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

10

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23 **Abstract**

24 1. Fine-roots play key roles in the capacity of plants to face environmental constraints and their traits reflect
25 adaptations to the environment, including soil structure, resource availability and climate. However, the
26 inaccuracy of global soil and climate databases to account for the large environmental variation occurring
27 at small spatial scale prevents accurate estimations of the linkages between environmental variables and
28 fine-root strategies.

29 2. Here, using two global databases on fine-root traits (Rhizopolis-db) and species phylogenetic
30 relatedness, and a regional database of species ecological indicator values (Baseflor), we quantified the
31 predictive value of ecological indicator values, as an alternative to classical coarse soil and climate
32 indicators, on the variation in four major fine-root traits.

33 3. A strong phylogenetic signal was found among species for fine-root mean diameter, specific root length
34 (SRL) and root tissue density (RTD), but less so for root nitrogen concentration (RNC). After accounting
35 for this relatedness, ecological indicators still explained a large part of trait variation in our dataset for SRL,
36 RTD and RNC. Multi-indicators best model R^2 reached 0.40 for SRL and RTD, and 0.44 for RNC, whereas
37 it was only 0.10 for diameter. Ecological indicators of nutrient availability and soil texture were those that
38 most strongly related to SRL, RTD and RNC. Specifically, plant fast resources use strategies characterized
39 by high SRL, RNC and low RTD occurred more frequently in nutrient-rich soils and in soils with light
40 sandy textures. Additionally, light availability and atmospheric temperature were negatively related with
41 SRL and continentality negatively influenced RNC.

42 4. With respect to both nutrient and water availability ecological indicator values, opposite adaptations
43 were observed between growth forms, particularly between woody and herbaceous species, limiting our
44 ability to define simple, widely applicable patterns of trait-environment relationships.

45 *Synthesis:* Our analysis demonstrates that species ecological indicator values are valuable predictors of
46 plant below-ground strategies. It provides original evidence that herbaceous species with fine-root traits
47 representative of fast resource use strategies typically occur in more favourable soil habitats (high nutrient
48 and water availability), meanwhile woody species may show the opposite trend. Other important
49 environmental parameters concomitantly influence fine-root trait variation in contrasting ways.

50

51 **Key words:** Plant-climate interactions, Plant-soil (below-ground) interactions, Ecological indicator values
52 (EiV), Environmental gradients, Fine-root traits, Root nitrogen concentration, Root tissue density, Specific
53 root length

55 Introduction

56 Understanding the strategies that allow species to establish and sustain a population in a habitat is a central
57 goal in ecology (Craine, Froehle, Tilman, Wedin & Chapin, 2001; Grime, 1977; Westoby, 1998). Plant
58 functional traits (*sensu* Violle et al. 2007) reflect species evolutionary history and, as a result, their
59 adaptation to a large range of environmental constraints (Cavender-Bares, Kozak, Fine, & Kembel, 2009;
60 Grime, 1977; McGill, Enquist, Weiher, & Westoby, 2006). They are key descriptors of plant strategies, by
61 controlling their capacity to pass through environmental and biotic filters (Keddy, 1992; Lortie et al.,
62 2004), and to sustain a population at the intersection of various environmental gradients (Reich, 2014). As
63 such, strong links have been previously identified at the global scale between the position of species
64 ecological niche (Hutchinson, 1957) along environmental gradients and their functional traits (Freschet et
65 al., 2017; Jager, Richardson, Bellingham, Clearwater, & Laughlin, 2015; Maire et al., 2015; Moles et al.,
66 2014; Ordoñez et al., 2009). Nonetheless, much remains to be done to refine our understanding of these
67 linkages, particularly with respect to plant below-ground features (Freschet et al., 2017; Iversen et al.,
68 2017).

69 From works on above-ground parts of plants, we know that species from environments with high nutrient
70 availability generally display fast resource acquisition strategies characterised by low leaf tissue density,
71 high specific leaf area (SLA) and high leaf nutrient concentration (Jager et al., 2015; Janse-Ten Klooster,
72 Thomas, & Sterck, 2007; Ordoñez et al., 2009). A contrasting trend occurs however with respect to light
73 availability, as species adapted to full light conditions generally harbour lower SLA than species from low
74 light conditions (Janse-Ten Klooster et al., 2007; Niinemets, 2010; Vojtkó et al., 2017). Besides these
75 patterns associated to critical above- and below-ground resources, leaf traits are also known to vary with
76 many other environmental factors such as temperature, precipitation, aridity or climatic extremes (Maire et
77 al., 2015). Above- and below-ground reproductive traits (e.g. seed mass, bud bank characteristics) also vary
78 according to environmental gradients (Herben, Tackenberg, & Klimešová, 2016; Vojtkó et al., 2017).
79 Vojtkó et al. (2017) demonstrated at the community level that bud bank size and depth are lower for
80 communities from habitats with high light and nutrient availability, whereas high moisture tends to have
81 the opposite effect. Parallel knowledge of the environmental drivers of species root trait variation is less
82 clear and appears to date largely inconsistent. On the one hand, tree species from more fertile habitats have
83 been shown to have lower specific root length (SRL) (Kramer-Walter et al., 2016; Ostonen et al., 2007),
84 lower root tissue density (RTD), higher mean fine-root diameter and no difference in root nitrogen
85 concentration (RNC) as compared to species of less fertile habitats (Kramer-Walter et al., 2016). On the
86 other hand, studies mostly based on graminoid and forb species highlighted a decrease in species RTD and
87 fine-root diameter and an increase in SRL and RNC with increasing habitat fertility (Craine et al., 2001;
88 Fort et al., 2016; Ryser, 1996). This was also confirmed by studies measuring root traits over entire

89 communities (i.e. community functional parameter; Prieto *et al.*, 2015; Fort *et al.*, 2016). These contrasting
90 results suggest that plants of distinct growth forms or phylogenetic groups may not respond homogeneously
91 to the same environmental gradients.

