.* 2008). However, in contrast to results from a previous synthesis (Kerkhoff *et al.* 2006; but see Salpagarova *et al.* 2014), we observe lower fine-root N in graminoid than in woody species, and no difference in fine-root N between forb and woody species. In light of fine-root economics, the low N concentration of graminoids, which is characteristic of resource-

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conservative species, is surprising since graminoids also show high SRL and low fine-root tissue density. This suggests that graminoid roots have relatively low metabolic activity and respiration rates (Reich et al. 2008; Roumet et al. 2016) and rely mostly on cost-efficient root morphological structure, rather than on high specific nutrient absorption rates (Bloom *et al.* 1992; Freschet *et al.* 2015) to acquire soil resources.

As expected, the main difference between N₂-fixing and non-fixing species relates to fine-root N concentration, which is higher globally in the Fabaceae than in the other plant groups. This result is consistent with previous work showing that N₂-fixers have higher leaf and stem N concentrations than other groups (Wright *et al.* 2005a; Cornwell *et al.* 2014). This high root N concentration could be explained by the positive effect that nutrient availability (e.g. via N₂-fixation) has on the nutrient concentration of all plant organs, in line with the luxury consumption hypothesis (Chapin 1980; Xia & Wan 2008). Additionally, the high metabolic cost of N₂ fixation should also contribute, although modestly, to the high N concentration in nodules and surrounding tissues of roots of N₂-fixing plants (Warembourg & Roumet 1989; Wardle & Greenfield 1991). Additionally, it cannot be entirely excluded that this trend would be linked to characteristics of the Fabaceae other than their N₂ fixation capacity.

Substantial mean differences in several key fine-root traits occur therefore among plant functional types. These classifications are partly redundant with phylogenetic relatedness (when this information is also available), but also include additional relevant information specific to root traits. Importantly, similar to observations made on leaf traits (Craine *et al.* 2001; Poorter *et al.* 2009; Díaz *et al.* 2016), the large overlap in fine-root traits among all plant functional types stresses that these global trends may not systematically occur at local scales.

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FIELD- AND POT-GROWN PLANTS DIFFER IN ROOT MORPHOLOGY

Due to the difficulty of measuring root structure and function in natural communities, comparative studies are often carried out under controlled conditions. While we know that growth conditions strongly affect aboveground plant traits (Garnier & Freijssen 1994; Mokany & Ash 2008), our results demonstrate that they also have effects on root morphological traits. The generally lower soil compaction and less frequent herbivore attacks in pots than is commonly found under more natural conditions could both contribute to the larger SRL observed here (Wahl & Ryser 2000; Alameda & Villar 2012). Plants grown in pots are also likely to have younger root systems than those in common-gardens or sampled in the field (Poorter *et al.* 2016). As a result, they may display a higher proportion of roots that are absorptive and have a high SRL (Pregitzer *et al.* 2002; Wells & Eissenstat 2002), as opposed to older roots with more secondary growth and xylem vessels (Hishi 2007).

Overall, the morphological trait differences found across growth conditions suggest a need for caution in using root trait values from pot studies to model plant and ecosystem functioning in natural conditions, or to parameterize and validate terrestrial biosphere models (Warren *et al.* 2015). The implementation of pot studies with prolonged plant development, realistic available rooting volume, soil density, moisture, fertility and micro-organism communities may be necessary to more adequately capture plant traits belowground in controlled conditions (see also Poorter *et al.* 2012; Poorter *et al.* 2016). Further experimental work should also determine to what degree differences between controlled and field studies can be reduced or accounted for by explicitly targeting fine roots of known age, developmental stage, and function (e.g. Ceccon *et al.* 2016). Studies are also needed that determine whether interspecific differences in root traits measured in controlled conditions are conserved under natural conditions (Freschet *et al.* 2013a; Valverde-Barrantes *et al.* 2013).

