

Peer Review File

Manuscript Title: Fine-root traits in the global spectrum of plant form and function

Editorial Notes: *none*

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referee #1 (Remarks to the Author):

This is a nice manuscript and I think one that has clear potential to be influential. The over-arching question motivating this research is a good one – as articulated on lines 39-40. “Thanks to the recent development of open-access fine root trait datasets, it is now possible to empirically ask how belowground traits relate to the GSPFF” [Diaz et al 2016’s Global spectrum of plant form and function – ref 3]. That is, this study is all about putting together two existing “global” datasets (one for aboveground traits, one for roots) and seeing what patterns emerge, using a variety of appropriate analyses.

The aboveground dataset (from Diaz et al 2016; ref 3 in bibliography) has information on several organs: seed mass, stem tissue density, typical adult height; and for leaves, their surface area, nitrogen concentration, and Specific Leaf Area (ratio of area to dry mass). The belowground dataset (Bergmann et al 2020; and other listed refs) concerns roots: tissue density, N concentration, diameter and Specific Root Length (ratio of length to dry mass). Diaz et al 2016 described a situation where most variation in their 6 traits was arrayed in a 2-D Principal Components plane (their Figure 2), in which a “leaf economics” (SLA – N) axis could be discerned, and also a “size axis” (seed mass, plant height). Leaf size and tissue density did not map neatly on to either of those axes. Bergmann et al 2020 found two axes in PC space: one defined by SRL and root diameter; another by root N and density (Fig 2a in that paper).

For this manuscript under review, Carmona et al sensibly combined data from these sources. All 10 traits were known for approx.. 300 species then, via statistical gap-filling (imputation), this was increased to approx.. 1200 species. Analysis of the combined datasets used both these versions (300 spp; 1200 spp).

Perhaps not surprisingly, Carmona et al’s chief analysis rediscovered the same multivariate patterns as Diaz et al (Fig 1a here; PC1 and PC2) and Bergmann et al (Fig 1b here; PC3, PC4). I have emphasised “perhaps” above, because this result certainly did not have to be the case. For example, one might reasonably have expected root N to be convincingly correlated with leaf N (e.g. as shown by Craine et al 2005 – ref. 20 here), or SRL to be correlated with SLA (as shown by a variety of past studies on herbaceous and woody seedlings) – in which case the total number of key multivariate trait dimensions might have dropped from four to three, or even perhaps two. But this was not the case. This is a seriously important result for plant functional ecology, and one counter to the somewhat glib narrative gaining popularity (despite mixed results) that there is a simple fast-slow economic trait spectrum across all tissues.

Follow-up analyses explored various additional aspects, for example demonstrating that family-level richness in aboveground traits was positively correlated with family-level richness in root traits (Fig. 3a), but considered at biome-level if anything the reverse was true (Fig. 3b). This result

is clear and interesting, as also (Lines 134-135) "...woodiness explained 36.3% of the variance of the position of species in the aboveground spectrum versus a mere 0.4% belowground, which means that the suites of fine-root traits of herbaceous and woody species are virtually undistinguishable".

COMMENTS

1. My chief concern for this analysis is whether the Varimax rotations applied to Principal Component analyses "forced" the finding that aboveground traits loaded on to different Components from those where root traits loaded. Indeed, I was very surprised not to see this aspect clearly explored/justified in a supplementary section. I would expect to see results (PC loadings) of non-rotated analyses compared with the rotated solutions. If the root traits still fall on different components to aboveground traits then, great, this make the chief finding all the more robust! If not, the authors will need to better justify considering the rotated solution as the "primary" finding. And, in reporting the results, find their way to a somewhat more nuanced description that acknowledges that the dramatic above- versus below-ground disconnect is partly artefactual.

2. My second concern for this analysis was triggered by the statement at Line 350 that "...we accounted for the study design (measurements performed on plants in situ, in pots or hydroponics)... by making a linear mixed model for each trait."

This seems potentially important. What proportion of root data were for seedlings, not for mature plants? What proportion of root data came from plants in pots? For seedlings grow with hydroponics? Put another way, what proportion of data were for field-grown plants, that is, for plants sampled in situations directly parallel to where the aboveground trait data came from? [note, for aboveground data, all data for seedlings etc were discarded] – see lines 310-312: "We removed observations that were marked as juveniles or seedlings and those done in non-natural conditions (e.g. growth chamber, greenhouse, field experiment, herbarium)..."

Why was this done for aboveground traits but not below ground traits? If it's because of the lack of root data for field situations then it should be clearly described as such, and then justified. For example, please demonstrate or cite to studies showing that root traits from pot studies (etc) reliably index root traits of field-grown plants. If this cannot be demonstrated then this potential problem should be acknowledged, discussed, etc. But perhaps there are also positives in this. Perhaps it may help reconcile the fact that seedling SLA and seedling SRL have been found tightly correlated in various past studies, but here SLA and SRL assorted on to different PCs, and were only quite weakly correlated, considered on their own (Table ED1).

