Matters arising

The importance of trait selection in ecology

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ARISING FROM C. P. Carmona et al. *Nature* https://doi.org/10.1038/s41586-021-03871-y (2021)

Two recent publications[1,2] have explored the importance of roots for understanding plant form and function, but reached opposite conclusions on the basis of largely overlapping data. Carmona et al.[1] concluded that their results "do not confirm the strong covariation between leaf and fine-root traits predicted by the plant economics spectrum hypothesis". By contrast, Weigelt et al.[2] 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 these studies and show that the rationale behind trait selection is vital for the conclusions.

In his 'traits manifesto', Reich[3] 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 and water). This proposed alignment of multiple organ strategies also seems inevitable 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 mass[4]. However, Carmona et al. conclude from their results that aboveground and root trait planes are decoupled[1]. Like Carmona et al., Weigelt et al. found a unique trait axis with root diameter and specific root length distinct from aboveground traits. However, Weigelt et al. also found consistent alignment of leaf and root nitrogen content, as well as leaf mass per area and root tissue density[2].

Indeed, in Fig. 1 in Carmona et al., 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"[1]. However, their correlation coefficient of leaf nitrogen to root nitrogen content (301 species, Extended Data Fig. 1 in ref. 1) is strongly positive with $r = 0.37$. This value (and most other pairwise correlation coefficients in ref. 1) are similar to those in Weigelt et al. (that is, $r = 0.38$ for leaf versus root nitrogen, 1,394 species (fig. S2 in ref. 2)). In addition, the positive correlation between leaf and root nitrogen is supported by a wealth of published studies (fig. 2 in ref. 2 and fig. 2 in ref. 5). Although the principal components analysis (PCA) plots of the two studies appear different, the underlying correlation coefficients are not, suggesting that the claim by Carmona et al. that aboveground and fine-root trait spaces are decoupled is to some extent unsupported. Here we expand on our thoughts regarding two potential causes for these apparent differences—trait selection and varimax rotation.

Carmona et al. draw conclusions on a comparison among aboveground and belowground traits, on the basis of six aboveground traits spanning a wide spectrum of plant form and function[6] and four fine-root traits linked to resource acquisition–conservation functions[7]. Notably, Carmona et al. included aboveground traits that are not directly related to resource acquisition, including stem specific density, plant height and seed mass[1]. In turn, Weigelt et al. used a stepwise approach (fig. 1 in ref. 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 Weigelt et al. first compared functionally analogous leaf and root traits exclusively related to resource investment (leaf and root nitrogen, leaf mass per area, root tissue density, specific root length and root diameter (fig. 3 in ref. 2)), and found significant correlations. Weigelt et al. subsequently included size-related traits (plant height and rooting depth), which yielded two additional trait gradients loading independently on principal component axes 3 and 4.

To substantiate the importance of trait selection, we reanalysed the 301 species used by Carmona et al. with these six traits, equally representing aboveground 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 Weigelt et al. 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 triggered primarily by the presence or absence of seed mass, a reproductive trait spanning a large range of variation that 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 Carmona et al. that trait variation is greater aboveground than belowground, as they find "greater

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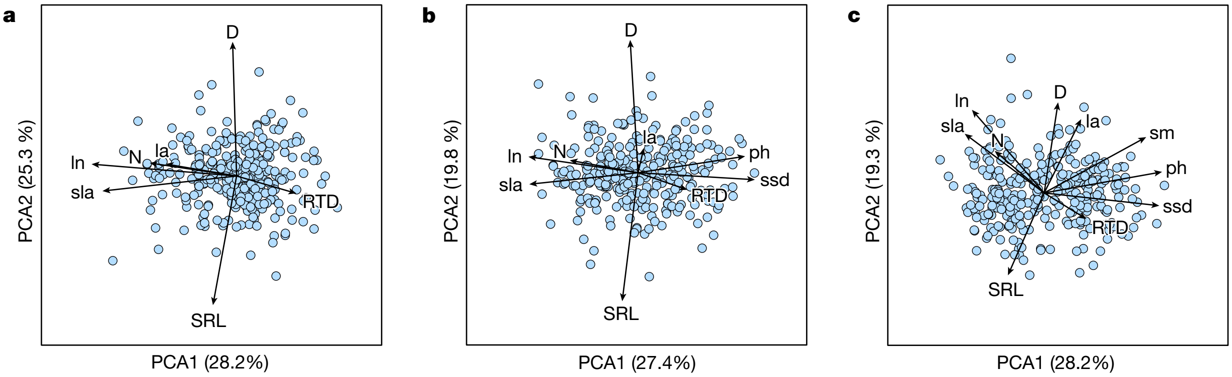