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CONCLUDING REMARKS

Our study provides the first comprehensive global picture of the variability of fine-root traits across plant functional types and geographic areas, and shows evidence for substantial selective pressures associated with climate and soil variables on fine-root traits. Based on these patterns of variation, we were able to demonstrate that (1) Climate conditions promoting soil fertility relate mostly negatively to fine-root traits favouring fast soil resource acquisition, with a particularly strong effect of temperature. (2) Soil bulk density strongly influences species fine-root morphology, by favouring thicker, denser fine-roots, with low SRL. (3) Herbaceous species generally display fine-roots typical of fast return on investment, as compared to more conservative fine-roots of woody species, and root N content is greater for plants with N₂-fixing capacity. (4) Plants growing in pots show higher SRL than those growing in the field.

Fine-root traits give us critical information on plant resource acquisition abilities (Chen *et al.* 2016), plant resource economics (Roumet *et al.* 2016), as well as plant impacts on ecosystem carbon and nutrient cycling (Freschet *et al.* 2013b). Consequently, incorporating the substantial root functional trait variation observed in our study appears to be a promising avenue towards better modelling of plant and ecosystem functioning. The large root trait variability observed within climatic areas and plant functional types also suggests that characterizing these parameters by single trait values in global vegetation models may be inaccurate (Violle *et al.* 2014), in a manner that has been previously emphasized for aboveground traits (Verheijen *et al.* 2013).

Overall, considering the large sampling and measurement bias potentially associated with fine-roots studies (e.g. as compared to studies of aboveground plants parts) and the lack of metadata related to root proximal environment, we note that the associations between environmental factors and fine-root traits may have been underestimated. One critical

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challenge for refining our understanding of these relationships will be to reduce uncertainties related to root sampling (McCormack et al 2015; Freschet & Roumet, in press), with the eventual goal to better separate the effect of environmental conditions on the distinct functional types of roots (e.g., apex, pioneer, nutrient acquisitive, or transport fine-roots). Future syntheses and modelling work will likely benefit from the development of more homogeneous characterisation of fine-root sampling methodologies, more accurate measurements of root functions, more consistent characterisation of on-site environmental conditions (or the use of high resolution maps of environmental variables), and a better understanding of plant internal trade-offs determining root trait covariation.

Authors' contributions

GTF and CR designed the study and wrote the first draft of the manuscript; all authors contributed data; GTF, CR and KRU gathered and formatted the data; GTF, CMT, FF and CV analysed the data; OJV, JMC, MLM and CBB substantially contributed to writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

The list and content of datasets used in this study is available in ‘Supporting information Table S1’. These datasets are available as part of the Fine-Root Ecology Database (FRED; <http://roots.ornl.gov>).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List and content of datasets used in this study. **Table S2.** Generalized least-square models without phylogenetic correction. **Fig. S1.** Variation in root trait values across a time-calibrated phylogenetic tree.

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Freschet, G., Valverde-Barrantes, O. J., Tucker, Craine, J., McCormack, M. L., Violle, Fort, F., Blackwood, Urban-Mead, Iversen, C. M., Bonis, A., Comas, L. H., Cornelissen, J. H. C., Dong, Guo, D., Hobbie, S. E., Holdaway, R., Kembel, S., Makita, N., Onipchenko, V. G., Picon-Cochard, C., Reich, P. B., De la Riva, E. G., Smith, S. W., Soudzilovskaia, N. A., Tjoelker,

Tables

Table 1. Significance (P -value), strength (X^2) and contribution to model explained variance (R^2) of drivers of fine-trait variation for the four most commonly measured traits, as obtained from phylogenetic generalized least-square models. ‘Study’ effect was removed a priori using the best linear unbiased predictor method.