Less importantly:

3. I found it hard to follow quite what was being reported in Figure 3. Is this species aggregation, is this species richness, is this species redundancy? (it seems different terms were used at different places). "SES" in caption of Figure 3 should perhaps be defined, to remind the reader, so they don't have to dig deep down in Methods. To what extent should we expect these analyses to mirror the comparisons of dissimilarity (Fig 3)? That is, are the different trends in Figs 2b and 3b surprising, important or unimportant? In seemingly discussing this (Lines 193-7) the authors instead emphasise that climate drives trait variation both above- and below-ground, which indeed seems true, but not germane to the Figs 2b vs 3b discrepancy. Perhaps all these issues could be made a bit more clear?

4. How best to describe the fact that there's one centre of data density in the multivariate analysis of root traits (Fig 1b). On lines 26-28 the authors write "...the diversity of syndromes on belowground plane is considerably lower, pointing towards a single optimal belowground strategy that is strongly selected across growth forms, families and biomes."

On face value this statement makes little sense. The phrase "a single, optimal strategy" suggests

that traits values converge so strongly that there is little or no meaningful variation. Clearly, that is not what is being reported. Or, put another way, what is this single “strategy”? – to take up water and nutrients from the soil?

Later (lines 2013), this result is reported in a more nuanced manner “Overall, these results are consistent with the idea that a relatively small number of trait syndromes are extremely prevalent, whereas many others, while viable, are rare”. This feels like a better choice of words!

I also pondered the use of the word “rare” for a while (finally figuring it’s ok), but still I was frustrated by the fact that there was no way to easily gauge how much variation there was in each root trait -- Figure ED1 has no axis tick marks or labels, which seems a bizarre omission.

Referee #2 (Remarks to the Author):

This is a most interesting manuscript that seeks to resolve variation in both above- and belowground plant traits worldwide, and specifically whether these two parts of plant functionality are linked. Such a potential link has been debated for some time but this is to my knowledge the first and best attempt to rigorously address the question.

The existence of a link between above- and belowground traits would reduce the dimensionality of current efforts to resolve global variation in plant functionality. Its absence would make the problem more difficult, or, at least, qualitatively different.

The general question posed is of fundamental importance for the rapidly emerging field of traits, plant function, and biome assembly. The overall analysis is thoughtful and important.

However, there are some potentially serious concerns which I address below. Perhaps most important is whether the argument – as presented – centers unnecessarily on a weaker part of the analysis?

Major issues:

1. Central message: It is not clear that the focus and central conclusion presented in the text and the title – lower diversity of trait syndromes below- than aboveground – is the most fundamental and potentially unbiased finding. First, this conclusion might be unnecessarily sensitive to the choice of specific traits considered in the analysis (addressed in #2, below). Second, the alternative and quantitatively strong conclusion “decoupling of the variation of above- and below-ground strategies” would seem of more fundamental significance and generality to the field. It also would seem less subject to concerns of selection bias.

Yes, the current emphasis on “diversity of trait syndromes” can be viewed as indirectly also communicating the more straight-forward above- vs. belowground decoupling message. But I fear that by centering the conclusions on the existence of a single additional dimension of trait variation above- vs. belowground, the central finding unnecessarily becomes sensitive to the biological differences introduced by the selection of traits, as described below.

A more rigorous way forward might be to first demonstrate as a central conclusion that, given the available global datasets, there is little to evidence of coupling between above- and belowground traits. This would be a new and significant finding of broad importance and interest to the field. The finding is well-supported by the quantitative analysis and less sensitive to selection bias. Parts of the text already successfully address this finding, including statements such as: “incorporating fine-root traits into the global spectrum of plant form and function adds fundamentally non-redundant information”.

This can then second be followed by a more open discussion about: (i) the potential dimensionality of the above- vs. belowground trait space, and (ii) how the results may relate to the important ecological concepts of “dissimilarity” or “functional richness/redundancy”.

2. Above- vs. belowground dimensionality: The quantitative PCA analysis appears carefully done and is impressive overall. But it is not clear whether the current central conclusion – greater above- than belowground dimensionality – is caused by biased selection of above- vs. belowground traits.

My concern is that the selected traits appear to differ qualitatively, with the aboveground trait group containing a major dimension of biological variability that is not included in the belowground group. The aboveground dataset consists of traits that do not depend strongly upon the organismal plant size (e.g., leaf nitrogen) but also a second group that are strongly size-dependent (e.g., plant height). In contrast, the belowground group includes only the former (size-independent traits) and is agnostic about the second dimension of trait variation.

This would appear a natural consequence of the difficulty of measuring size-dependent belowground traits in nature – root system biomass, sum of fine root length per plant, or rooting depth demands substantial excavation, especially for large plants. This dimension of trait variation therefore is not available in global trait datasets.

But readers will still ask: If the equivalent size-dependent traits were available also for roots, then would the analysis show that also the belowground trait space is organized in two dimensions (as the aboveground space)? And, if this is the case, then is the current focus of the manuscript on a dimensionality comparison misplaced, if not artifactual, in an otherwise important analysis?

