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RESEARCH ARTICLE

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Plant ecological indicator values as predictors of fine-root trait variations

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Abstract

1. Fine roots play key roles in the capacity of plants to face environmental constraints and their traits reflect adaptations to the environment, including soil structure, resource availability and climate. However, the inaccuracy of global soil and climate databases to account for the large environmental variation occurring at small spatial scale prevents accurate estimations of the linkages between environmental variables and fine-root strategies.
2. Here, using two global databases on fine-root traits (Rhizopolis-db) and species phylogenetic relatedness, and a regional database of species ecological indicator values (Baseflor), we quantified the predictive value of ecological indicator values, as an alternative to classical coarse soil and climate indicators, on the variation in four major fine-root traits.
3. A strong phylogenetic signal was found among species for fine-root mean diameter, specific root length (SRL) and root tissue density (RTD), but less so for root nitrogen concentration (RNC). After accounting for this relatedness, ecological indicators still explained a large part of trait variation in our dataset for SRL, RTD and RNC. Multi-indicators best model R^2 reached .40 for SRL and RTD, and .44 for RNC, whereas it was only 0.10 for diameter. Ecological indicators of nutrient availability and soil texture were those that most strongly related to SRL, RTD and RNC. Specifically, plant fast resources use strategies characterized by high SRL, RNC and low RTD occurred more frequently in nutrient-rich soils and in soils with light sandy textures. Additionally, light availability and atmospheric temperature were negatively related with SRL and continentality negatively influenced RNC.
4. With respect to both nutrient and water availability ecological indicator values, opposite adaptations were observed between growth forms, particularly between woody and herbaceous species, limiting our ability to define simple, widely applicable patterns of trait–environment relationships.
5. *Synthesis*. Our analysis demonstrates that species ecological indicator values are valuable predictors of plant below-ground strategies. It provides original evidence that herbaceous species with fine-root traits representative of fast resource use strategies typically occur in more favourable soil habitats (high nutrient and water availability); meanwhile, woody species may show the opposite trend. Other

important environmental parameters concomitantly influence fine-root trait variation in contrasting ways.

KEYWORDS
ecological indicator values, environmental gradients, fine-root traits, plant–climate interactions, plant–soil (below-ground) interactions, root nitrogen concentration, root tissue density, specific root length

1 | INTRODUCTION

Understanding the strategies that allow species to establish and sustain a population in a habitat is a central goal in ecology (Craine, Froehle, Tilman, Wedin, & Chapin, 2001; Grime, 1977; Westoby, 1998). Plant functional traits (sensu Violle et al., 2007) reflect species evolutionary history and, as a result, their adaptation to a large range of environmental constraints (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Grime, 1977; McGill, Enquist, Weiher, & Westoby, 2006). They are key descriptors of plant strategies, by controlling their capacity to pass through environmental and biotic filters (Keddy, 1992; Lortie et al., 2004), and to sustain a population at the intersection of various environmental gradients (Reich, 2014). As such, strong links have been previously identified at the global scale between the position of species ecological niche (Hutchinson, 1957) along environmental gradients and their functional traits (Freschet et al., 2017; Jager, Richardson, Bellingham, Clearwater, & Laughlin, 2015; Maire et al., 2015; Moles et al., 2014; Ordoñez et al., 2009). Nonetheless, much remains to be done to refine our understanding of these linkages, particularly with respect to plant below-ground features (Freschet et al., 2017; Iversen et al., 2017).

From works on above-ground parts of plants, we know that species from environments with high nutrient availability generally display fast resource acquisition strategies characterized by low leaf tissue density, high SLA and high leaf nutrient concentration (Jager et al., 2015; Janse-Ten Klooster, Thomas, & Sterck, 2007; Ordoñez et al., 2009). A contrasting trend occurs however with respect to light availability, as species adapted to full-light conditions generally harbour lower SLA than species from low-light conditions (Janse-Ten Klooster et al., 2007; Niinemets, 2010; Vojtkó et al., 2017). Besides these patterns associated to critical above- and below-ground resources, leaf traits are also known to vary with many other environmental factors such as temperature, precipitation, aridity or climatic extremes (Maire et al., 2015). Above- and below-ground reproductive traits (e.g. seed mass, bud bank characteristics) also vary according to environmental gradients (Herben, Tackenberg, & Klimešová, 2016; Vojtkó et al., 2017). Vojtkó et al. (2017) demonstrated at the community level that bud bank size and depth are lower for communities from habitats with high light and nutrient availability, whereas high moisture tends to have the opposite effect. Parallel knowledge of the environmental drivers of species root trait variation is less clear and appears to date largely inconsistent. On the one hand, tree species from more fertile habitats have been shown to have lower specific root length (SRL) (Kramer-Walter et al., 2016; Ostonen et al., 2007), lower root tissue density (RTD), higher mean fine-root diameter and no difference in root nitrogen concentration (RNC) as compared to species of less fertile habitats (Kramer-Walter et al., 2016). On the other hand, studies mostly based on graminoid and forb species highlighted a decrease in species RTD and fine-root diameter and an increase in SRL and RNC with increasing habitat fertility (Craine et al., 2001; Fort et al., 2016; Ryser, 1996). This was also confirmed by studies measuring root traits over entire communities (i.e. community functional parameter; Fort et al., 2016; Prieto et al., 2015). These contrasting results suggest that plants of distinct growth forms or phylogenetic groups may not respond homogeneously to the same environmental gradients.