92 Recently, two meta-analyses on fine roots and very fine roots (Freschet *et al.*, 2017; Valverde-Barrantes *et*
93 *al.*, 2017, respectively) suggested that climate conditions relate to fine-root traits representative of soil
94 resource acquisition, with a particularly strong positive effect of temperature on fine-root diameter and
95 negative effect on SRL, and a negative effect of rainfall on RNC. However, relationships between fine-root
96 traits and soil properties were more ambiguous (Freschet *et al.*, 2017), likely owing to the use of coarse-
97 scale soil data inadequate to capture fine-scale soil heterogeneity. Most root studies and therefore root
98 databases are lacking a common set of descriptors of soil properties (Iversen *et al.*, 2017). Therefore, while
99 current knowledge on the climatic drivers of species root trait values contrasts with expectations from the
100 “fast-slow” root economics spectrum theory (Reich, 2014; Weemstra *et al.*, 2016), our understanding of
101 soil drivers of root trait values remains largely incomplete. This is despite fine-scale environmental
102 variations, particularly in soil properties, are known to have strong effects on species traits (e.g. Freschet,
103 Cornelissen, van Logtestijn, & Aerts, 2010; Hill, Simpson, Moore, & Chapman, 2006) and community
104 functional parameters (i.e., trait values measured at the plant community level) (Fort *et al.*, 2016) and may
105 mitigate the effects of more global environmental gradients (Conti, de Bello, Lepš, Acosta, & Carboni,
106 2017). Acknowledging the limitation of current global root trait and soil databases regarding soil
107 properties, one way to gain further insight into the relationships between species root traits and
108 environmental features is to assess linkages between species trait values and species ecological indicator
109 values (Ellenberg *et al.*, 1991; Garnier *et al.*, 2016).

110 Ecological indicators values (EiV), generally established at the regional scale, characterise the ecological
111 optimum of species along major environmental gradients using ordinal scales. They are highly useful
112 indices to assess species niche position along environmental gradients without direct measurement
113 (Bartelheimer & Poschlod, 2016; Diekmann, 2003; Herben *et al.*, 2016). These EiV are derived from long-
114 term vegetation surveys, expert knowledge and measurements of soil parameters. They reflect
115 environmental conditions where a plant species is most likely to sustain a population, i.e. species optimal
116 niche position along environmental gradients (Bartelheimer & Poschlod, 2016; Fort, Jouany, & Cruz, 2015;
117 Silvertown, Dodd, Gowing, Lawson, & McConway, 2006). Since species EiV are estimated across entire
118 populations of individuals occurring across a range of environments, they can be meaningfully related to
119 trait data coming from heterogeneous databases where traits have been measured in a range of growth
120 conditions. Recent studies highlighted that EiV are related with key functional traits, such as relative
121 growth rate, net carbon assimilation rate, and reproductive strategies (Bartelheimer & Poschlod, 2016;
122 Herben *et al.*, 2016; Shipley *et al.*, 2017). Bartelheimer & Poschlod (2016) demonstrated for instance a

123 positive relationship between EiV related to nutrient availability, pH and soil water and plant relative
124 growth rate and SLA, and a negative relationship between light availability EiV and these same traits.
125 Vojtkó et al. (2017) confirmed further the robustness of these relations between SLA and nutrient, pH and
126 light EiV at the community level. The relationships between these traits and EiV were however weaker for
127 continentality and temperature (Bartelheimer & Poschlod, 2016; Vojtkó et al., 2017) and the relationship
128 between SLA and light or water EiV appeared to be impacted by plant growth form (Shipley et al., 2017).
129 Except for reproductive and regenerative traits (Herben et al., 2016; Vojtkó et al., 2017), relationships
130 between EiV and plant strategies were for most part established based on plant above-ground
131 characteristics, highlighting above-ground level adaptations to species niche along environmental gradients
132 (Bartelheimer & Poschlod 2016 and references therein). However, root system characteristics represent key
133 aspects of species adaptation to various environmental constraints and especially soil resources (Bauhus &
134 Messier, 1999; Forde & Lorenzo, 2001; Ostonen et al., 2007). In this context, extending the known
135 relationships between EiV and plant characteristics to below-ground traits would be critical to further our
136 understanding of processes driving the differentiation of species ecological niches.

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

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

149 **Materials and Methods**

150 DATA COLLECTION

151 The first step of our study was to collect functional trait data using a global database of fine-root traits
152 spanning 1115 species (Rhizopolis database; Freschet et al., 2017). We restricted our selection of species to
153 these presenting at least one of the four most commonly measured root functional traits: root diameter,
154 SRL, RTD and RNC. To improve the homogeneity of our trait data, we further restricted our selection of
155 species to those with roots sampled as < 2mm in diameter (i.e., the most common sampling classification in
156 our database; Freschet & Roumet 2017). The trait data were categorized, depending on species growth
157 conditions, as in “pot” (indoors or outdoors), in “common garden” (outdoor plantations) or in “field”
158 conditions (natural conditions), in order to differentiate between different degrees of climate and soil
159 manipulation.