And any such effect could likely cascade further into the inferences that extend to growth form (woody vs. herbaceous plants) or between-family differences. Inclusion of size-dependent traits only in the aboveground analysis risk the generation of statistical signals across any variables that correlate with size, including the statistical differences reported in the “functional space analysis” between woody vs. herbaceous plants (lines 126-135), and possibly between plant families (if they differ in stature; e.g., lines 135-137).

It would be helpful to see how the authors respond to these potential concerns, and whether they can address them in the text and perhaps also the quantitative analysis. Such an effort should also consider that some root traits – specifically the percent mycorrhizal colonization at a given root diameter (Fig. 1c in Ma et al., 2019, *Nature*) – have been shown to differ significantly between woody and herbaceous plant species, raising the possibility of an additional dimension of variation in belowground traits that were not considered in this analysis.

3. Redundancy and dissimilarity: The last 1/3 of manuscript offers a very interesting analysis of “redundancy” and “dissimilarity” patterns in the above- and belowground trait space. The analysis evaluates the distribution of species traits relate spatially within the PCA scaling analysis, either in 2 dimensions (above- and belowground plane analyzed separately) or 3-dimensions (total dataset analyzed).

This analysis offers some really interesting patterns by itself and when compared against climate/biome dissimilarity. The quantitative approach is described well in the methods section. However, the main text treatment of this analysis reads relatively abstract despite the long-standing importance of the “redundancy” and “dissimilarity” terms within the field of ecology.

A reader of the main text gets the sense that what is presented is an analysis of clouds of points and their distances or overlap. And this, of course, is the case, but underlying these points are real-world biological species and traits that are distributed across biomes. I would welcome a bit more effort to bring in biological realism, to the degree possible. Beyond the natural question of

whether the woody vs. herbaceous distinction (discussed above) drives the major results are issues such as: “what are the most dissimilar species pairs, and what biological characteristics appear to drive these differences?” Or, “what is the biological reason for why herbaceous species display greater redundancy belowground than woody species?” You get the idea.

4. Relation to previous work: The trait literature is vast, and it would be difficult to properly represent all previous findings and ideas. And it is understandable that comparisons are done against recent publications that have used the same fine root datasets.

The treatment could benefit, however, from comparing the ideas and results against recent similar studies. One such study (Ma et al. 2019) looked at a global dataset of 369 species with additional root traits based on first-order roots only (instead of root orders 1-3 combined). Using a two-dimensional PCA analysis similar to the present study, Ma et al. inferred “root trait organization that is functionally decoupled from the leaf economic spectrum” but based on a different set of reasoning than the present study (with emphasis on the functional role of nitrogen vs. structural traits in roots vs. leaves).

The study also observed a different organization of belowground traits than the present study. Of particular importance is the finding “that woody and herbaceous plants occupy different parts of the SRL versus root diameter relationship” and that woody and herbaceous plants differ in the pattern of mycorrhizal colonization (Fig. 1c) and in root tissue density (Fig. 1d).

This difference in findings ought to be addressed in a revised version, since the existence of a woody vs. herbaceous plants difference in root traits might introduce a second dimension of variability, analogous to what is observed aboveground. If so, the dimensional comparison may not be fundamentally different.

5. Summary: This is a potentially exceptional contribution that addresses fundamental questions about the global organization of plant traits. The dataset is strong and this is the first effort to explicitly combine above and below-ground trait data, derived symmetrically from each species, and then exposed to rigorous quantitative analysis.

However, the focus may have been placed on a weaker part of the analysis, rather than the quantitatively more powerful comparison of above vs. below-ground trait organization, as well as issues of biological redundancy and dissimilarity. If appropriately revised, the manuscript has great potential to move this field forward through a creative and new analysis.

Referee #3 (Remarks to the Author):

Vascular plant trait diversity is globally higher above- than belowground

Carmona et al.

In this manuscript, the authors combined the global spectrum of plant form and function (GSPFF), representing the functional space aboveground and the root economic space (RES) representing the functional space belowground. The combination of above and belowground functional spaces is a fundamental step towards understanding whole-plant strategies, with this study providing interesting new insights. For instance, the authors found that above and belowground functional spaces are not analogous to each other, with the belowground space providing additional information regarding plant form and function. Further, the authors provide evidence of whole-plant coordination based on their analysis of dissimilarity and redundancy among families and biomes. Overall, I find the integration of above and belowground functional spaces a priority. In addition, the authors used robust statistical analysis accompanied by a clear explanation, the code

and the data. However, I am concerned that the paper's main conclusion, i.e., that vascular plant trait diversity is globally higher above- than belowground (as stated by the title, the abstract and the conclusion), may be misleading.