Recently, two meta-analyses on fine roots and very fine roots (Freschet et al., 2017; Valverde-Barrantes, Freschet, Roumet, & Blackwood, 2017, respectively) suggested that climate conditions relate to fine-root traits representative of soil resource acquisition, with a particularly strong positive effect of temperature on fine-root diameter and negative effect on SRL, and a negative effect of rainfall on RNC. However, relationships between fine-root traits and soil properties were more ambiguous (Freschet et al., 2017), likely owing to the use of coarse-scale soil data inadequate to capture fine-scale soil heterogeneity. Most root studies and therefore root databases are lacking a common set of descriptors of soil properties (Iversen et al., 2017). Therefore, while current knowledge on the climatic drivers of species root trait values contrasts with expectations from the ‘fast–slow’ root economics spectrum theory (Reich, 2014; Weemstra et al., 2016), our understanding of soil drivers of root trait values remains largely incomplete. This is despite fine-scale environmental variations, particularly in soil properties, are known to have strong effects on species traits (e.g. Freschet, Cornelissen, van Logtestijn, & Aerts, 2010; Hill, Simpson, Moore, & Chapman, 2006) and community functional parameters (i.e. trait values measured at the plant community level; Fort et al., 2016) and may mitigate the effects of more global environmental gradients (Conti, de Bello, Lepš, Acosta, & Carboni, 2017). Acknowledging the limitation of current global root trait and soil databases regarding soil properties, one way to gain further insight into the relationships between species root traits and environmental features is to assess linkages between species trait values and species ecological indicator values (Ellenberg et al., 1991; Garnier et al., 2016).

Ecological indicators values (EiV), generally established at the regional scale, characterize the ecological optimum of species along major environmental gradients using ordinal scales. They are highly useful indices to assess species niche position along environmental gradients without direct measurement (Bartelheimer & Poschlod, 2016; Diekmann, 2003; Herben et al., 2016). These EiV are derived from long-term vegetation surveys, expert knowledge and measurements of soil parameters. They reflect environmental conditions where a plant species is most likely to sustain a population, that is, species optimal niche position along environmental gradients (Bartelheimer & Poschlod, 2016; Fort, Jouany, & Cruz, 2015; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006). Since species EiV are estimated across entire populations of individuals occurring across a range of environments, they can be meaningfully related to trait data coming from heterogeneous databases where traits have been measured in a range of growth conditions. Recent studies highlighted that EiV are related with key functional traits, such as relative growth rate, net carbon assimilation rate and reproductive strategies (Bartelheimer & Poschlod, 2016; Herben et al., 2016; Shipley et al., 2017). Bartelheimer and Poschlod (2016) demonstrated, for instance, a positive relationship between EiV related to nutrient availability, pH and soil water and plant relative growth rate and SLA, and a negative relationship between light availability EiV and these same traits. Vojtkó et al. (2017) confirmed further the robustness of these relations between SLA and nutrient, pH and light EiV at the community level. The relationships between these traits and EiV were, however, weaker for continentality and temperature (Bartelheimer & Poschlod, 2016; Vojtkó et al., 2017) and the relationship between SLA and light or water EiV appeared to be impacted by plant growth form (Shipley et al., 2017). Except for reproductive and regenerative traits (Herben et al., 2016; Vojtkó et al., 2017), relationships between EiV and plant strategies were for most part established based on plant above-ground characteristics, highlighting above-ground level adaptations to species niche along environmental gradients (Bartelheimer & Poschlod, 2016 and references therein). However, root system characteristics represent key aspects of species adaptation to various environmental constraints and especially soil resources (Bauhus & Messier, 1999; Forde & Lorenzo, 2001; Ostonen et al., 2007). In this context, extending the known relationships between EiV and plant characteristics to below-ground traits would be critical to further our understanding of processes driving the differentiation of species ecological niches.

The general aim of this study was to determine (a) whether fine-root traits representing different aspects of root resource use strategies are related to species niche position along environmental gradients. More specifically, we hypothesized that (b) fine-root traits would be most related with nutrient and water availability EiV, due to the central role of roots in the uptake of these resources; and that (c) species with fine-root traits favouring fast soil resource use (high SRL and RNC, low RTD and fine-root diameter) would typically occur in environments with favourable soil conditions (high nutrient and water availability, low soil density).

To test these hypotheses, we studied the relationships between four fine-root traits (fine-root diameter, RNC, RTD and SRL) of ecological importance (Freschet & Roumet, 2017), as taken from a world-wide database of fine-root traits (Rhizopolis-db; Freschet et al., 2017), and species ecological niche position along environmental gradients across 249 species with available EiV (Julve, 2015), accounting for species phylogenetic relatedness.

2 | MATERIALS AND METHODS

2.1 | Data collection

The first step of our study was to collect functional trait data using a global database of fine-root traits spanning 1,115 species (Rhizopolis database; Freschet et al., 2017). We restricted our selection of species to these presenting at least one of the four most commonly measured root functional traits: root diameter, SRL, RTD and RNC. To improve the homogeneity of our trait data, we further restricted our selection of species to those with roots sampled as <2 mm in diameter (i.e. the most common sampling classification in our database; Freschet & Roumet, 2017). The trait data were categorized, depending on species growth conditions, as in 'pot' (indoors or outdoors), in 'common garden' (outdoor plantations) or in 'field' conditions (natural conditions), to differentiate between different degrees of climate and soil manipulation.

The second step was to cross species root trait data with EiV data from the Baseflor database (Julve, 2015). Baseflor is a floristic database indexing about 10,000 taxa from the French vascular flora. For each taxon, the database includes ecological and biological descriptions (Julve, 2015). In the Baseflor database, the F, K, L, N, R and T Ellenberg's indicators values (Ellenberg et al., 1991) are modified to take into account the French ecological context of each taxon, and extended to species typical of the French flora. Additionally, soil organic matter content, soil texture and atmospheric humidity EiVs were established using the same methodology as Ellenberg's indicators values (Ellenberg et al., 1991) based an extensive collection of data on species ecology coming from flora and others published sources, the author's field experience and scientific exchanges with ecologists, especially phytosociologists (Julve, 2009). The relationships between Baseflor EiV and original Ellenberg's EiV, for a common subset of species and EiV, are strong, with R^2 ranging from .32 for continentality to .84 for pH and temperature EiVs ($p < .001$; Figure S1). Baseflor also includes additional EiV describing climate, that is, atmospheric moisture, and soil characteristics, that is, soil texture and organic matter content, which are of strong interest for explaining root traits. Species from the Rhizopolis database (Freschet et al., 2017) were crossed with the EiV database to identify species presenting both types of data. Based on this selection of 357 species, we identified nine EiV for which we had enough observations to perform robust analyses. These EiV could be separated into three groups: (a) EiV related to resource availability, that is, light, nutrients and soil water; (b) EiV related to climate, that is, atmospheric humidity, continentality and temperature, and (c) EiV related to soil properties, that is, pH, organic matter content and soil texture. For resource availability, low EiV indicate low resource availability, whereas high values indicate high resource availability. For climatic conditions, low EiV for atmospheric moisture and temperature indicate low air humidity and temperature, whereas high EiV indicate high air humidity and temperature, respectively; low values of continentality indicate that species occurred in oceanic habitats, whereas high values indicate that species occurred in continental habitats. For soil properties, low pH and organic matter EiV indicate acid pH and low organic matter content, whereas high EiV indicate high pH and organic matter content, respectively; low EiV of soil