160 The second step was to cross species root trait data with EiV data from the Baseflor database (Julve, 2015).
161 Baseflor is a floristic database indexing about 10,000 taxa from the French vascular flora. For each taxon,
162 the database includes ecological, and biological descriptions (Julve, 2015). In the Baseflor database, the F,
163 K, L, N, R and T Ellenberg’s indicators values (Ellenberg et al., 1991) are modified to take into account the
164 French ecological context of each taxon, and extended to species typical of the French flora. Additionally,
165 soil organic matter content, soil texture and atmospheric humidity EiVs were established using the same
166 methodology as Ellenberg’s indicators values (Ellenberg et al., 1991) based an extensive collection of data
167 on species ecology coming from flora and others published sources, the author’s field experience and
168 scientific exchanges with ecologists, especially phytosociologists (Julve, 2009). The relationships between
169 Baseflor EiV and original Ellenberg’s EiV, for a common subset of species and EiV, are strong, with R^2
170 ranging from 0.32 for continentality to 0.84 for pH and Temperature EiVs (p -value < 0.001, Fig. S1).
171 Baseflor also includes additional EiV describing climate, i.e. atmospheric moisture, and soil characteristics,
172 i.e. soil texture and organic matter content, which are of strong interest for explaining root traits. Species
173 from the Rhizopolis database (Freschet *et al.*, 2017) were crossed with the EiV database to identify species
174 presenting both types of data. Based on this selection of 357 species, we identified nine EiV for which we
175 had enough observations to perform robust analyses. These EiV could be separated into three groups: i)
176 EiV related to resource availability, i.e. light, nutrients and soil water; ii) EiV related to climate, i.e.
177 atmospheric humidity, continentality and temperature, and iii) EiV related to soil properties, i.e. pH,
178 organic matter content and soil texture. For resource availability, low EiV indicate low resource
179 availability, whereas high values indicate high resource availability. For climatic conditions, low EiV for
180 atmospheric moisture and temperature indicate low air humidity and temperature, whereas high EiV
181 indicate high air humidity and temperature, respectively; low values of continentality indicate that species
182 occurred in oceanic habitats, whereas high values indicate that species occurred in continental habitats. For

183 soil properties, low pH and organic matter EiV indicate acid pH and low organic matter content, whereas
184 high EiV indicate high pH and organic matter content, respectively; low EiV of soil texture indicate that
185 species occurred in loamy soil, whereas value around 5 indicate that species occurred in sandy soil and
186 values higher than 6 indicate that species occurred in scree or stone. Repartition of species among the EiV
187 were provided in the Figure S2. Non-surprisingly, the median classes of EiV were most represented,
188 whereas extreme EiV had fewer observations. This trend was particularly pronounced for low temperature,
189 low light availability and high soil texture EiV (species from gravel and stone habitats) and less so for
190 nutrient and organic matter EiV (Fig. S2). This may result from the fact that a limited number of species
191 have their ecological optimum in extreme environmental conditions (although present in extreme
192 environments), but also from the lack of studies on roots in extreme habitats.

193 In order to estimate the phylogenetic signal on species root traits and take it into account in our analyses we
194 constructed a phylogenetic tree using the comprehensive species-level phylogeny from Zanne et al. (2014),
195 as updated by Qian & Jin (2016). This time-calibrated tree includes nearly all families of extant seed plants:
196 species placement relied on seven gene regions, with orders and families constrained by the APG III
197 (2016). We used S.PhyloMaker (Qian & Jin, 2016) to generate a phylogeny containing species from the
198 Rhizopolis database from this megaphylogeny. Where species or genera were not represented in the larger
199 tree, they were added as uninformative (e.g. basal) polytomies. The final tree was ultrametric with time-
200 calibrated branches.

201

202 As a result, we selected 249 species from 62 families (Fig. 1) and from 34 datasets for which we collected
203 at least one mean value of one of the four traits (root diameter, SRL, RTD, RNC), the nine values of the
204 ecological indicators and the position along the phylogenetic tree. This represented 218 species for SRL,
205 182 for fine-root diameter, 172 for RTD and 144 species for RNC (Table 1).

206

207 **Data analysis**

208 Recent papers have highlighted the importance of phylogenetic corrections for meta-analyses and similar
209 comparative analyses (Chamberlain et al., 2012), as it can represent a significant source of non-
210 independence between observations. We tested for phylogenetic signal (Pagel's λ) in the values of each of
211 the four root traits (phylosig() in 'phytools' (Revell, 2012)). Values of Pagel's λ close to zero indicate
212 phylogenetic independence and larger values (approaching 1) indicate increasingly strong relationships
213 between trait values and the phylogeny (Münkemüller et al., 2012).

214 The potential effects of plant growth conditions and datasets were corrected using a random-effect model
215 with growth condition and dataset as random factors to calculate a best linear unbiased predictor (BLUP) of

216 the log-transformed mean trait value of each species and its standard error (see Freschet *et al.*, 2017). The
217 BLUP were calculated with mixed linear models (`lmer()` in 'lme4' package; Bates, Mächler, Bolker, &
218 Walker, 2015). We then examined the link between the estimated species trait values (BLUP) and species
219 habitat position along ecological gradients (i.e. EiVs) by using a model averaging procedure (Johnson &
220 Omland, 2004). Models used within this procedure are general least square (gls) models in which the
221 correlation structure is a phylogenetic tree reflecting the evolutionary relationships between all species
222 present in the dataset (using `gls()` from 'nlme' package; Pinheiro, Bates, DebRoy, Sarkar, & Team, 2016).
223 These models recognize that trait values may have non-zero covariances between them as a result of shared
224 evolutionary history between species, and so transform the data to reflect this. Linear regression is then
225 applied to the transformed data (Stone, Nee, & Felsenstein, 2011). The weight of each species within the
226 models was proportional to the inverse of the standard error of its BLUP to take into account the
227 uncertainty of the mean trait value estimates. For each trait, the complete models included all the EiV. The
228 set of all possible models were run and ranked according their corrected Akaike information criterion
229 (AICc) (using `dredge()` from 'MuMin' package; Bartoń, 2016). For each trait, we first extracted the results
230 of the best model (based on AICc). Then, we estimated the effect of each EiV on each trait by calculating
231 the means and confidence intervals (95%) of the estimates associated with the EiV among the models
232 representing 95% of the total AICc weight. The relative importance (RI) of EiV effect on trait values was
233 estimated by the sum of the AICc weights of the models in which the EiV appears (the more the RI value of
234 an ecological indicator is close to 1 the more the models where it is represented have high AICc weights,
235 i.e. represent well the fitted data). For each trait the best model was used to calculate an R^2 with the method
236 proposed by Nakagawa & Schielzeth (2013). The same procedure of model selection was also conducted
237 independently for each plant growth form to test the effect of plant growth forms on the relationship
238 between trait values and EiV.