As the authors stated clearly in the introduction, the aboveground functional space included traits associated with plant size, aboveground organs, and the leaf economic spectrum while the belowground space reflects fine roots; as the authors stated fine roots are equivalent to leaves due to their role in resource acquisition. The authors tested species aggregation in above and belowground spaces, finding higher aggregation when compared with null models for above and belowground spaces. For aboveground, species were clustered in two hotspots associated mostly with plant size (i.e. plant height, specific stem density, and seed mass, with a bimodal distribution separating herbaceous and trees) as shown in Díaz et al 2016. For belowground, species were clustered in one hotspot as observed in Bergmann et al 2020. Based on species aggregation and further comparisons between dissimilarity between families and biomes and PERMANOVAs, the authors conclude that vascular plant trait diversity is globally higher above than belowground. Yet, for this study, the belowground space is limited to fine roots (which will be more comparable to the leaf economic spectrum). Therefore, it is difficult to know if there is higher plant trait diversity above than belowground or if this reflects that relevant traits belowground are missing in the analysis (with this point only briefly mentioned in lines 229 - 231).

For example, strong influence of plant size included aboveground and the absence of potential analogous traits belowground could explain differences in dissimilarities between above and belowground. The authors mentioned that "21% of the family pairs presented higher dissimilarities below- than aboveground. These cases mostly belonged to pairs of families including almost exclusively herbaceous species or woody species" (lines 141 - 143); this could highlight how differences in term of plant trait diversity above and belowground may be associated with plant size and to a lesser extent to more diverse strategies in nutrient acquisition when comparing leaf and fine-roots (as mentioned in lines 220 - 222). Therefore, for me, to make a statement as the "Vascular plant trait diversity is globally higher above- than belowground", it would be required to include belowground traits which could be analogous to plant size aboveground and/or traits which represent the root system. In contrast, the authors could clearly state that, i.e., "many species with the same fine-root syndrome display contrasting aboveground traits" (as mentioned in lines 129 - 130), which maybe be less impactful but more accurate.

Referee #4 (Remarks to the Author):

The aim of the manuscript is to link the global spectrum of plant form and function (GSPFF) to the root economic space (RES) taking advantage of the recently published database on global fine root traits. After decades of functional trait research which primarily focused on the aboveground plant organs more recent advances in belowground trait analysis widened the perspective of the field. Numerous recent papers search to understand belowground trait correlations and their relationship to ecosystem functioning and there is strong interest in the question of if and how above and belowground organs align and how these functional relationships can be expressed using plant traits. It is within this light that the submitted manuscript offers a very timely analysis with importance to a broad scientific field. There have been other attempts to the same question (which are referenced) but none so far with as large a dataset as the offered manuscript. Given the large and global representation of species, this enables the authors for the first time to also draw conclusions on the distribution of various groups of plants (families, biomes) in total trait space. In addition to this general fit to the scope of the Journal, the manuscript is very clear and well written and overall good to follow. Statistical analyses appear technically sound to the best of my knowledge though I do not agree with some of the decisions in the analysis procedure or at least think there is room for better reasoning in some cases (see below). However, the overall approach is valid, the quality of data is very good and the presentation of results is of very high quality.

Despite this overall praise to the authors, I do have two points of major critique I would like to bring forth. First, I am not convinced the main or one of the main conclusions of the paper that “functional trait differentiation is consistently lower belowground than aboveground” is true. I think the paper is inherently written from an aboveground perspective while claiming a fair comparison of above and belowground traits. Yet aboveground the full spectrum of traits representing also growth form and most importantly size is considered in the analysis and compared with what belowground would only account for the leaf economics space – the fine root traits or a selection thereof. In the very last sentence of the paper it is concluded that more root traits need to be taken into account to further evaluate above- belowground trait variation and correlation but the remainder of the paper is giving the impression of equal comparison of the above and belowground plant compartments. The GSPFF includes growth form as stated by the name and this is via traits of seed mass and plant height while belowground only traits concerning economic space are included in the analysis. As stated in line 40 of the paper – “fine roots are functionally comparable to leaves” – not stems or tree trunks or seed mass or leaf size. I believe that including more and inherently different traits aboveground than belowground does not allow a “fair” comparison of the importance of root to the GSPFF and as such that the conclusions drawn from the paper when it comes to roots being less variable or explaining less variance in the data, are not sound and perhaps even partly wrong. I realize my own perspective might not be neutral on this ground, given that I am more of a root ecologist myself. Yet, being familiar with the larger part of multivariate trait analysis presented I am also aware that the number and identity of traits included in the analysis might have a large effect and in this manuscript this effect is totally dominated by plant height, seed and leaf area which is why the first axes mainly separates woody and non-woody plants while belowground this option is not available given the selected traits. With this I do not want to indicate that the analysis is not sound, I only suggest that the conclusions are better tuned to the results presented.