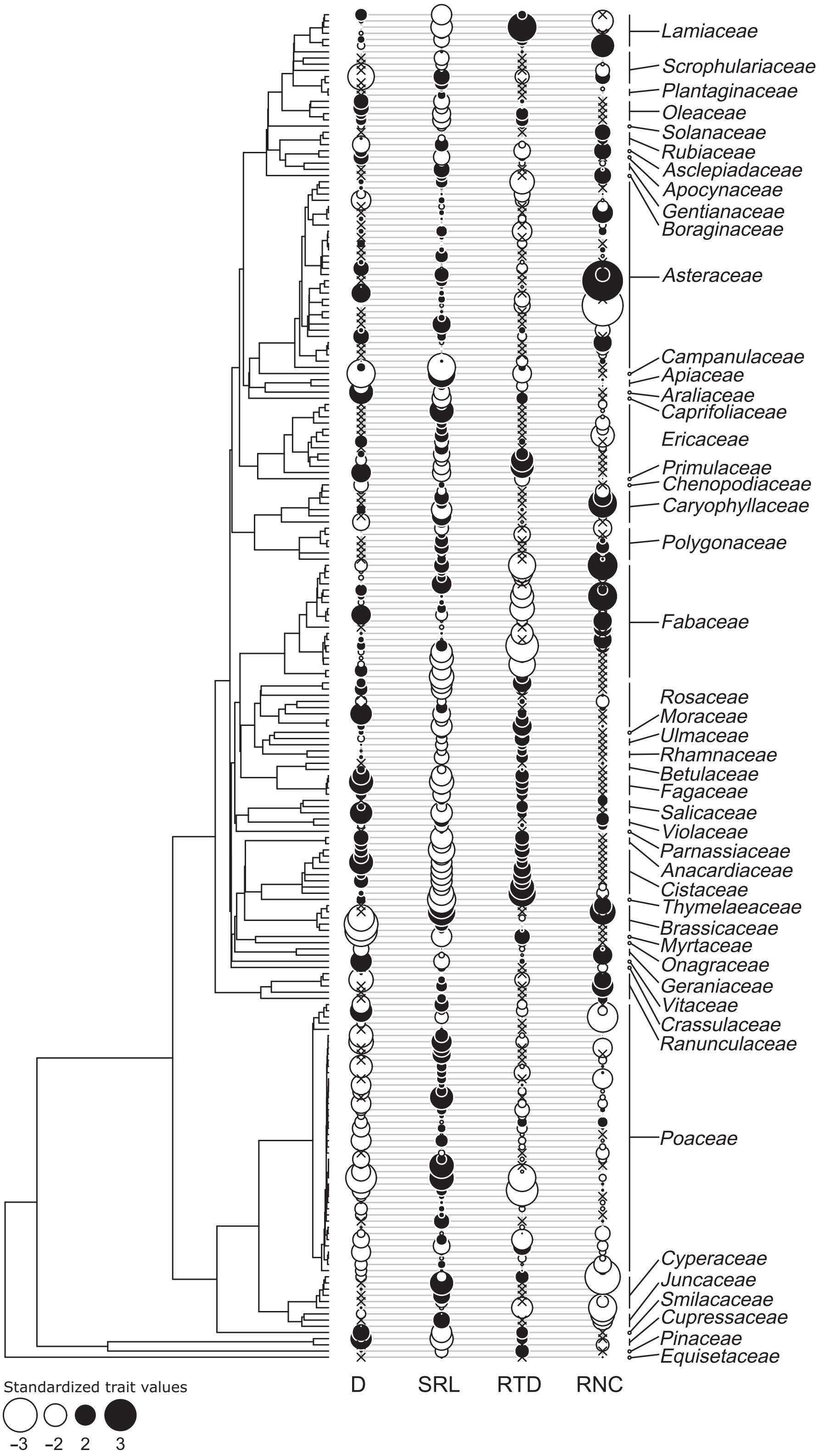

FIGURE 1 Phylogeny of the 249 species of this study (only family names are displayed). Estimated values of the four functional traits (Best Linear Unbiased Predictor estimated by mixed models) are represented at the tips of the phylogeny (in centred and standardized format). Black circles represent high values and white circles represent low values (magnitude is scaled by circle diameter). Missing trait values are represented by an X. D, mean root diameter; RNC, root nitrogen concentration; RTD, root tissue density; SRL, specific root length

TABLE 1 Description of dataset main characteristics for each trait after crossing all three databases

Traits	Min	Mean	Max	Cv	Number of datasets	Number of families	Number of species	Phylogenetic signal λ	Phylogenetic signal *p*
D (mm)	0.14	0.30	0.55	0.29	19	44	182	0.80	<.001
SRL (m/g)	6.17	104.8	936.4	1.07	24	49	218	0.84	<.001
RTD (g/cm^3)	0.04	0.29	1.18	0.69	16	44	172	0.76	<.001
RNC (mg/kg)	3.15	12.36	42.2	0.48	18	33	144	0.59	<.001

Abbreviations: D, mean root diameter; RNC, root nitrogen concentration; RTD, root tissue density; SRL, specific root length.

texture indicate that species occurred in loamy soil, whereas value around five indicate that species occurred in sandy soil and values higher than 6 indicate that species occurred in scree or stone. Repartition of species among the EiV is provided in Figure S2. Not surprisingly, the median classes of EiV were most represented, whereas extreme EiV had fewer observations. This trend was particularly pronounced for low temperature, low light availability and high soil texture EiV (species from gravel and stone habitats) and less so for nutrient and organic matter EiV (Figure S2). This may result from the fact that a limited number of species have their ecological optimum in extreme environmental conditions (although present in extreme environments) but also from the lack of studies on roots in extreme habitats.