	Root nitrogen content			Mean root diameter			Root tissue density			Specific root length						
	n	R^2	P	n	R^2	P	n	R^2	P	n	R^2	P				
PGLS Model	808	0.11	<0.001	916	0.36	<0.001	875	0.22	<0.001	926	0.24	<0.001				
Model variables	df	χ^2	R^2	P	df	χ^2	R^2	P	df	χ^2	R^2	P				
Climatic area	3	33.1	0.07	<0.001	3	285.1	0.34	<0.001	3	20.9	0.02	<0.001	3	95.1	0.12	<0.001
Plant growth form	2	8.8	0.02	0.01	2	5.6	0.01	0.06	2	82.4	0.13	<0.001	2	14.1	0.02	<0.001
N ₂ -fixation ability	1	0.0	0.00	0.83	1	1.3	0.00	0.25	1	0.1	0.00	0.82	1	0.6	0.00	0.45
Conditions of growth	2	0.1	0.00	0.97	2	0.6	0.00	0.73	2	18.2	0.03	<0.001	2	19.3	0.03	<0.001
Residuals	353			515			493			518						

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Table 2. Significance (P -value), strength (X^2) and contribution to model explained variance (R^2) of drivers of fine-root trait variation for the four most commonly measured traits, as obtained from phylogenetic generalized least-square models. ‘Study’ effect was removed a priori using the best linear unbiased predictor method. (+/-) indicates the sign of the relationship.

	Root nitrogen content					Mean root diameter					Root tissue density					Specific root length				
	n		R^2	P		n		R^2	P		n		R^2	P		n		R^2	P	
PGLS Model	664		0.19	<0.001		663		0.43	<0.001		658		0.45	<0.001		738		0.33	<0.001	
Model variables	df	+/-	χ^2	R^2	P	df	+/-	χ^2	R^2	P	df	+/-	χ^2	R^2	P	df	+/-	χ^2	R^2	P
Plant growth form	2		37.1	0.10	<0.001	2		40.1	0.07	<0.001	2		119.7	0.19	<0.001	2		47.8	0.07	<0.001
Mean annual temperature	1	-	5.9	0.02	0.02	1	+	180.9	0.29	<0.001	1	+	12.9	0.02	<0.001	1	-	107.7	0.17	<0.001
Mean annual precipitation	1	-	37.9	0.10	<0.001	1	-	9.1	0.01	0.003	1	-	1.8	0.00	0.18	1	+	0.6	0.00	0.44
Soil pH	1	-	15.9	0.04	<0.001	1	+	0.0	0.00	0.96	1	-	18.3	0.03	<0.001	1	-	0.2	0.00	0.65
Soil cation exchange capacity	1	-	0.4	0.00	0.52	1	-	5.8	0.01	0.02	1	+	82.3	0.13	<0.001	1	+	0.0	0.00	0.88
Soil bulk density	1	-	0.1	0.00	0.75	1	+	5.6	0.01	0.02	1	+	84.0	0.13	<0.001	1	-	12.7	0.02	<0.001
Residuals	301					354					352					437				

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Figure captions

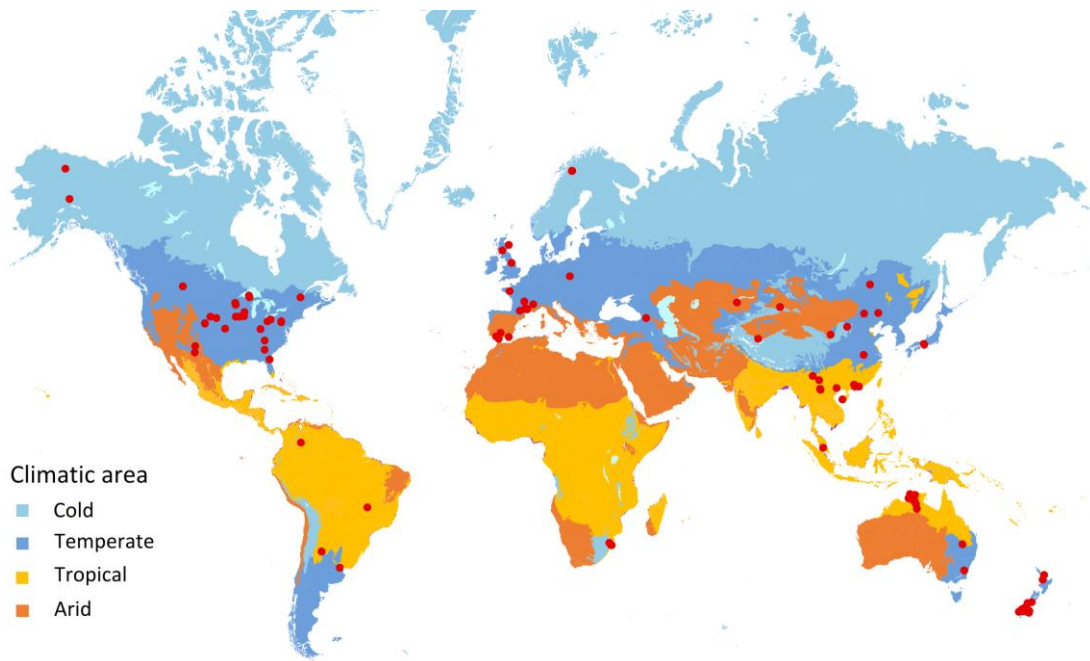
Fig. 1. Location of all sites (red dots) from which the data were obtained, as distributed across the major climatic areas of the globe.