My second point of criticism is the large number of inferences drawn from the imputed dataset and the additional species put in the original PCA without changing the trait axes (which had been calculated based on the 301 species with full trait coverage). Basically, from line 120 onwards in the main text all further discussion is based on the imputed dataset of 1218 species. I think it is an interesting aspect of the manuscript to look at the distribution of different groups of species in the trait space. I also think that this aspect of the paper does need a critical mass of species which is higher than 300. However, to impute the data you do use phylogenetic information and the imputed dataset contains 54 more families than the dataset with full information. Still you project all additional 917 species on the same functional space created with the complete dataset of only 301 species (line 125) rather than calculate a second PCA based on the imputed data. All the following conclusions are based on this procedure of which I am not fully convinced.

Further comments:

- Line 71: Varimax rotation is not without criticism in the community. I am not saying I would advise not to use it as in this case but I think a good justification beyond just “where traits are best related to axes” would be recommendable. This is especially important as you later map species positions in your so called trait planes. I am sure you are fully aware of this discussion and also guess that there has been a discussion in the group of authors about this point, but rotated PCA axes are strictly speaking not orthogonal which does have important implications for your conclusions. I recommend to give your line of thought more justification including perhaps also the original PCA for reference.
- I do wonder why the authors did not use phylogenetically corrected data for the analysis. They do use phylogenetic information for the imputed data but not the main analysis. Why not? Non-phylogenetic data might exaggerate the result of the main PCA were most variance on the first axis explains the divergence between herbaceous species and angiosperm trees.
- Line 87 ff: It is not entirely clear from this paragraph which subset of species (301, imputed data set or other) was mapped and analysed here. The methods refer to the 301 for observed which should be mentioned also in the figure legend for clarity.
- Line 113: which traits have been dropped?
- Line 122ff: The imputed dataset is a critical issue for me. Extended table 1 states the number of species per trait from which data needed to be imputed. From that table it is hard to see how only

15.4 % of data was imputed overall given that e.g. for root N more than 30% of trait info was missing. Please explain.

- Line 129 ff: this is the type of conclusion I am referring to above. I am not convinced this is true.
- Line 217: " we found that plants differentiate preferentially in the above- rather than in the belowground part of this functional trait space" while before in most cases the correct relation between GSPFF and fine root traits is mentioned, this sentence is much more general. See my first major comment.
- Line 339: did you at some point calculate species mean trait values? I did not see this mentioned.
- Line 377: Why did you use phylogenetic information here but not use phylogenetically corrected data?
- Line 414: It appears that the examination of the belowground plane is a repetition of the Bergmann et al. paper. Why would you exactly repeat that here? To show they were correct of that those results can be reproduced? Seems strange to me.
- Line 484: Did I understand correctly that you mapped the imputed data onto the original trait space (300 species) and calculated dissimilarities based on these matrices?
- Extended Data Fig 1: While this figure nicely shows the difference between the shared species and the full dataset, it does not show the difference between the imputed (on which a large part of the manuscript is based) and the full dataset. Distribution of data for plant height differs clearly for subset and full set. Subset height is more dichotomous than full set?
- Figure 2b – enlarge writing in the graph.

Author Rebuttals to Initial Comments:

We are very grateful for the opportunity to submit a revised version of our manuscript to be considered for publication in *Nature*. We would like to thank all referees for their very constructive comments that have greatly aided us in producing an improved version of our manuscript. Below, we provide extended explanations to each particular point, explaining in deeper detail our methodological choices and how we have modified the analyses and the manuscript following the referees' recommendations (**response text is in black font colour and referees' comments in blue**).

Referees' comments:

Referee #1 (Remarks to the Author):

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because this result certainly did not have to be the case. For example, one might reasonably have expected root N to be convincingly correlated with leaf N (e.g. as shown by Craine et al 2005 – ref. 20 here), or SRL to be correlated with SLA (as shown by a variety of past studies on herbaceous and woody seedlings) – in which case the total number of key multivariate trait dimensions might have dropped from four to three, or even perhaps two. But this was not the case. This is a seriously important result for plant functional ecology, and one counter to the somewhat glib narrative gaining popularity (despite mixed results) that there is a simple fast-slow economic trait spectrum across all tissues.

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R1: We understand the reviewer’s concern here and agree that we should have explained in greater detail the reasons that led us to choose to perform the varimax rotation. When performing our original analyses, we started examining the correlation matrix between traits considering the full database including 1,719 species with at least one aboveground and one fine-root trait measured (as reported in the manuscript and shown as “full dataset” in ED Fig. 1). Note that these correlations between pairs of variables did not include any imputed information, but rather considered all observations (species) that had empirical information for the considered pair of traits. We then performed an eigenanalysis (singular value decomposition) on the pairwise correlation matrix, which is shown in full detail in Table R1 below and Fig. R1a, and

included as ED Table 2 in the new version of the manuscript. Results suggested that four principal components should be retained (eigenvalues being > 1 , and accounting for 75% of the total variation). The eigenvectors of the traits in these four first principal components revealed the general structure that we report in our manuscript: a first principal component associated with size-related traits analogous to the first principal component in the GSPFF of Díaz et al. (2016); a second principal component related to leaf traits, also analogous to the second component of Díaz et al. (2016) (see ED Table 1 in Díaz et al. 2016 for the loadings of the aboveground traits in the GSPFF); a third principal component reflecting the specific root length-root diameter trade-off, corresponding with the first component in Bergmann et al. (2020), and also in Ma et al. (2018); and a fourth principal component reflecting the root tissue density-root nitrogen content per mass trade-off, again analogous the second principal component in Bergmann et al. (2020). These results strongly suggested that the four-dimensional space can be interpreted as being organised in two planes: one (PC1-PC2) corresponding with the aboveground traits and the other one (PC3-PC4) with the fine-root traits. As very well pointed out by the referee, this result is far from trivial and is against the notion of a single “whole-plant economics” spectrum.