To estimate the phylogenetic signal on species root traits and take it into account in our analyses, we constructed a phylogenetic tree using the comprehensive species-level phylogeny from Zanne et al. (2014), as updated by Qian and Jin (2016). 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 (2016). We used S.PhyloMaker (Qian & Jin, 2016) to generate a phylogeny containing species from the Rhizopolis database from this megaphylogeny. 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.

As a result, we selected 249 species from 62 families (Figure 1) and from 34 datasets for which we collected at least one mean value of one of the four traits (root diameter, SRL, RTD, RNC), the nine values of the ecological indicators and the position along the phylogenetic tree. This represented 218 species for SRL, 182 for fine-root diameter, 172 for RTD and 144 species for RNC (Table 1).

2.2 | Data analysis

Recent papers have highlighted the importance of phylogenetic corrections for meta-analyses and similar comparative analyses (Chamberlain et al., 2012), as it can represent a significant 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() in ‘PHYTOOLS’ (Revell, 2012)). Values of Pagel's λ close to zero indicate phylogenetic independence and larger values (approaching 1) indicate increasingly strong relationships between trait values and the phylogeny (Münkemüller et al., 2012).

The potential effects of plant growth conditions and datasets were corrected using a random-effect model with growth condition and dataset as random factors to calculate a best linear unbiased predictor (BLUP) of the log-transformed mean trait value of each species and its standard error (see Freschet et al., 2017). The BLUP were calculated with mixed linear models (lmer() in ‘LME4’ package; Bates, Mächler, Bolker, & Walker, 2015). We then examined the link between the estimated species trait values (BLUP) and species habitat position along ecological gradients (i.e. EiVs) using a model averaging procedure (Johnson & Omland, 2004). Models used within this procedure are general least square (gls) models in which the correlation structure is a phylogenetic tree reflecting the evolutionary relationships between all species present in the dataset (using gls() from ‘NLME’ package; Pinheiro, Bates, DebRoy, Sarkar, & Team, 2016). These models recognize that trait values may have non-zero covariances between them as a result of shared evolutionary history between species, and so transform the data to reflect this. Linear regression is then applied to the transformed data (Stone, Nee, & Felsenstein, 2011). The weight of each species within the models was proportional to the inverse of the standard error of its BLUP to take into account the uncertainty of the mean trait value estimates. For each trait, the complete models included all the EiV. The set of all possible models were run and ranked according to their corrected Akaike information criterion (AICc) (using dredge() from ‘MUMIN’ package; Bartoń, 2016). For each trait, we first extracted the results of the best model (based on AICc). Then, we estimated the effect of each EiV on each trait by calculating the means and confidence intervals (95%) of the estimates associated with the EiV among the models representing 95% of the total AICc weight. The relative importance (RI) of EiV effect on trait values was estimated by the sum of the AICc weights of the models in which the EiV appears (the more the RI value of an ecological indicator is close to 1 the more the models where it is represented have high AICc weights, i.e. represent well the fitted data). For each trait, the best model was used to calculate an R^2 with the method proposed by Nakagawa and Schielzeth (2013). The same procedure of model selection was also conducted independently for each plant growth form to test the effect of plant growth forms on the relationship between trait values and EiV.

Finally, to test the multivariate relationship between the set of root traits and EiV, we performed a phylogenetic canonical correlation analysis (pCCA, using phyl.cca() in 'PHYTOOLS'; Revell, 2012) on a subsample of 68 species for which we had BLUP values for each of the four traits.

3 | RESULTS

3.1 | Phylogenetic signal

All four traits showed large and significant ($p < .001$) phylogenetic signals (Figure 1; Table 1). SRL showed the strongest signal with a Pagel's λ of 0.84, whereas RNC had the weakest signal with a Pagel's λ of 0.59. This was consistent with significant differences in root traits among species and families (Figure 1 and Figure S3). *Brasicaeae* and *Poaceae* families displayed the thinnest roots (highest SRL and low diameter), whereas *Cistaceae*, *Fagaceae* and *Oleaceae* had the coarsest roots within the dataset. *Fabaceae* were characterized by their low RTD and high RNC (Figure 1 and Figure S3).

3.2 | Ecological indicators

Ecological indicator values were good estimators of RNC (R^2 of the best model (AIC based) equal to 0.45), SRL and RTD (best model R^2 of .41 and .40, respectively). All three traits appeared to be related to at least four ecological indicators (Figure 2). In contrast, fine-root diameter was only modestly estimated by EiV (for the best model R^2 = .11) and was significantly related to one EiV only (Figure 2; Table S1). These results were impacted by species growth form (Figure 2), as discussed in more detail below.

Among ecological indicators related with climate, continentality EiV had a strong negative effect on RNC for both the whole