Fig. 2. Comparison of global fine-root trait variation (box-plot in bold = all fine-root < 2 mm observations in our database) to this of a subset of local datasets (each other box-plot=fine-root observations for at least 15 species sampled within the same site) for the four most commonly measured traits in our database. Box-plots: middle lines, boxes and whiskers represent the median and the 50% and 95% confidence intervals, respectively. The displayed local datasets were selected on the basis of highest data counts and are not consistently the same across all four traits owing to change in available data among traits.

Fig. 3. Distribution of fine-root trait values (raw trait values), as observed for a wide range of species from different climatic areas, functional groups and growth conditions. Bottom and top parts of the boxes indicate the first and third quartiles, the two whiskers the 10th and the 90th percentile, and the horizontal line within the boxes the median value. The total number of observations per group is indicated at the top of each box.

Fig. 4. Differences in least square means (\pm SE) of fine-root traits (i.e. predicted trait values) across climatic areas, plant growth forms and plant growth conditions, as measured by post-hoc Tukey's test on phylogenetic generalized least-square models for each trait. These bar charts are displayed for the purpose of group comparisons only, not for predictions of group means. Distinct letters indicate significant differences in trait means at $P < 0.05$, while 'ns' indicates no significant differences among groups.

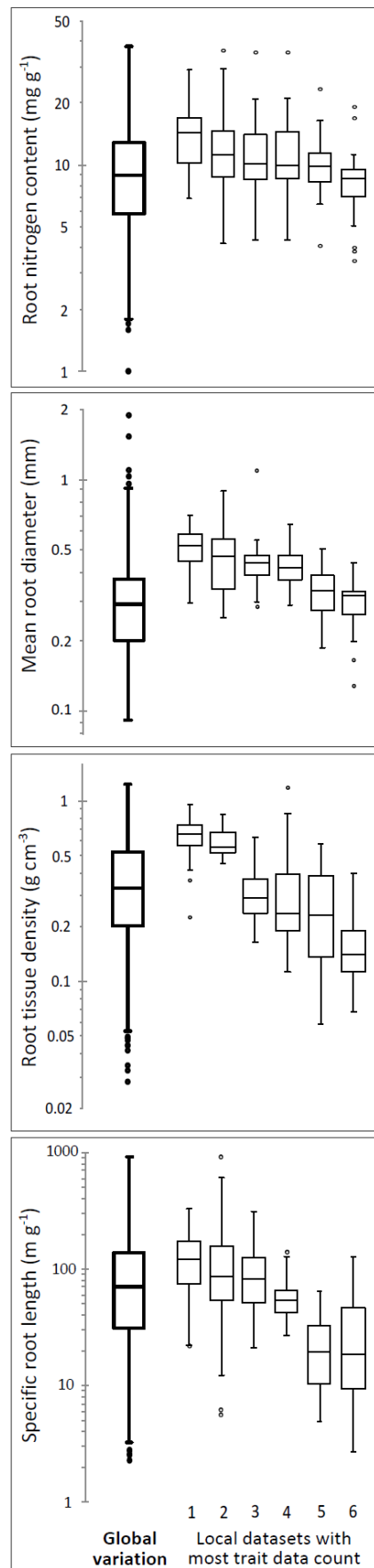
Fig. 1.