Indeed, the lack of completeness of the full dataset did not allow us to find scores for the species in the space created this way. Because this is the first time that these general patterns are reported, we opted for the most conservative approach possible, which was to present a functional space based on the 301 species with complete empirical trait measurements for the ten traits considered (the “complete” dataset). When performing this analysis, we started with a simple, non-rotated, PCA. In agreement with the PCA based on the full dataset, our analyses revealed that the space based on the 301 complete species has fundamentally four dimensions of variation, as we report in the manuscript. The loadings of the first four principal components of the non-rotated PCA (Table R2, which is also included in ED Table 2) have a correlation of 0.98 with the loadings of the PCA based on the full dataset that we report above, showing that they reflect the same fundamental structure. Despite this, there were some inconsistencies regarding the loadings of leaf-related traits, which showed a less clear linkage to PC2, with loadings somewhat evenly divided between PC2 and PC3. We think that these inconsistencies are due to minor differences in the correlation between some pairs of traits in the full and complete dataset, which are shown in ED Fig. 1, as pointed out by referee #4 below. These inconsistencies reflect slight differences in the structure of trait data between the full and complete datasets. For example, the full dataset includes a higher proportion of species of small stature, reflecting the fact that larger species tend to be better studied than smaller species. As a result, the

simple structure revealed in the eigenanalysis of the full dataset was somewhat “hidden” in the complete species dataset (Fig. R1c).

Table R1. Results of the eigenanalysis (eigenvalues and eigenvectors) of the correlation matrix between pairs of traits in the full dataset (1,719 species with at least one measurement for both the aboveground and fine-root traits considered). The first four principal components (PC) encompass > 75% of the variation in the data and are the only ones with eigenvalues > 1. We have underscored in bold the highest loading of each trait in these four PCs, revealing a general pattern of separation between aboveground and fine-root traits in two orthogonal planes. Aboveground traits are specific leaf area (sla), leaf nitrogen concentration (ln), leaf area (la), seed mass (sm), plant height (ph) and stem specific density (ssd). Fine-root traits are specific root length (SRL), root diameter (D), root tissue density (RTD) and nitrogen concentration (N).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
eigenvalue	2.70	1.96	1.72	1.14	0.89	0.48	0.41	0.36	0.22	0.13
% cumulative variation	27.04	46.61	63.77	75.17	84.03	88.82	92.92	96.51	98.68	100
ph	0.5	0.15	-0.24	0.12	-0.06	-0.05	0.24	-0.41	-0.66	0.04
ssd	0.52	-0.08	-0.17	0.14	0.12	-0.19	0.15	-0.31	0.71	-0.03
sm	0.44	0.29	-0.12	0.01	0.11	-0.35	-0.29	0.69	-0.08	-0.01
la	0.16	0.45	-0.26	-0.23	-0.36	0.69	-0.08	0.06	0.19	-0.04
ln	-0.27	0.44	-0.23	-0.19	0.29	-0.26	-0.53	-0.45	0.02	-0.1
sla	-0.32	0.35	-0.29	-0.26	-0.13	-0.37	0.66	0.13	0.1	0.13
SRL	-0.18	-0.29	-0.57	0.26	-0.22	-0.05	-0.05	0.1	-0.04	-0.65
D	0.08	0.36	0.6	0.03	-0.21	-0.15	0.14	-0.09	0.03	-0.64
RTD	0.17	-0.25	-0.04	-0.69	0.49	0.15	0.18	0.06	-0.09	-0.35
N	-0.14	0.31	-0.04	0.51	0.64	0.34	0.26	0.12	0	-0.1

Table R2. Loadings (eigenvectors) of the considered traits in the four selected principal components in the PCA (unrotated) considering the 301 species with complete empirical information for all traits.