Fig. 1 | PCA of the 301 species analysed in Carmona et al.[1] using differing trait subsets and no varimax rotation. a, Traits strictly related to resource acquisition aboveground (leaf nitrogen content (ln), leaf area (la) and specific leaf area (sla)) and belowground (root nitrogen content (N), root tissue density (RTD), root diameter (D) and specific root length (SRL)) show strong aboveground–belowground correlation, as in Weigelt et al.[2]. **b**, Addition of stem traits (plant height (ph) and stem specific density (ssd)). **c**, Inclusion of seed mass (sm), without strong aboveground and belowground correlation as in ref. 1. Details are shown in Supplementary Table 1.

differentiation in aboveground trait syndromes than in fine roots [...]"[1]. We expect that this outcome is again related primarily to their aboveground trait selection, which encompasses a wider trait gradient for potential variation than the selected belowground traits. Carmona et al. acknowledge this in the article, but the overall conclusion still hints at a systematic difference in trait variation aboveground compared with belowground. Here we caution against such a generalization on the basis of statistical inference rather than biological understanding.

A second cause for the differences in PCAs could be that Carmona et al. use a varimax rotation of the PCA axes, whereas Weigelt et al. do not. Theoretically, this rotation should not change the outcome of the analysis, but should improve the interpretability as individual traits are better aligned with the main axes[8]. However, PCA axes after varimax rotation may not perfectly reflect the position of the original variables. As a result, although rotated PCA axes remain orthogonal, the representation of underlying variables may not[9]. This seems to be the case in Carmona et al., 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 in ref. 1)). Similarly, there are clear differences in primary trait association with the second and third axes between the rotated and unrotated analysis for 301 species. Notably, the full decoupling between root and leaf traits is visible only in the rotated form. However, we note that root traits linked to the conservation gradient[10] (root tissue density and root nitrogen) also load to other principal component axes, irrespective of axis rotation[1,2], indicating flexibility in the biological coordination of these traits.

Despite our concerns regarding some of the conclusions of Carmona et al., we admire the extent and depth of data and analyses provided. As plant ecologists, we all wish 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 unknown functions of aboveground and belowground plant traits. A better functional understanding of traits above and belowground will improve our understanding of the role of plant traits in shaping the responses of plant communities and ecosystems in a rapidly changing world.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06148-8.

Reporting summary

Further information on experimental design is available in the Nature Portfolio Reporting Summary linked to this Article.

Data availability

The data to reproduce Fig. 1 and Supplementary Table 1 are available according to the statement in Carmona et al.[1] in the Figshare repository: https://doi.org/10.6084/m9.figshare.13140146.

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Additional information
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Reply to: The importance of trait selection in ecology

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REPLYING TO A. Weigelt et al. *Nature* https://doi.org/10.1038/s41586-023-06148-8 (2023)

In the accompanying Comment[1], Weigelt et al. (2023) claim that the different conclusions of two studies—Weigelt et al. (2021)[2] and Carmona et al. (2021)[3]—presenting global integrations of aboveground and belowground plant traits are due to methodological issues in Carmona et al. Specifically, ref. 2 concluded that leaf and fine-root traits are coordinated, whereas ref. 3 reported weak covariation between these traits. In their Comment, Weigelt et al. attribute these divergent conclusions to the selection of traits and the use of varimax rotation in ref. 3. Here we estimate angles between pairs of traits in different functional spaces to show that these objections are not supported by the data.