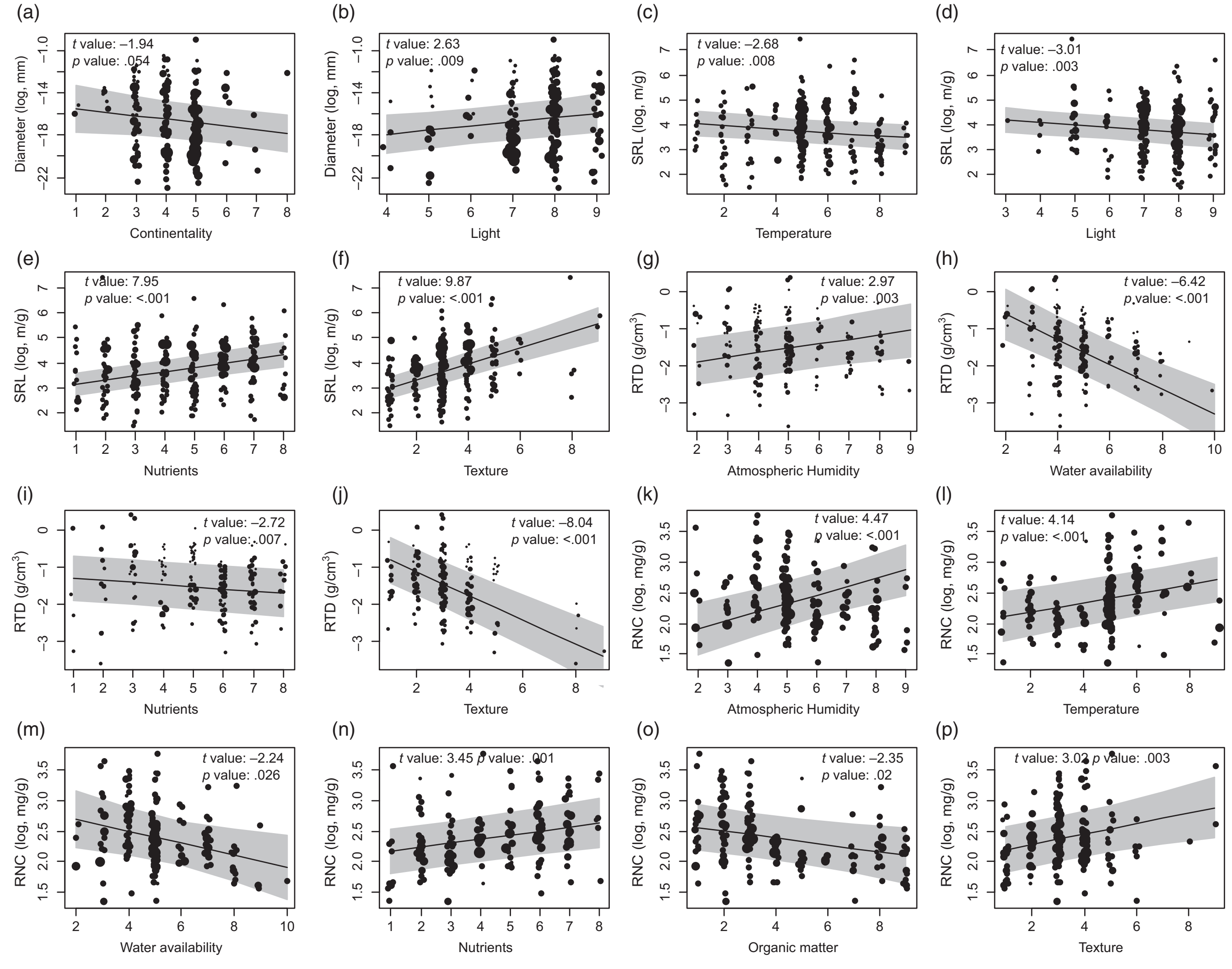

FIGURE 2 Biplots of relationships between ecological indicator values (EiV) and (phylogenetically corrected) trait values for those EiV that were retained in the best multivariate models (lowest AICc) explaining mean root diameter (a–b), specific root length (SRL) (c–f), root tissue density (RTD) (g–j) and root N concentration (RNC) (k–p). Each point represents the Best Linear Unbiased Predictor (BLUP) of the phylogenetically corrected mean trait value of one species. The size of the points represents their weight within the model based on the inverse of the standard error of the estimation of the mean

dataset and grasses only, highlighting that species from continental climate had lower RNC than species from more oceanic conditions (Figure 3). Continentality also had a negative effect on the mean root diameter of shrubs and trees, highlighting that woody species from continental habitats had thinner absorptive roots than woody species from oceanic habitats (Figure 3). Atmospheric humidity EiV had a positive effect on RTD and RNC, indicating that species generally present in humid climates displayed higher RTD and RNC than average, independently of their phylogenetic relatedness (Figure 3). The same relation was observed when grasses were analysed alone, but the estimates did not significantly differ from zero for other growth forms (Figure 3). Finally, the temperature EiV had a negative influence on SRL, indicating that species from cold environments generally displayed higher SRL than average. At the level of growth forms, temperature had a negative effect on root diameter of trees, and displayed contrasting effects