	PC1	PC2	PC3	PC4
ph	0.501	0.111	-0.217	0.159
ssd	0.488	-0.067	-0.182	0.253
sm	0.433	0.294	-0.141	0.003
la	0.154	0.381	-0.411	-0.194
ln	-0.306	0.437	-0.292	-0.025
sla	-0.334	0.309	-0.353	-0.202
SRL	-0.152	-0.427	-0.501	0.246
D	0.058	0.471	0.515	0.114
RTD	0.167	-0.128	-0.028	-0.715
N	-0.201	0.212	-0.065	0.496

In this sense, we think it is also important to show that when the PCA is performed using the dataset with imputed species (1,218 species), as we do now (following the suggestions of referee #4; see **R12**), the loadings of individual traits in the principal components are again more clearly aligned with a single principal component (as in the case of the full dataset), so that the varimax rotation does not add to the interpretation in this case (Fig. R1e-f). Moreover, in the light that our imputation procedure has very high accuracy (see **R16** below, new Supplementary Methods 1: Reliability of the imputation procedure, and lines 425-429 in the new version of the manuscript), it could be argued that the PCA based on the imputed dataset is actually more closely replicating the underlying “real” functional structure of the dataset. In fact, it has been shown that imputed datasets are better able to reflect underlying fundamental relationships among traits than datasets in which species with missing values are removed (Penone *et al.* 2014).

Following these observations, we decided to perform a varimax rotation of the retained four components, to facilitate the interpretation of results. In cases like the one we have here, in which the data follow a clear model of organization with clear orthogonality between groups of variables (see more detailed analyses in Supplementary Methods 2: Exploration of the structure of the functional space), varimax rotation is likely to provide a more replicable solution, which is less subject to particularities of the considered dataset (Abdi & Williams 2010). This is clearly exemplified by the similarity between the varimax-rotated PCAs for the full, complete and imputed datasets shown in Fig. R1 b, d and f, respectively. Note that varimax is an orthogonal rotation, which means that the relative position of species after the rotation is unchanged (the Procrustes correlation between the position of species in the functional space before and after rotation is 0.995). The main advantage of this

approach is that each original trait is now fundamentally associated with one component, and each component represents only a reduced number of traits. Most importantly, the varimax procedure does not “force” the separation of aboveground and fine-root traits. In fact, the algorithm does not “know” how the original variables (traits) are classified into such groups, which in turn means that the set of traits with high loadings in the same component does not depend on *a priori* trait grouping (i.e. is not artefactual). Rather, it retrieves the fundamental structure of trait variation in the dataset in a more interpretable and consistent (i.e. less dependent on the specific subset of species considered) way.

In summary, we are confident that the disconnection between aboveground and fine-root traits is real, and not an artefact of our analysis, and we believe that we show this point more clearly now. In the new version of the manuscript, we have described in detail the reasoning for performing the varimax rotation, and we have included a new section (Supplementary Methods 2) explaining the data exploration procedure that led us to prefer the use of the varimax rotation, as well as a new ED Table 2 reporting the non-rotated and rotated PCA spaces for the full (1,719 species), imputed (1,218 species) and complete (301 species) datasets.

