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Matters Arising

The importance of trait selection in ecology

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Recently, two papers^{1,2} have emerged that explore the importance of roots for understanding plant form and function, but reach opposite conclusions based on largely overlapping data. Carmona *et al.*¹ (hereafter "CN") concluded that "[their] results do not confirm the strong covariation between leaf and fine-root traits predicted by the plant economics spectrum hypothesis". In contrast, Weigelt *et al.*² (hereafter "WNP") concluded that "key leaf and fine-root traits were aligned" along the expected [fast-slow] conservation gradient of plant economic investment". Here, we reflect on the causes for the apparent discrepancies of both studies and show that the rationale behind trait selection is vital for the conclusions.

Ecological inference. In his 'traits manifesto' Reich³ hypothesized that strong selection along trait trade-offs must result in convergence for any taxon on a uniformly fast, medium or slow strategy for all organs (leaves, stems and roots) and all resources (carbon, nitrogen, water)'. This proposed alignment of multiple organ strategies seems inevitable also for stoichiometric reasons: fast carbon-fixation in leaves without high nitrogen-uptake rates in roots would result in low plant nitrogen concentration which would reduce carbon-fixation per unit leaf mass⁴. However, CN conclude from their results that aboveground and root trait planes are decoupled. Like CN, WNP found a unique trait axis with root diameter and specific root length distinct from aboveground traits. However, WNP also found consistent alignment of leaf and root nitrogen content, as well as leaf mass per area and root tissue density.

Indeed, in Fig. 1 in CN it seems as if "four dimensions are needed to explain the non-redundant information in the dataset, [which] can be summarized in an aboveground and a fine-root plane". However, their correlation coefficient of leaf nitrogen to root nitrogen content (301 species, Extended data Fig. 1 in ¹) is strongly positive with $r = 0.37$. This value (and most other pairwise correlation coefficients in ¹) are similar to those in the study of WNP (i.e. $r = 0.38$ for leaf vs. root nitrogen, 1394 species, Fig. S2 in ²). In addition, the positive correlation between leaf and root nitrogen is supported by a wealth of published studies (Fig. 2 in ^{2,5}). Though, the Principal Components Analysis (PCA) plots of the two studies appear different, the underlying correlation coefficients are not, suggesting that the claim by CN that aboveground and fine-root trait spaces are decoupled is to some extent unsupported. We expand on our thoughts regarding two potential causes for these apparent differences – trait selection and varimax rotation.

Trait selection: CN draw conclusions on a comparison among above- and belowground traits, based on six aboveground traits spanning a wide spectrum of plant form and function⁶ and four fine-root traits linked to resource acquisition-conservation functions⁷. Importantly, CN included aboveground traits that are not directly related to resource acquisition, including stem specific density, plant height, and seed mass¹. In turn, WNP used a stepwise approach (Fig. 1 in ²) to first compare traits that are proposed to be functionally relevant, and then increased complexity with additional traits not directly related to resource acquisition. This means that WNP first compared functionally analogous leaf- and root traits exclusively related to resource investment (leaf and root nitrogen, leaf mass per area and root tissue density, specific root length, root diameter, Fig. 3 in ²), and found significant correlations. WNP subsequently included size-related traits (plant height and rooting depth), which yielded two additional trait gradients loading independently on PC axes 3 and 4.

To substantiate the importance of trait selection, we reanalysed the 301 species used by CN with these six traits, equally representing above- and belowground aspects of plant form and

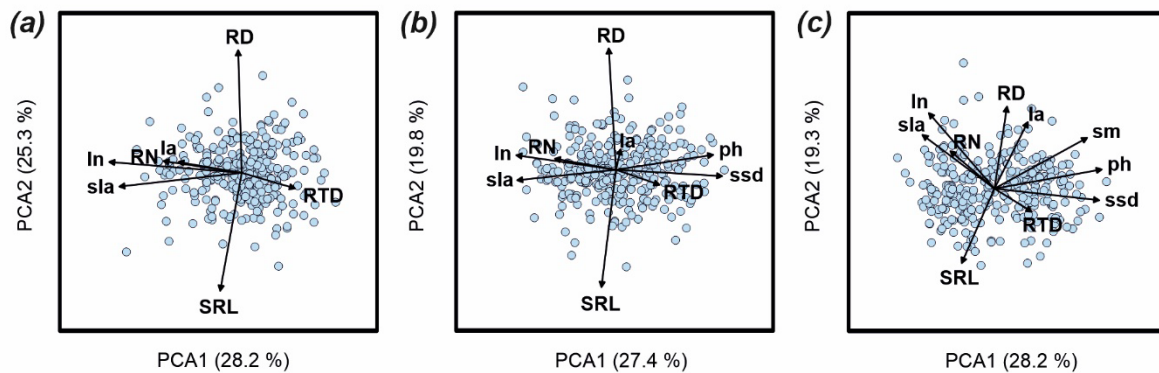
function (Fig. 1a). By selecting the same traits in a PCA, we observed a correlation between the leaf and root trait spaces, similar to WNP. Stepwise inclusion of size-related traits (Fig. 1b) and seed mass (Fig. 1c) then changed the interpretation of the study results. Our reanalysis shows that the rationale leading to the trait selection is a critical factor in such studies. The apparent discrepancies in conclusions between the two studies seem to be primarily triggered by the presence or absence of seed mass, a reproductive trait spanning a large range of variation which might mask the more subtle changes in acquisitive traits. Our stepwise analysis (Fig. 1a-c) reconfirms that results of multivariate analyses depend on the type and number of traits included. We argue that trait selection requires careful ecological consideration and should be based on knowledge of trait functionality.