The two studies analysed the same data using principal components analysis (PCA) to determine the necessary dimensions for explaining non-redundant plant trait information. Although we appreciate the points raised in the Comment, we found inconsistencies in the arguments and analyses. For example, consider the relationship between leaf nitrogen content (ln) and root nitrogen content (N). Weigelt et al. view these traits as having "a strong positive correlation coefficient" ($r = 0.37$), supporting Reich's plant economics spectrum hypothesis[4], which predicts coordination between ln and N. Although the arguments behind the hypothesis are strong, empirical support for it is mixed[5–11], which prompted us to test it against the most comprehensive trait dataset[3]. If two traits are highly coordinated, knowing the value of one we could precisely estimate the value of the other. However, the common amount of variation in ln and N is low ($r^2 = 0.137$), so we maintain our original conclusion of no strong coordination between these traits[3].

Characterizing the coordination between pairs of traits after selecting relevant principal components is more complex than analysing individual correlations, because all dimensions should be considered simultaneously. To better understand relationships between traits, we propose to consider the angle they form in the appropriate dimensionality of the space: highly coordinated traits should form a low angle, whereas independent traits should be nearly orthogonal (Fig. 1a and Supplementary information). We address the specific arguments in the Comment using this approach.

Weigelt et al.[1] consider that the space in Carmona et al.[3] is inadequate for testing a single acquisition–conservation gradient across leaves and roots, arguing that seed mass is not related to resource acquisition. We included seed mass along with five other aboveground traits because our primary aim was to reveal patterns at the level of whole-plant form and function, rather than comparing fully analogous organs of resource acquisition[3] (an important plant function, but not the only one). In the Comment, Weigelt et al. claim that the inclusion of seed mass distorts the estimated relationships between other traits. They base this claim on a stepwise PCA analysis in which traits are included sequentially. Although the stepwise analysis seems reasonable, Weigelt et al. do not consider the appropriate dimensionalities when interpreting differences between consecutive PCAs (compare their Fig. 1 with their Supplementary Table 1 (ref. 1)). Instead, they interpret projections of three- and four-dimensional vectors in two-dimensional planes, reaching distorted interpretations of trait relationships. In Fig. 1b, we show how the relationship between ln and N can look very different when considering two dimensions versus three dimensions. Indeed, when all significant dimensions are considered in the sequential PCAs[1], the angles between traits strictly related to resource acquisition are essentially the same, regardless of whether size-related traits are considered or not (Fig. 2a). Therefore, the selection of traits in Carmona et al. did not alter ecological inference.

The Comment also question the finding of greater differentiation in aboveground traits than fine-root traits, without providing any supporting analysis. We stand by our conclusion from Carmona et al.[3], which is supported by our analyses here. The mere order of PCA axes in Fig. 1 in Carmona et al.[3] indicates that variation aboveground (axes 1 and 2) is larger than for fine-root traits (axes 3 and 4). Moreover, differentiation between families and biomes is higher for the traits and the component of space related to plant size (C1), followed by the component reflecting the leaf economics spectrum (C2) (Extended Data Fig. 1). Of note, fine-root traits and related components (C3 and C4) are those for which differentiation was smallest, even when individual traits were analysed.

In Carmona et al., we performed a PCA based on ten key aboveground and fine-root traits, finding four fundamental dimensions of variation. This PCA was followed by a varimax rotation of the four-dimensional space (original space) to enhance its interpretability (rotated space). Weigelt et al. argue[1] that the varimax rotation of the principal components distorts the relationship between traits. However, although the rotation results in different loadings between the original and rotated spaces, it should not change the relationship among traits (on which ecological inference should be based). By comparing the angles between traits in both the original and rotated spaces (Supplementary Information), we demonstrate that the relationships between traits are completely unaffected by the rotation (Fig. 2b). Therefore, rather than distorting inference, the use of varimax rotation helped Carmona et al. to identify the space configuration in which intrinsic differences between traits are most apparent, aiding their correct interpretation and ecological inference.

Weigelt et al. (2023) claim that despite using the same data, the results of refs. 2,3 are fundamentally different. Here we have used data from the