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

242

243 Results

244 Phylogenetic signal

245 All four traits showed large and significant (p -value <0.001) phylogenetic signals (Fig. 1, Table 1). SRL
246 showed the strongest signal with a Pagel's λ of 0.84, whereas RNC had the weakest signal with a Pagel's λ
247 of 0.59. This was consistent with significant differences in root traits among species and families (Fig. 1,
248 Fig. S3). *Brassicaceae* and *Poaceae* families displayed the thinnest roots (highest SRL and low diameter)
249 whereas *Cistaceae*, *Fagaceae* and *Oleaceae* had the coarsest roots within the dataset. *Fabaceae* were
250 characterized by their low RTD and high RNC (Fig. 1, Fig. S3).

251 Ecological indicators

252 Ecological indicator values were good estimators of RNC (R^2 of the best model (AIC-based) equal to 0.45),
253 SRL and RTD (best model R^2 of 0.41 and 0.40, respectively). All three traits appeared to be related to at
254 least four ecological indicators (Fig. 2). In contrast, fine-root diameter was only modestly estimated by EiV
255 (for the best model $R^2 = 0.11$) and was significantly related to one EiV only (Fig. 2; Table S1). These
256 results were impacted by species growth form (Fig. 2), as discussed in more detail below.

257 Among ecological indicators related with climate, continentality EiV had a strong negative effect on RNC
258 for both the whole dataset and grasses only, highlighting that species from continental climate had lower
259 RNC than species from more oceanic conditions (Fig. 3). Continentality also had a negative effect on the
260 mean root diameter of shrubs and trees, highlighting that woody species from continental habitats had
261 thinner absorptive roots than woody species from oceanic habitats (Fig. 3). Atmospheric humidity EiV had
262 a positive effect on RTD and RNC, indicating that species generally present in humid climates displayed
263 higher RTD and RNC than average, independently of their phylogenetic relatedness (Fig. 3). The same
264 relation was observed when grasses were analysed alone, but the estimates did not significantly differ from
265 zero for other growth forms (Fig. 3). Finally, the temperature EiV had a negative influence on SRL,
266 indicating that species from cold environments generally displayed higher SRL than average. At the level
267 of growth forms, temperature had a negative effect on root diameter of trees, and displayed contrasting
268 effects on the RNC of grasses and forbs: i.e. grass species from cold habitats had higher RNC than grasses
269 from warmer habitats, whereas the opposite trend occurred for forbs (Fig. 3).

270 Among EiV related to resource availability, nutrient EiV had strong effects ($RI \geq 0.94$) on SRL, RNC and
271 RTD. Across all species, plants found in nutrient-rich soils had higher SRL and RNC and lower RTD
272 values than species from nutrient-poor soils. At the level of plant growth forms, grasses and forbs showed
273 the same trend than at the whole dataset level, whereas trees displayed lower diameter, higher SRL and
274 RNC values at lower nutrient EiV. Soil water EiV had a strong and negative effect on RTD and RNC for

275 both the whole dataset and grasses only, showing that species from environments with high water
276 availability or water-logged environments had lower RTD and RNC than other species. In contrast, tree and
277 shrub species analysed separately displayed higher RNC values, and forbs displayed lower diameter and
278 SRL values in case of high water EiV. Light EiV was negatively related with SRL and positively related
279 with root diameter, indicating that species ability to establish viable population in shaded environments is
280 associated with low root diameter and high SRL. The increase of light EiV for trees and shrubs was related
281 with an increase of tissue density and a decrease of RNC.

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

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

294 **Discussion**

295 Our analyses demonstrate that species ecological indicator values, together with phylogenetic information,
296 are valuable predictors of plant below-ground strategies. They shed light on several environmental
297 parameters strongly connected to fine-root trait variation: nutrient and water availability and soil texture
298 below-ground, as well as light and temperature above-ground. As hypothesised, ecological indicators
299 related to nutrient availability and soil texture were the most strongly related to fine-root trait values,
300 highlighting the importance of these traits for species adaptation to the availability of soil resources.
301 Importantly, species growth forms had a strong impact on the relationships between traits and EiV, with
302 woody species sometimes displaying opposite responses to herbaceous species, especially for resource-
303 related ecological indicators. All four traits, root diameter, SRL, RTD and RNC, considered as major traits
304 supporting the “fast-slow” root economic spectrum (together with root lifespan and root respiration rate;
305 Reich, 2014; Roumet et al., 2016) and/or the trade-off between building thin roots or thick roots relying on
306 mycorrhiza (Kong et al., 2019; McCormack & Iversen, 2019), were (at least partly) differently related to
307 species habitat in terms of climate, nutrient availability and other soil properties. This finding of multiple

308 determinants of fine-root trait global distribution implies that root trait values cannot be simply represented
309 by one single strong environmental axis.