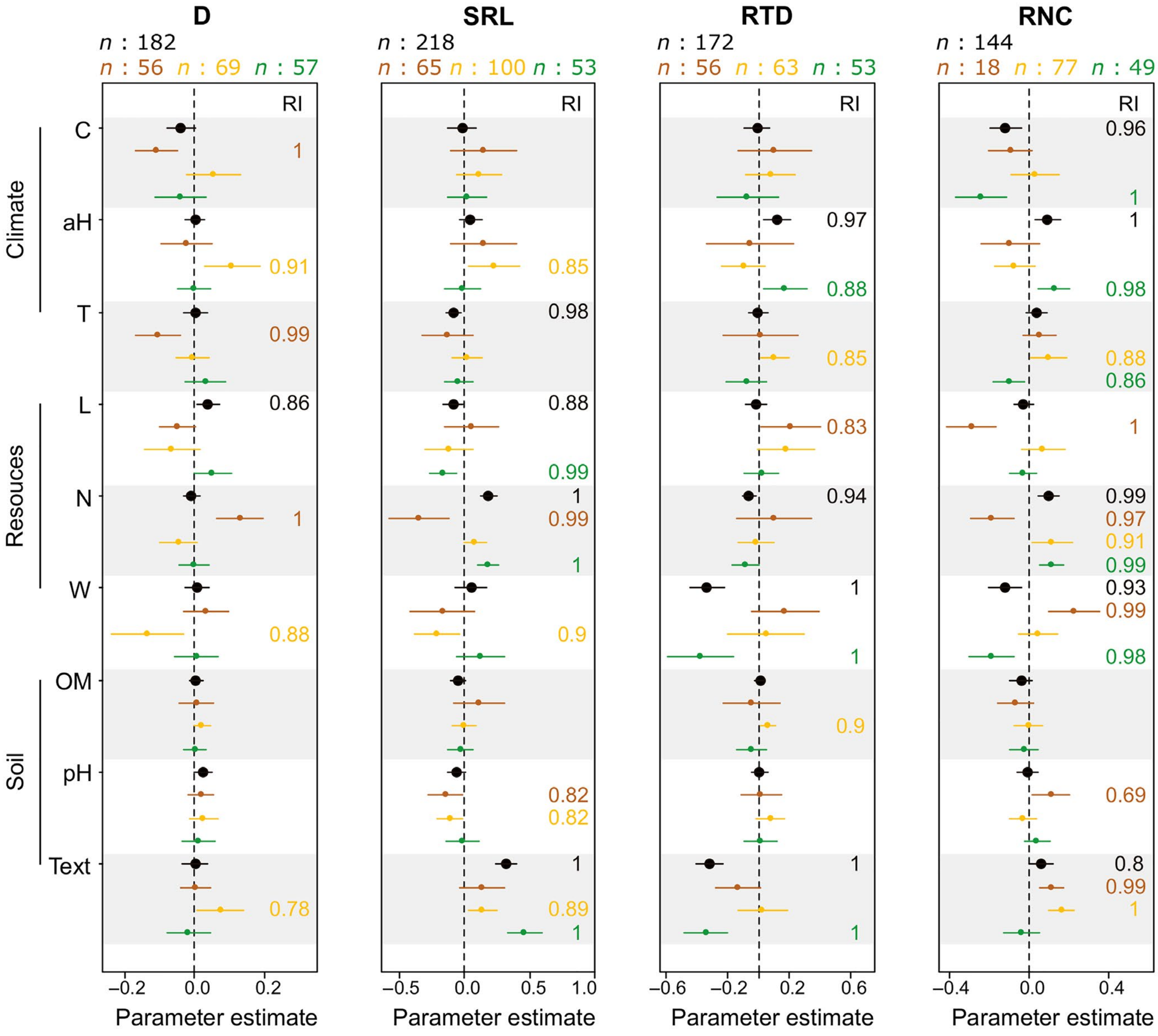

FIGURE 3 Effects of ecological indicator values (EiV) on fine-root traits across all species. Regression coefficients for models fitted separately for D: mean root diameter, RTD: root tissue density, SRL: specific root length and RNC: root N concentration (dots show average estimates, lines show 95% confidence intervals). Symbol colours differentiate between our analysis of the whole dataset (black) and its subsets: shrubs and trees only (brown), forbs only (yellow) and grasses only (green). The parameter estimates represent the magnitude of an ecological indicator effect on the standardized trait values. The RI (relative importance) varies from 0 to 1 and represents the sum of the Akaike weights of the models in which the ecological indicator appears (the more the RI value of an ecological indicator is close to 1 the more the models where it is represented have high Akaike weights, i.e. well represent the fitted data). EiV are separated into three groups: (i) EiV related to climate, that is, atmospheric moisture (aH), continentality (C) and temperature (T), (ii) EiV related to resource availability, that is, light (L), nutrients (N) and soil water (W) availability; and (iii) EiV related to soil properties, pH (pH), organic matter content (OM) and soil texture (Text) [Colour figure can be viewed at wileyonlinelibrary.com]

on the RNC of grasses and forbs, that is, grass species from cold habitats had higher RNC than grasses from warmer habitats, whereas the opposite trend occurred for forbs (Figure 3).

Among EiV related to resource availability, nutrient EiV had strong effects (RI ≥ 0.94) on SRL, RNC and RTD. Across all species, plants found in nutrient-rich soils had higher SRL and RNC and lower RTD values than species from nutrient-poor soils. At the level of plant growth forms, grasses and forbs showed the same trend than at the whole dataset level, whereas trees displayed lower diameter, higher SRL and RNC values at lower nutrient EiV. Soil water EiV had a strong and negative effect on RTD and RNC for both the whole dataset and grasses only, showing that species from environments with high water availability or water-logged environments had lower RTD and RNC than other species. In contrast, tree and shrub species analysed separately displayed higher RNC values, and forbs displayed lower diameter and SRL values in case of high water EiV. Light EiV was negatively related with SRL and positively related with root diameter, indicating that species ability to establish viable population in shaded environments is associated with low root diameter and high SRL. The increase in light EiV for trees and shrubs was related with an increase in tissue density and a decrease in RNC.

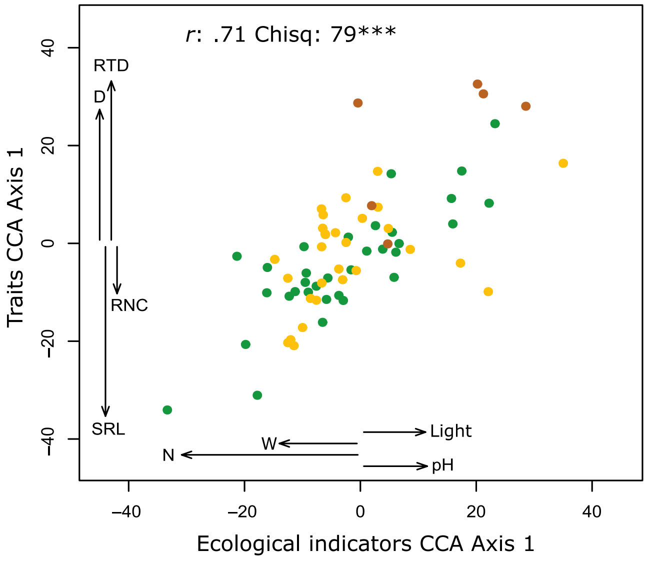

FIGURE 4 Relationship between species scores among the ecological indicator values (EiV; *x*-axis) and root trait values (*y*-axis) from a phylogenetic canonical correlation analysis (pCCA). Brown points are shrub and tree species, yellow points are forb species and green points are grass species. The strength and direction of correlations between EiV and the *x*-axis species scores, and between root traits and the *y*-axis species scores, are represented by the direction and length of arrows. Only those variables significantly correlated with the axis species scores are represented. The significance of the relationship was assessed by Chi-square method, $n = 68$, $p < .001$: ***. D, mean root diameter; Light, light availability EiV; N, nutrient availability EiV; pH, pH EiV; RNC, root nitrogen concentration; RTD, root tissue density; SRL, specific root length; W, soil water availability EiV [Colour figure can be viewed at wileyonlinelibrary.com]

Regarding soil properties, only the soil texture EiV was strongly related to root traits, with a substantial effect on SRL, RTD and RNC both at the level of the whole dataset and for most growth forms. Species from more sandy soils showed high SRL, RNC and low RTD in comparison with species from more loamy soils. Additionally, the root diameter of forbs was positively related with soil texture EiV. At the level of plant growth forms, the organic matter EiV was positively related with RTD for forbs only; and the pH EiV was negatively related with SRL of trees, shrubs and forbs and positively related with RNC of trees and shrubs (Figure 3).