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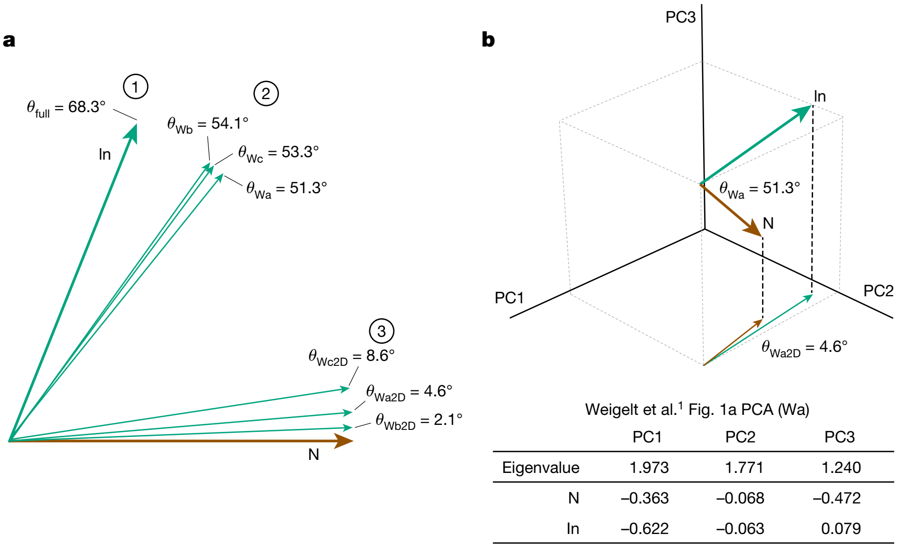

Weigelt et al.[1] Fig. 1a PCA (Wa)

	PC1	PC2	PC3
Eigenvalue	1.973	1.771	1.240
N	–0.363	–0.068	–0.472
In	–0.622	–0.063	0.079

Fig. 1 | The effect of dimensionality reduction and trait selection on the ln–N relationship. a, The relationship between leaf nitrogen (ln) and root nitrogen (N) expressed as an angle *θ*, which is estimated considering different dimensionalities and accompanying traits. (1) Raw trait values (full PCA space). In geometric terms, the correlation coefficient between ln and N (0.37) corresponds to (is the cosine of) the angle the two traits form in a full PCA space (that is, without dimensionality reduction; θ_{full} = 68.3°). (2) In the Comment[1], the data are fit to three PCAs, starting with only leaf and fine-root traits (Wa), and adding sequentially stem traits (Wb) and seed mass (Wc). The angle between ln and N is similar in these three spaces when all significant dimensions (those with eigenvalues greater than 1) are considered (θ_{Wa}, θ_{Wb}, θ_{Wc}), indicating that trait selection did not alter ecological inference. (3) When interpreting the relationship between traits, Weigelt et al. consider only projections of the traits in the first two components of their PCAs (see fig. 1 in ref. 1). This leads to large overestimations of the degree of coordination between ln and N (θ_{Wa2D}, θ_{Wb2D}, θ_{Wc2D}). **b**, Unjustified reduction of dimensionality can lead to inferring misleading relationships between traits. The ln–N relationship from the first PCA in ref. 1 (with three significant dimensions) differs strongly from the relationship when only two dimensions are considered.

phylogenetically informed PCA reported in Table S4 of ref. 2 to estimate the angles between all pairs of traits reported in the two studies and compared them. The results are remarkably similar in this analysis (the correlation between angles from both studies is 0.97; Fig. 2c), which means that the main difference between them lies in how the functional spaces are interpreted. In the Comment, projections for the first two components are used to explore a space of three dimensions, leading to the conclusion that some aboveground and fine-root traits—such as ln and N or specific leaf area and root tissue density—were aligned[1]. However, when the appropriate dimensionalities are considered, ln and N are not strongly aligned (Fig. 1b) in either of the studies[2,3], whereas specific leaf area and root tissue density are close to orthogonal (95 degrees; Fig. 2c).

A comprehensive understanding of the relationship among plant traits can only be achieved by considering all relevant dimensions. For this, examining the angles between traits is less prone to errors than