310 *Relevance of accounting for phylogenetic relatedness*

311 This work confirms that root functional traits carry a strong phylogenetic signal (Comas et al., 2012),
312 although the strength of this signal for all four traits differed between this and other datasets (e.g. Freschet
313 et al., 2017; Valverde-Barrantes et al., 2017; Ma et al., 2018) following distinct representations of the
314 global species set and different entities of root studied. This substantial phylogenetic signal was generally
315 consistent with ancient history of root-mycorrhiza coevolution (Ma et al., 2018) and historical evolution of
316 tissue organisation and development (Comas, Callahan, & Midford, 2014), such as the capacity of dicot
317 species to perform secondary growth in contrast to monocots, or the tendency of *Fabaceae* to accumulate
318 root N potentially relating to their ability to associate with N₂-fixing symbionts (Freschet et al., 2017).

319 *Root traits vary according to ecological indicators values*

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

334 Specific root length is strongly related with mean root diameter following a general nonlinear asymmetric
335 relation (Ma et al., 2018). However, our results suggest that across all plant growth forms SRL is more
336 strongly related to species adaptation to a range of environmental gradients than fine-root diameter (see
337 also Valverde-Barrantes et al., 2017). The positive relationship between SRL and the nutrient EiV
338 highlights that having high SRL values is one of the key for plants to succeed in nutrient-rich
339 environments. Indeed, high SRL may provide higher competitive ability, at least among grassland species
340 (Mommer et al., 2011). The strong negative relationship observed between the temperature EiV and SRL

341 strengthens the patterns observed with global climatic variables (Freschet et al., 2017; Valverde-Barrantes
342 et al., 2017) or at finer scales, such as in studies comparing root traits of tree species from different latitudes
343 (Ostonen et al., 2007). High SRL is further associated with faster root elongation rates and higher potential
344 to proliferate in nutrient patches (Eissenstat, 1992; Eissenstat, Kucharski, Zadworny, Adams, & Koide,
345 2015; Hodge, 2006). These characteristics should be particularly useful to acquire resources in colder
346 environments where strong seasonality and soil freezing could lead to heterogeneous and intermittent soil
347 microbial activity and nutrient availability (Bardgett, Bowman, Kaufmann, & Schmidt, 2005; Chen, Zeng,
348 Eissenstat, & Guo, 2013).

349 Specific root length is also strongly and positively related to soil texture EiV, that is, it decreases as soil
350 texture becomes dominated by silt and clay. Soil texture is one of the major driver of bulk soil density, and
351 water, nutrient and air contents and movement in soil (Alameda & Villar, 2012; Arvidsson, 1998; Pabin,
352 Lipiec, Wlodek, Biskupski, & Kaus, 1998). All these parameters are known to have complex influences on
353 root growth and root traits. Bulk density for instance, which is negatively related to soil clay and silt
354 content, is known to increase the resistance to root penetration and limit root growth (Dexter, 2004; Jones,
355 1983); and species with thicker fine-roots, and therefore lower SRL, are generally better adapted to denser
356 soils because of their higher soil penetration strengths (Bengough, McKenzie, Hallett, & Valentine, 2011;
357 Materechera, Alston, Kirby, & Dexter, 1992). The negative relation between RTD and the soil texture EiV
358 also strengthens the idea that dense roots with a high investment in structural tissues, and therefore of lower
359 SRL, are beneficial in soil with high content of clay and silt (Freschet et al., 2017) where even low soil
360 penetration resistance and bulk density may limit root growth (Pabin et al., 1998).

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

370 Root tissue density and nitrogen concentration are also strongly but negatively related to water availability
371 EiV, indicating that species characterised by low RTD and RNC are more represented in high water
372 availability environments. More specifically, wetland species display the lowest RTD values, which can be

373 related to their capacity to produce aerenchyma in order to limit tissues hypoxia in waterlogged conditions
374 (Justin & Armstrong, 1987).

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

382 Largely consistent with the univariate analyses, our multivariate approach shows that the trait spectrum
383 separating species with high SRL and RNC but low RTD (and also low root diameter) and species with the
384 opposite characteristics relates to an axis separating species from nutrient-rich, humid, low soil pH and
385 shaded habitats to those with the opposite ecological preferences. These results, essentially derived from
386 data on herbaceous species, strengthen the idea that fast use of soil resources through low tissue density and
387 thin elongated roots (and therefore short root lifespan; McCormack *et al.*, 2012; Ma *et al.*, 2018) and high
388 nitrogen concentration (associated to high respiration rates; Reich *et al.*, 2008) is an efficient way to avoid
389 being suppressed by competitors in nutrient-rich habitats (Fort, Cruz, & Jouany, 2014; Grime, 1977; Reich,
390 2014). In contrast, the opposite root trait syndrome (low RNC, SRL and high RTD) would allow plants to
391 strive in nutrient-poor conditions where fast resource use is less suitable. However, more work is needed to
392 assess the generality of this trend across woody species. Additionally, future analyses would strongly
393 benefit from the inclusion of data from a wider range of environmental conditions (providing that future
394 studies increasingly consider extreme environmental conditions) and a wider range of species, so as to
395 extend our analysis to better capture non-linear patterns of trait-environment relationships.