A related point of concern is the claim by CN that trait variation is greater aboveground compared to belowground, as they state to find “Greater differentiation in aboveground trait syndromes than in fine roots [...]”. We expect that this outcome is again primarily related to the aboveground trait selection of CN which encompasses a wider trait gradient for potential variation than the selected belowground traits. The authors acknowledge this fact in their paper, but the overall conclusion still hints at a systematic difference in trait variation above-compared with belowground. Here, we caution against such a generalization based on statistical inference rather than biological understanding.

Effects of varimax rotation: A second cause for the differences in PCAs could be that CN use a varimax rotation of the PCA axes, while WNP did not. Theoretically, this rotation should not change the outcome of the results, but improve the interpretability as individual traits are better aligned with the main axes⁸. However, PCA axes after varimax rotation may not perfectly reflect the position of the original variables. As a result, while rotated PCA axes remain orthogonal, the representation of underlying variables may not⁹. This seems to be the case in CN where the high correlation of leaf nitrogen and root nitrogen with the axis representing the leaf economics spectrum (PCA2; loadings 0.44 and 0.31 for leaf and root nitrogen, respectively) disappears for root nitrogen after varimax rotation (loadings 0.59 and 0.08 for leaf and root nitrogen, respectively, Extended Data Table 2). Similarly, there are clear differences in primary trait association with the second and third axes between the rotated and unrotated analysis for 301 species. Importantly, the full decoupling between root and leaf traits is only visible in the rotated form. However, we note that root traits linked to the conservation gradient¹⁰; root tissue density and root nitrogen) also load to other PC axes, irrespective of axis rotation^{1,2} indicating flexibility in the biological coordination of these traits.

Finally, we would like to highlight that, despite our concerns regarding some of the conclusions drawn from the CN study, we admire the extent and depth of data and analyses provided. As plant ecologists, we are all eager to improve our understanding and quantification of plant trait variation, and particularly belowground plant traits, which have lagged behind their showier aboveground counterparts^{11–13}. Progress will be built on critical and open conversations on the role of both known and yet unknown functions of above- and belowground plant traits. A better functional understanding of traits – above and belowground - will dramatically improve our understanding of the role of plant traits in shaping the responses of plant communities and ecosystems in a world that is rapidly changing.

Figure 1: PCA of the 301 species in CN¹ using differing trait subsets and no varimax rotation. **(a)** Traits strictly related to resource acquisition aboveground (ln = leaf nitrogen content, la = leaf area, sla = specific leaf area) and belowground (RN = root nitrogen content, RTD = root tissue density, RD = root diameter, SRL = specific root length) showing strong above-: belowground correlation as in WNP². **(b)** Addition of stem traits (ph = plant height, ssd = stem specific density). **(c)** Inclusion of seed mass (sm), without strong above- and belowground correlation as in ¹. Details supplementary data table 1.



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Supplementary table 1: Analysis of the complete dataset (301 species) with full information for all traits based on species mean trait data. Given are results from the first four principal components as shown in **figure 1a, b and c** where ln is leaf nitrogen concentration, sla is specific leaf area, la is leaf area, SRL is specific root length, RD is average root diameter, RTD is root tissue density, RN is root nitrogen concentration, ssd is stem specific density, ph is maximum plant height and sm is seed mass. Results for PC4 for figure 1a are given in grey to indicate its Eigenvalue is smaller than 1. All data derived from Carmona *et al.* (2021).

	Figure 1a				Figure 1b				Figure 1c			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Eigenvalue	1.973	1.771	1.240	0.912	2.464	1.782	1.593	1.157	2.818	1.933	1.702	1.157
Variance	0.282	0.253	0.177	0.130	0.274	0.198	0.177	0.129	0.282	0.193	0.170	0.116
ln	-0.622	-0.063	0.079	0.170	0.464	-0.084	0.379	0.024	0.306	-0.437	-0.292	0.025
sla	-0.573	0.080	0.202	0.033	0.460	0.060	0.340	0.202	0.334	-0.309	-0.353	0.202
la	-0.291	-0.061	0.582	-0.410	-0.020	-0.107	0.663	0.191	-0.154	-0.381	-0.411	0.194
SRL	-0.101	0.684	-0.196	-0.216	0.068	0.680	0.080	-0.245	0.152	0.427	-0.501	-0.246
RD	-0.017	-0.711	-0.107	-0.148	0.034	-0.704	-0.087	-0.115	-0.058	-0.471	0.515	-0.114
RTD	0.242	0.087	0.585	0.687	-0.196	0.084	-0.014	0.716	-0.167	0.128	-0.028	0.715
RN	-0.363	-0.068	-0.472	0.512	0.280	-0.063	0.077	-0.495	0.201	-0.212	-0.065	-0.496
ssd					-0.496	0.037	0.295	-0.255	-0.488	0.067	-0.182	-0.253
ph					-0.453	-0.086	0.441	-0.162	-0.501	-0.111	-0.217	-0.159
sm									-0.433	-0.294	-0.141	-0.003