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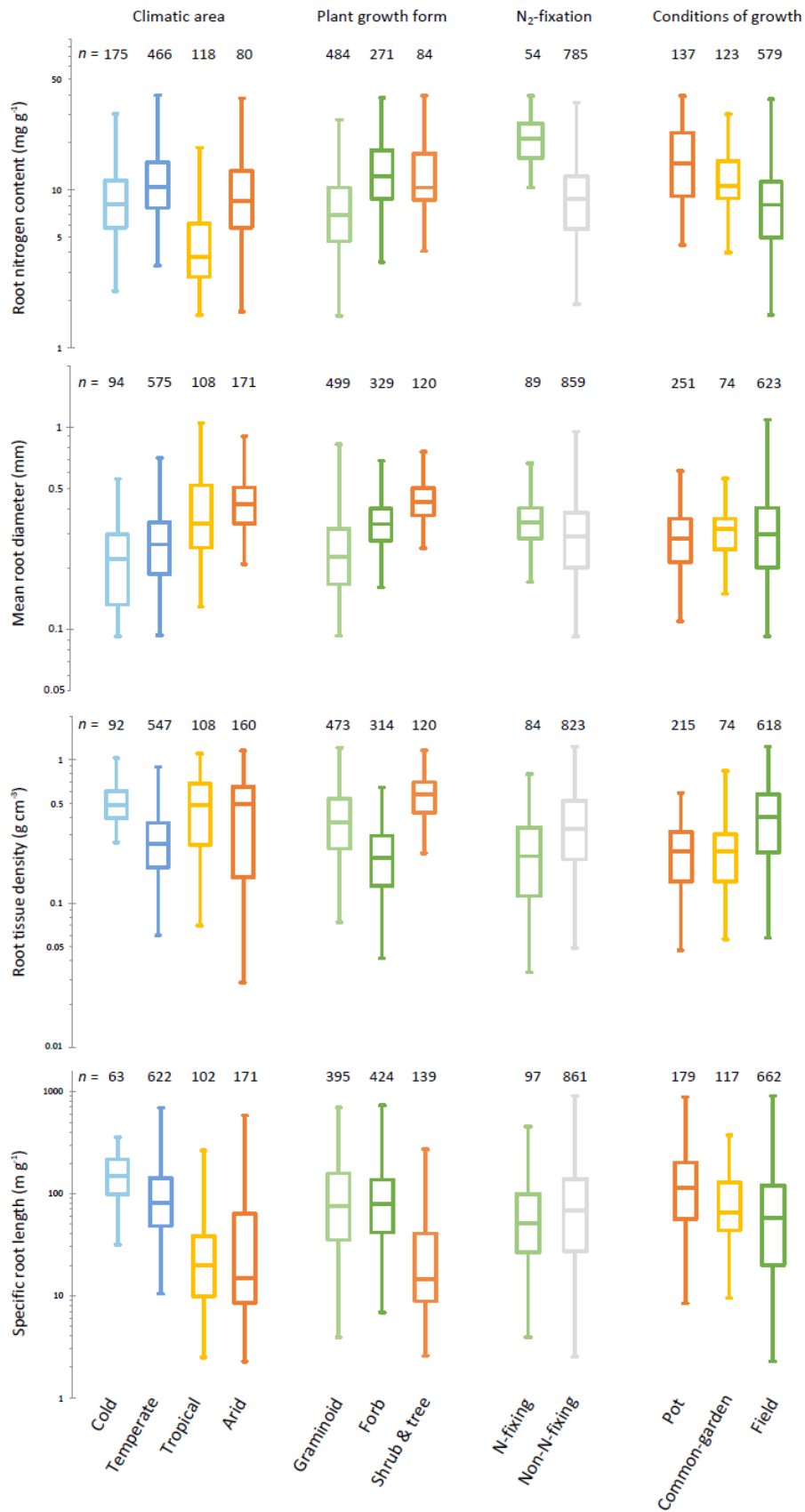
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Fig. 2