396 *Opposite patterns between woody and herbaceous species*

397 Beyond the general patterns observed across all species, growth forms had a strong impact on the
398 relationships between traits and ecological indicators, with woody species sometimes displaying opposite
399 responses to herbaceous species, especially for resource-related EiV. Most particularly, in nutrient-rich
400 environments, woody species tended to rely on high-diameter, low SRL and low RNC roots, which
401 contrasted strongly with herbaceous species, especially grasses. Plant root systems have multiple ways to
402 deal with low soil nutrient availability (e.g. increasing SRL, Bauhus & Messier, 1999; root hair length and
403 density, Yang *et al.*, 2015; mycorrhizal association and cluster roots, Lambers, Raven, Shaver, & Smith,
404 2008). In this context, our results might reflect a higher reliance of woody species on mycorrhizal
405 association (McCormack & Iversen, 2019) in nutrient-rich conditions, whereas grasses would typically

406 adopt high SRL roots, with higher metabolic activities. Grass species also showed lower RNC and RTD in
407 high water availability environments, whereas the contrary was true for woody species, suggesting different
408 adaptations of grasses and woody species to high water conditions, including higher reliance on
409 aerenchyma for grasses. Overall, these results suggest that plant species adaptation to their environment
410 may depend on a larger set of plant characteristics linked to growth forms (e.g., among many other
411 potential traits, size, lifespan, woodiness) that set different constraints on plants in view to overcome the
412 same stresses and limitations. Such results limit our ability to define simple, widely applicable patterns of
413 trait-environment relationships and illustrate how different plant community assembly processes may apply
414 to contrasting sets of species.

415 *Conclusion*

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

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436 **Authors' contributions**

437 FF and GTF conceived the ideas, designed the methodology, analysed the data and wrote the manuscript.

438 **Data Availability Statement**

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

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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	
								Lambda	p-value
D (mm)	0.14	0.30	0.55	0.29	19	44	182	0.80	<0.001
SRL (m g ⁻¹)	6.17	104.8	936.4	1.07	24	49	218	0.84	<0.001
RTD (g cm ⁻³)	0.04	0.29	1.18	0.69	16	44	172	0.76	<0.001
RNC (mg kg ⁻¹)	3.15	12.36	42.2	0.48	18	33	144	0.59	<0.001

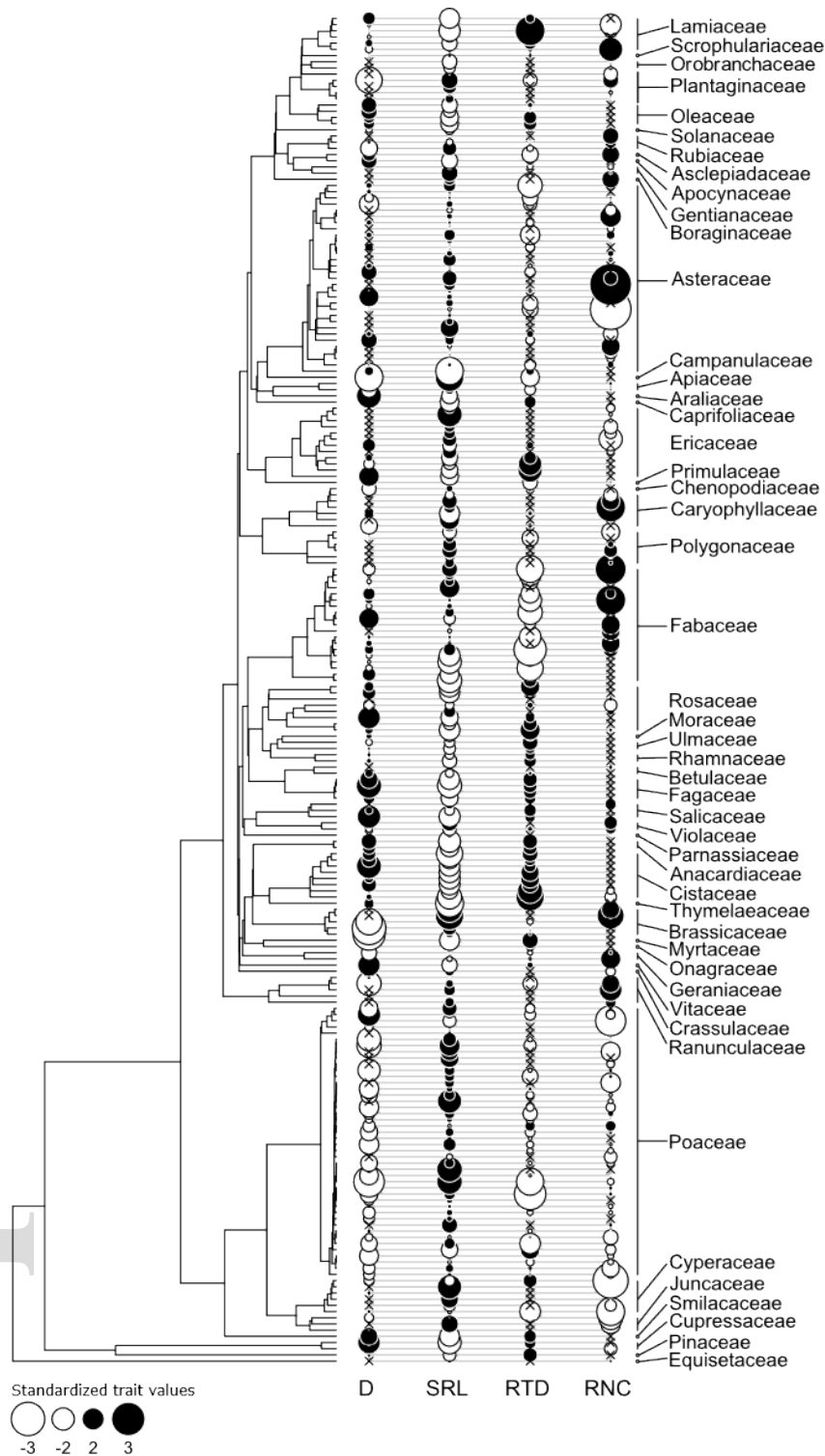


Figure 1: Phylogeny of the 249 species of this study (only family names are displayed). Estimated values of the four functional traits (Best Linear Unbiased Predictor estimated by mixed models) are represented at the tips of the phylogeny (in centred and standardised format). Black circles represent 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; SRL: specific root length; RTD: root tissue density; RNC:
root nitrogen concentration.