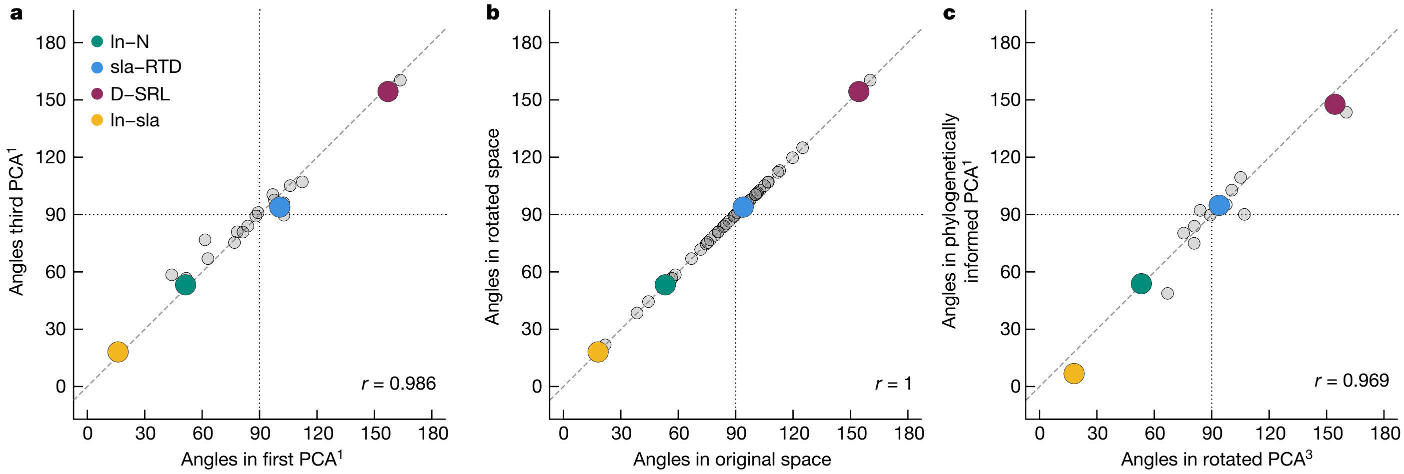

Fig. 2 | Rotation and trait selection do not affect trait relationships. a, The ‘first PCA’ (resource-acquisition traits) and ‘third PCA’ (all traits used in Carmona et al.) in the accompanying Comment[1]) show almost identical angles between pairs of traits (n = 21; r = 0.986), refuting the idea that including ph, ssd and especially sm affects the relationships between resource-acquisition traits. **b**, The angles between all pairs of traits in the non-rotated PCA and varimax-rotated spaces from Carmona et al.[2] are identical, demonstrating that varimax rotation has no effect on the inferred relationships. **c**, The angles between the common traits in the phylogenetically informed PCA in the Comment[1] and the rotated PCA in Carmona et al.[3] are almost identical (n = 15; r = 0.969), indicating that Carmona et al.[3] and Weigelt et al.[1,2] arrived to different conclusions owing to different interpretations. The ln–N (green) and sla–RTD (blue) pairs are closer to 90° than to 0° or 180°, indicating weak relationships. To facilitate comparison, four pairs of traits are displayed in different colours.

directly interpreting their loadings in PCA components; we recommend this approach to ecologists analysing multivariate trait spaces. The varimax rotation, rather than changing the characteristics of this space, can help to identify the perspective from which the genuine relationships among traits are most evident. On the basis of the available information, our results and reassessment of the results reported in Weigelt et al.[2] do not support the existence of a fast–slow conservation gradient at a global scale in which leaf and fine-root traits are aligned. Instead, we confirm that the aboveground and fine-root traits considered are not strongly correlated at a global scale, but rather organized in four main dimensions of functional variation reflecting differences in size, leaf economics, symbiosis and root tissue economics. Finally, we note that although we disagree on trait selection and data processing, the comprehensive analyses by Weigelt et al. undoubtedly advance plant trait research.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06149-7.

Reporting Summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All the data used in this paper are from Carmona et al. (2021)[3] and are available in the Figshare repository at https://doi.org/10.6084/m9.figshare.13140146.

Code availability

The code used is available in the Supplementary Information.