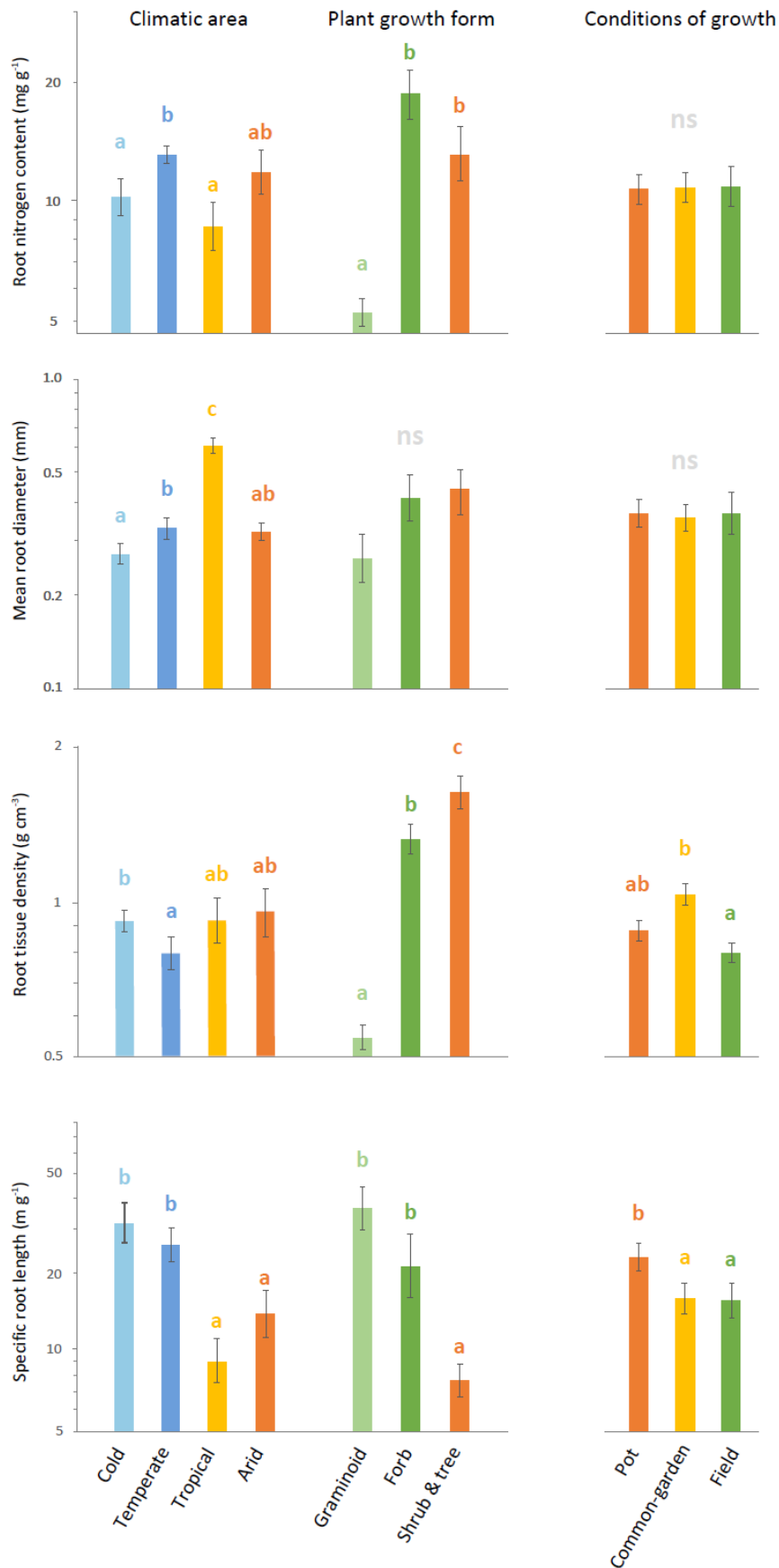
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Fig. 3.



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Fig. 4.



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