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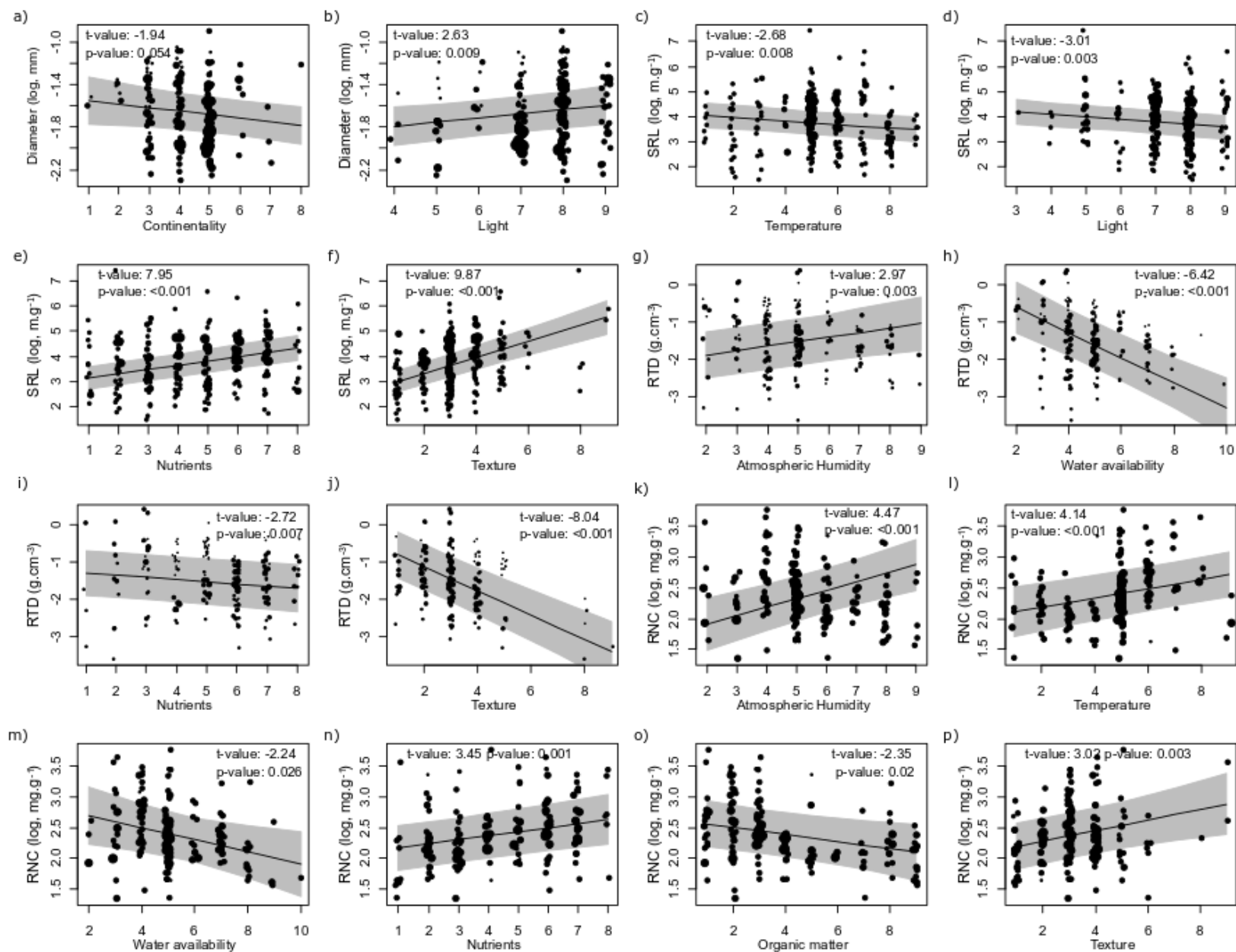


Figure 2: Biplots of relationships between ecological indicator values (EiV) and (phylogenetically corrected) trait values for those EiV that were retained in the best multivariate models (lowest AICc) explaining mean root diameter (a-b), specific root length (SRL) (c-f), root tissue density (RTD) (g-j) 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.