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Additional information
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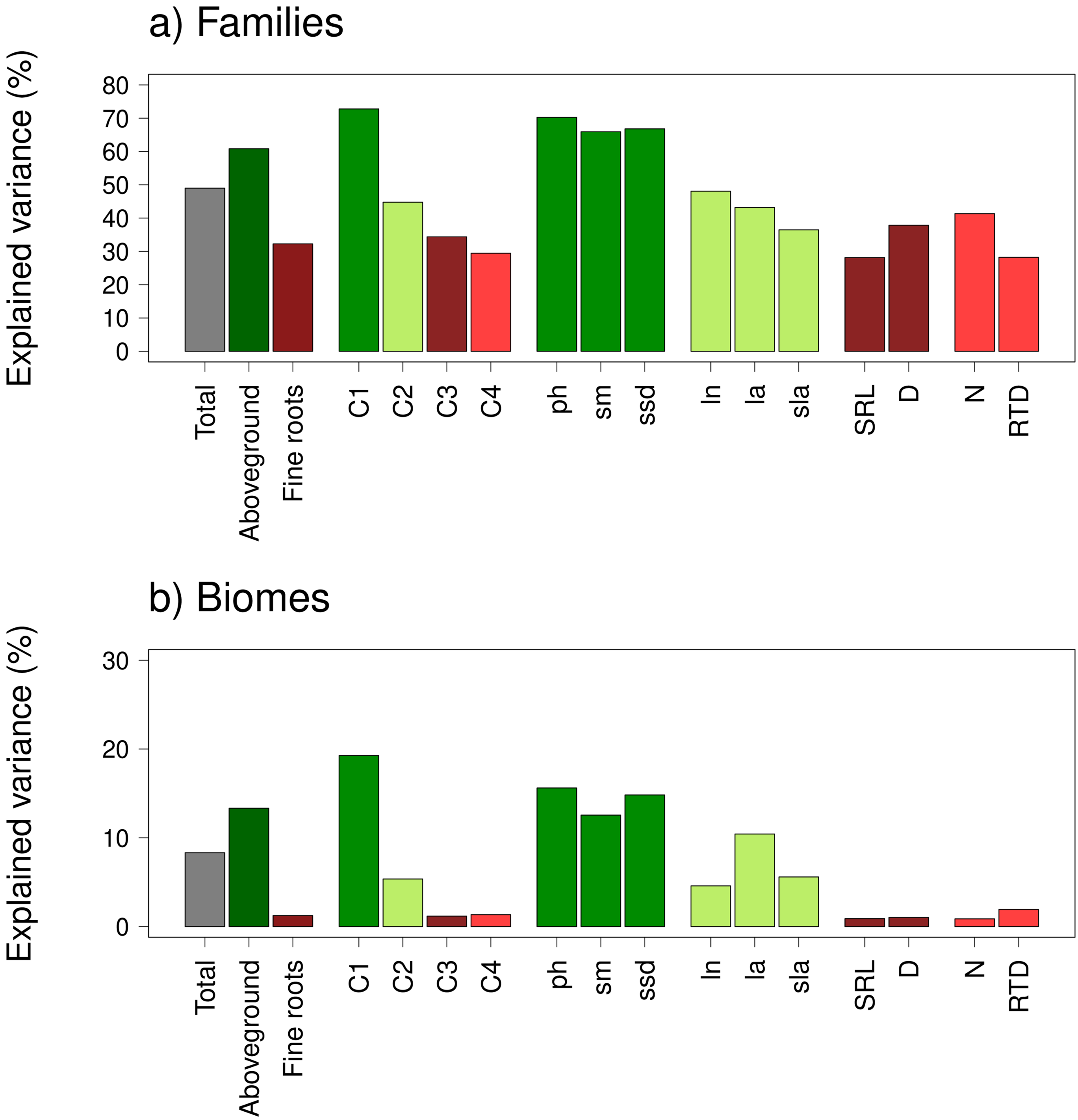

Extended Data Fig. 1 | Larger differentiation in aboveground than fine-root traits. Proportion of variance explained in PERMANOVA analyses by differences among groups of species (families and biomes, see Carmona et al.[3] for details), considering the whole functional space (Total), the aboveground and fine-root planes, individual components of the functional space and individual traits. This way, fine-root axes (C3 and C4) and traits (SRL, D, N and RTD), and leaf economics spectrum axis (C2) and traits (ln, la, sla) can be compared after removing the dominant effect of size (C1) and size-related traits (ph, sm, ssd) on differences between groups of species. High values of explained variance mean that differences between the members of one group (e.g. differences between families) account for a large proportion of the total variance (in the total space, a specific plane, a specific component or a specific trait). **a**, Differences between families in the functional space considering different scales: four-dimensional space (total), aboveground plane (in green) and fine-roots plane (in red), the individual components of the trait space (C1 to C4), and the individual traits. **b**, Differences between biomes.