Finally, the multivariate analysis of correlation (pCCA based on a 68 species subsample) demonstrated further a strong link between EiV values and root traits along a trade-off between species building thin, light roots with high SRL and these presenting coarse and dense roots (Figure 4). This functional trade-off was related to an EiV axis separating denser (i.e. shaded) and more fertile habitats (nutrient-rich, humid soils, although with low pH), from more open habitats with drier and poorer soil conditions.

4 | DISCUSSION

Our analyses demonstrate that species ecological indicator values, together with phylogenetic information, are valuable predictors of plant below-ground strategies. They shed light on several environmental parameters strongly connected to fine-root trait variation: nutrient and water availability and soil texture below-ground, as well as light and temperature above-ground. As hypothesized, ecological indicators related to nutrient availability and soil texture were the most strongly related to fine-root trait values, highlighting the importance of these traits for species adaptation to the availability of soil resources. Importantly, species growth forms had a strong impact on the relationships between traits and EiV, with woody species sometimes displaying opposite responses to herbaceous species, especially for resource-related ecological indicators. All four traits, root diameter, SRL, RTD and RNC, considered as major traits supporting the 'fast–slow' root economic spectrum (together with root life span and root respiration rate; Reich, 2014; Roumet et al., 2016) and/or the trade-off between building thin roots or thick roots relying on mycorrhiza (Kong et al., 2019; McCormack & Iversen, 2019) were (at least partly) differently related to species habitat in terms of climate, nutrient availability and other soil properties. This finding of multiple determinants of fine-root trait global distribution implies that root trait values cannot be simply represented by one single strong environmental axis.

4.1 | Relevance of accounting for phylogenetic relatedness

This work confirms that root functional traits carry a strong phylogenetic signal (Comas et al., 2012), although the strength of this signal for all four traits differed between this and other datasets (e.g. Freschet et al., 2017; Ma et al., 2018; Valverde-Barrantes et al., 2017) following distinct representations of the global species set and different entities of root studied. This substantial phylogenetic signal was generally consistent with ancient history of root-mycorrhiza coevolution (Ma et al., 2018) and historical evolution of tissue organization and development (Comas, Callahan, & Midford, 2014), such as the capacity of dicot species to perform secondary growth in contrast to monocots, or the tendency of *Fabaceae* to accumulate root N potentially relating to their ability to associate with N_2-fixing symbionts (Freschet et al., 2017).

4.2 | Root traits vary according to ecological indicators values

Fine-root diameter is a major determinant of plant species resource use strategies (Eissenstat, 1992; Ma et al., 2018; McCormack et al., 2017). Large fine-root diameters are generally associated with slow resource use (Eissenstat, 1992; Roumet et al., 2016), high storage and water transport capacities (Fort et al., 2017; Hernández, Vilagrosa, Pausas, & Bellot, 2010) and high dependence on mycorrhiza to acquire soil resources (Kong et al., 2019; McCormack & Iversen, 2019). Despite such evidence of the role of fine-root diameter in species strategies, our analysis did not reveal strong links between fine-root diameter and species ecological indicators values (except for light). This is potentially due to our accounting of fine-root diameter strong phylogenetic signal, which may overlap with the ecological information carried by this trait. Across all plant growth forms, root diameter only related with light EiV, with shade tolerant species displaying thinner root diameter. This relation could be related to a change in carbon economy along light availability gradients, that is, fine-root diameter generally associated with high SRL (Ma et al., 2018) could be advantageous within shaded environments where carbon supply is limiting (Vernay, 2017). The large representation of short plants among shade tolerant species (mainly grasses, forbs and shrubs) could also contribute to the observed link between species light exigency and root diameter.

Specific root length is strongly related with mean root diameter following a general nonlinear asymmetric relation (Ma et al., 2018). However, our results suggest that across all plant growth forms SRL is more strongly related to species adaptation to a range of environmental gradients than fine-root diameter (see also Valverde-Barrantes et al., 2017). The positive relationship between SRL and the nutrient EiV highlights that having high SRL values is one of the key for plants to succeed in nutrient-rich environments. Indeed, high SRL may provide higher competitive ability, at least among grassland species (Mommer et al., 2011). The strong negative relationship observed between the temperature EiV and SRL strengthens the patterns observed with global climatic variables (Freschet et al., 2017; Valverde-Barrantes et al., 2017) or at finer scales, such as in studies comparing root traits of tree species from different latitudes (Ostonen et al., 2007). High SRL is further associated with faster root elongation rates and higher potential to proliferate in nutrient patches (Eissenstat, 1992; Eissenstat, Kucharski, Zadworny, Adams, & Koide, 2015; Hodge, 2006). These characteristics should be particularly useful to acquire resources in colder environments where strong seasonality and soil freezing could lead to heterogeneous and intermittent soil microbial activity and nutrient availability (Bardgett, Bowman, Kaufmann, & Schmidt, 2005; Chen, Zeng, Eissenstat, & Guo, 2013).

Specific root length is also strongly and positively related to soil texture EiV, that is, it decreases as soil texture becomes dominated by silt and clay. Soil texture is one of the major driver of bulk soil density, and water, nutrient and air contents and movement in soil (Alameda & Villar, 2012; Arvidsson, 1998; Pabin, Lipiec, Wlodek, Biskupski, & Kaus, 1998). All these parameters are known to have complex influences on root growth and root traits. Bulk density for instance, which is negatively related to soil clay and silt content, is known to increase the resistance to root penetration and limit root growth (Dexter, 2004; Jones, 1983); and species with thicker fine roots, and therefore lower SRL, are generally better adapted to denser soils because of their higher soil penetration strengths (Bengough, McKenzie, Hallett, & Valentine, 2011; Materechera, Alston, Kirby, & Dexter, 1992). The negative relation between RTD and the soil texture EiV also strengthens the idea that dense roots with a high investment in structural tissues, and therefore of lower SRL, are beneficial in soil with high content of clay and silt (Freschet et al., 2017) where even low soil penetration resistance and bulk density may limit root growth (Pabin et al., 1998).