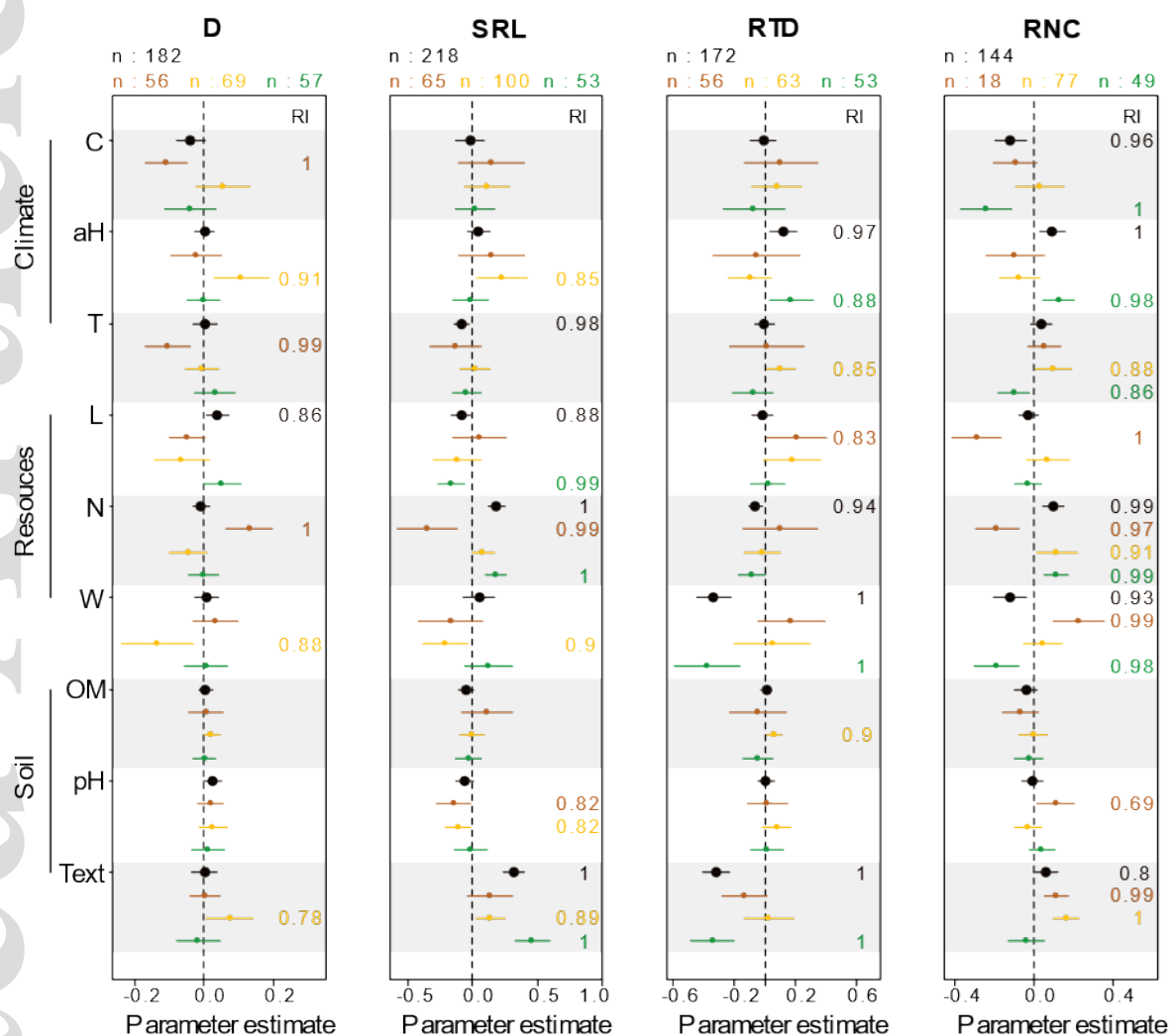


Figure 3: Effects of ecological indicator values (EiV) on fine-root traits across all species. Regression coefficients for models fitted separately for D: mean root diameter, RTD: root tissue density, SRL: specific root length and RNC: root N concentration (dots show average estimates, lines show 95% 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 standardised 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, i.e. atmospheric moisture (aH), continentality (C) and temperature (T), ii) EiV related to resource availability, i.e. 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).

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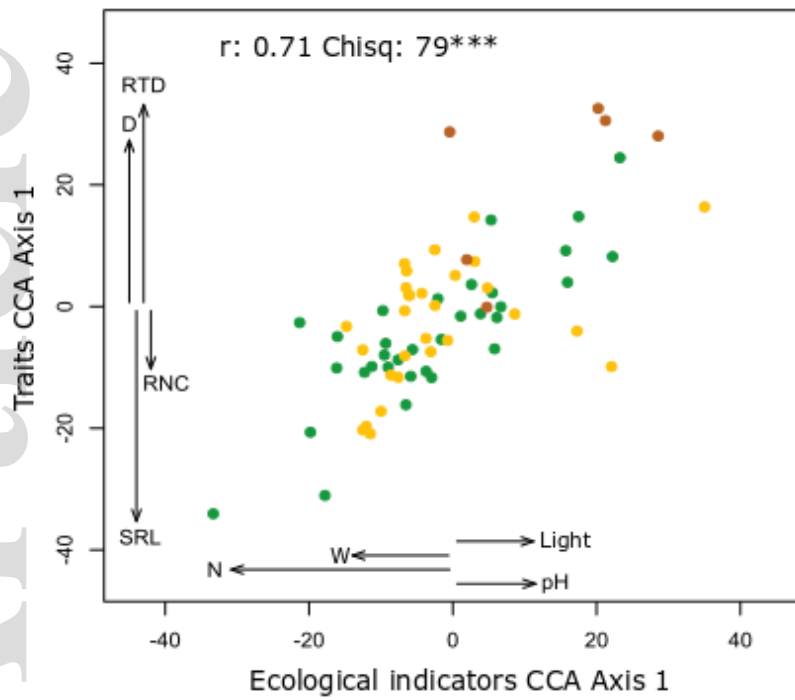


Figure 4: Relationship between species scores among the ecological indicator values (EiV; x-axis) and root trait values (y-axis) from a phylogenetic canonical correlation analysis (pCCA). Brown points are shrub and tree species, yellow points are forb species and green points are grass species. The strength 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 -value < 0.001 : ***. D: mean root diameter, RNC: root nitrogen concentration, RTD: root tissue density, SRL: specific root length. Light: light availability EiV, W: soil water availability EiV, N: nutrient availability EiV, pH: pH EiV.