Across all species, RTD is with RNC one of the two traits that relate to atmospheric humidity EiV. Species adaptation to atmospheric humidity is linked to their management of water vapour pressure deficit (Kupper et al., 2017; Sellin et al., 2017). At the intraspecific level, changes in vapour deficit affect hydraulic properties of roots and leaves (Claverie, Schoppach, & Sadok, 2016). The higher RTD of species from high atmospheric humidity may be related to higher investment in root stele relative to cortex tissues (Kong et al., 2016), to facilitate water fluxes across plant organs (Oksanen et al., 2018). The positive relationship between RNC and the atmospheric humidity EiV could be related to a stronger investment in root metabolic activity in conditions where nutrients are less mobile due to limited water flux from the soil to the atmosphere (Oksanen et al., 2018).

Root tissue density and nitrogen concentration are also strongly but negatively related to water availability EiV, indicating that species characterized by low RTD and RNC are more represented in high water availability environments. More specifically, wetland species display the lowest RTD values, which can be related to their capacity to produce aerenchyma to limit tissues hypoxia in waterlogged conditions (Justin & Armstrong, 1987).

In support of our first hypothesis, ecological indicators of soil resource availability were strongly related to fine-root trait values, with water and nutrient EiV showing a strong influence on SRL, RTD and RNC. Nonetheless, they were not the only environmental variables connected to fine-root trait variation. Light EiV appeared also important for fine-root diameter and SRL. All three climate EiV, temperature, continentality and atmospheric humidity, were related to at least one of the four traits studied and, although classical soil EiV such as pH and organic matter content appeared poorly linked to fine-root trait values, soil texture showed a strong link with SRL, RTD and RNC.

Largely consistent with the univariate analyses, our multivariate approach shows that the trait spectrum separating species with high SRL and RNC but low RTD (and also low root diameter) and species with the opposite characteristics relates to an axis separating species from nutrient-rich, humid, low soil pH and shaded habitats to those with the opposite ecological preferences. These results, essentially derived from data on herbaceous species, strengthen the idea that fast use of soil resources through low tissue density and thin elongated roots (and therefore short root life span; Ma et al., 2018; McCormack, Adams, Smithwick, & Eissenstat, 2012) and high nitrogen concentration (associated to high respiration rates; Reich et al., 2008) is an efficient way to avoid being suppressed by competitors in nutrient-rich habitats (Fort, Cruz, & Jouany, 2014; Grime, 1977; Reich, 2014). In contrast, the opposite root trait syndrome (low RNC, SRL and high RTD) would allow plants to strive in nutrient-poor conditions where fast resource use is less suitable. However, more work is needed to assess the generality of this trend across woody species. Additionally, future analyses would strongly benefit from the inclusion of data from a wider range of environmental conditions (providing that future studies increasingly consider extreme environmental conditions) and a wider range of species, so as to extend our analysis to better capture nonlinear patterns of trait–environment relationships.

4.3 | Opposite patterns between woody and herbaceous species

Beyond the general patterns observed across all species, growth forms had a strong impact on the relationships between traits and ecological indicators, with woody species sometimes displaying opposite responses to herbaceous species, especially for resource-related EiV. Most particularly, in nutrient-rich environments, woody species tended to rely on high-diameter, low SRL and low RNC roots, which contrasted strongly with herbaceous species, especially grasses. Plant root systems have multiple ways to deal with low soil nutrient availability (e.g. increasing SRL, Bauhus & Messier, 1999; root hair length and density, Yang et al., 2017; mycorrhizal association and cluster roots, Lambers, Raven, Shaver, & Smith, 2008). In this context, our results might reflect a higher reliance of woody species on mycorrhizal association (McCormack & Iversen, 2019) in nutrient-rich conditions, whereas grasses would typically adopt high SRL roots, with higher metabolic activities. Grass species also showed lower RNC and RTD in high water availability environments, whereas the contrary was true for woody species, suggesting different adaptations of grasses and woody species to high water conditions, including higher reliance on aerenchyma for grasses. Overall, these results suggest that plant species adaptation to their environment may depend on a larger set of plant characteristics linked to growth forms (e.g. among many other potential traits, size, life span, woodiness) that set different constraints on plants in view to overcome the same stresses and limitations. Such results limit our ability to define simple, widely applicable patterns of trait–environment relationships and illustrate how different plant community assembly processes may apply to contrasting sets of species.

5 | CONCLUSIONS

Our results demonstrate that ecological indicators describing species habitat have the potential to explain trait variation among a large range of species from various families and environments. Since species EiV are estimated across entire populations of individuals occurring across a range of environments, they can be meaningfully related to trait data coming from heterogeneous databases where traits have been measured in a range of plant growth conditions. While EiV do not allow to precisely predict species trait values due to their categorical nature, they are nonetheless useful to explain trait variations among species and habitats and help improve our knowledge about root trait ecological significance. In this context, the development of homogenized EiV bridging locally based systems is further needed to improve the value of ecological indicators over large scales. Here, this original approach showed that fine-root trait variations were related to species adaptation to a range of environmental parameters including resource availability, climate and soil texture. Traits supporting the concept of ‘fast–slow’ root economics spectrum were strongly related to soil nutrient availability. However, such relations differed strongly between woody and herbaceous species. Moreover, our results showed a range of other covariations between fine-root traits and environmental parameters, indicating that the global distribution of fine-root traits cannot be simply synthetized by one single axis of trait–environment covariation.

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AUTHORS' CONTRIBUTIONS

F.F. and G.T.F. conceived the ideas, designed the methodology, analysed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

All data used in the preparation of this manuscript, such as Rhizopolis database (Freschet et al., 2017; available as part of the Fine-Root Ecology database, http://roots.ornl.gov), Baseflor database (Julve, 2015; http://philippe.julve.pagesperso-orange.fr/catminat.htm) and the phylogenetic tree (Zanne et al., 2014; https://doi.org/10.5061/dryad.63q27), are freely accessible.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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