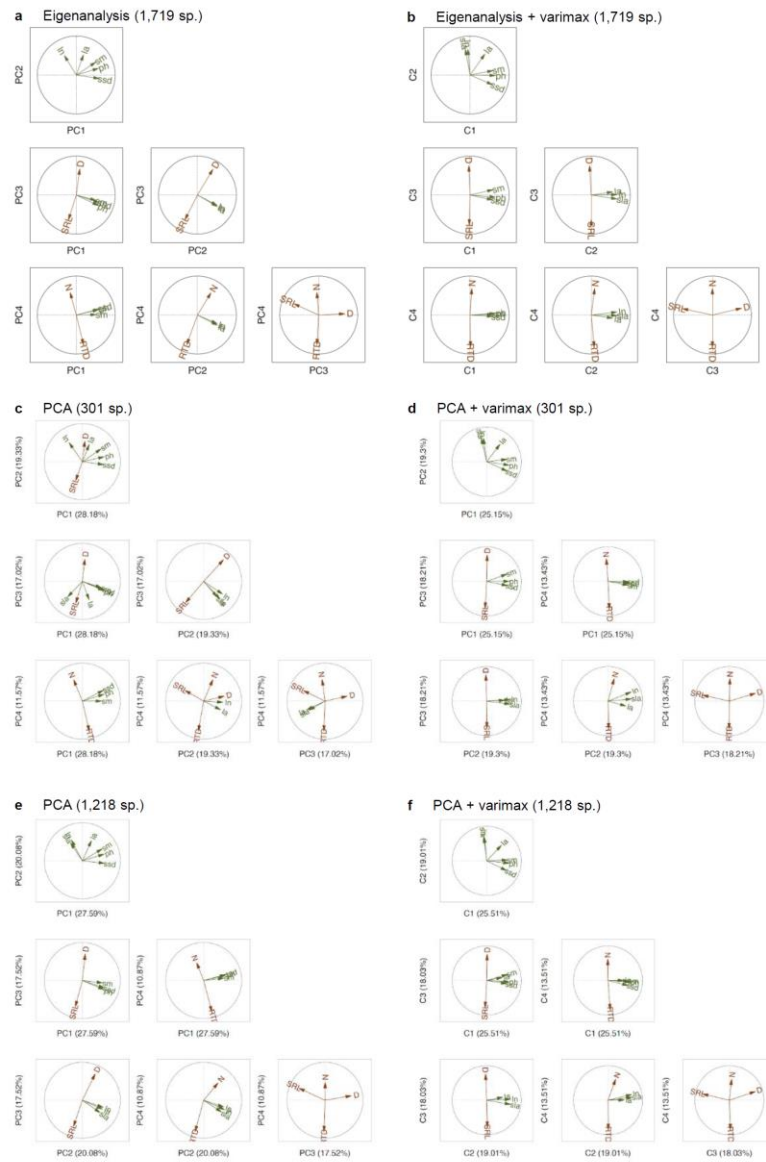


Fig. R1. Functional space considering aboveground and fine-root traits of species for different datasets. **a** eigenanalysis considering the species common to both the aboveground and fine-root traits datasets ($n = 1,719$), **b** followed by varimax rotation. **c** original PCA without rotation considering species with complete information for all selected traits ($n = 301$), **d** followed by varimax rotation. **e** original PCA without rotation considering species with complete information for all selected traits plus species with imputed trait values ($n = 1,218$), **f** followed by varimax rotation. Aboveground traits are shown in green colour and fine-root traits in brown. Each panel shows a combination of two of the four principal components that define the full plant spectrum. Only those traits that had a loading of at least 0.35 in any of the represented components are shown to improve visualization.

2. My second concern for this analysis was triggered by the statement at Line 350 that “...we accounted for the study design (measurements performed on plants in situ, in pots or hydroponics)... by making a linear mixed model for each trait.”

This seems potentially important. What proportion of root data were for seedlings, not for mature plants? What proportion of root data came from plants in pots? For seedlings grow with hydroponics? Put another way, what proportion of data were for field-grown plants, that is, for plants sampled in situations directly parallel to where the aboveground trait data came from? [note, for aboveground data, all data for seedlings etc were discarded] – see lines 310-312: “We removed observations that were marked as juveniles or seedlings and those done in non-natural conditions (e.g. growth chamber, greenhouse, field experiment, herbarium)...”

Why was this done for aboveground traits but not below ground traits? If it's because of the lack of root data for field situations then it should be clearly described as such, and then justified. For example, please demonstrate or cite to studies showing that root traits from pot studies (etc) reliably index root traits of field-grown plants. If this cannot be demonstrated then this potential problem should be acknowledged, discussed, etc. But perhaps there are also positives in this. Perhaps it may help reconcile the fact that seedling SLA and seedling SRL have been found tightly correlated in various past studies, but here SLA and SRL assorted on to different PCs, and were only quite weakly correlated, considered on their own (Table ED1).

R2: We aimed to prepare the data in the same way as the previous papers by Diaz et al. (2016) for aboveground traits and Bergmann et al. (2020) for fine-root traits. Therefore, there were slight differences in how the data was processed prior to analyses between the aboveground and fine-root datasets.

Unfortunately, the GRooT database does not provide information on whether the root data were measured on seedlings or on mature plants. Since fine roots are relatively young regardless of plant age (Wells & Eissenstat 2002), we expect that the data is not strongly affected by plant age (Garbowski *et al.* 2021). On the other hand, we removed seedling data for aboveground traits since plant age has strong impacts on most aboveground traits (plant height, leaf area) and seed mass cannot be measured for seedlings.

After removing ferns and dead roots from the GRooT database, and retaining only fine-root data, a majority of the trait measurements were done in natural conditions (67% of observations, including field observations and field experiments), 32% of observations came from potted experiments and <0.1% from hydroponic experiments. The rest (~0.5%) were unspecified. Hydroponic

experiment data only included 2 species (*Oryza sativa* and *Citrus volkameriana*), both of which also had data from field studies and pot experiments. Note that these different data exclusion approaches apply to raw data and have less impact on the estimated species averages used in the final analyses since most species have data from different sources. Moreover, for both aboveground and fine-root data, outliers ($\pm 3SD$ of species average) were also removed, further diminishing the effect of differential raw data origins.

Although trait values measured in different environmental conditions vary, the species rankings generally remain the same (see examples for plant species in Australia Mokany & Ash 2008, and in Europe Dostál *et al.* 2020). Field data was available for 69%-83% (depending on the considered trait) of the species in the GRooT database. In fact, considering only field data, the species average root trait values were highly correlated with the data in which also other data sources were included ($r > 0.97$; Table R3).

Table R3. Number of species including field and pot data and only field data for each fine-root trait, and correlation (Pearson) between the trait values estimated from both sources.

Trait	No. of species (all)	No. of species (only field data)	%	r
SRL	1736	1224	0.71	0.98
D	1592	1150	0.72	0.97
RTD	1390	929	0.69	0.97
N	1253	1043	0.83	0.98

For comparison, we repeated the procedure to estimate the functional space (PCA followed by varimax rotation) after excluding fine-root data that did not come from field observations. However, the resulting functional space was extremely similar to the one reported in the manuscript (the Pearson correlation between the loadings of traits in the components was 0.97, whereas the comparison of the relative position of species common to both analyses through Procrustes analysis yielded a value of 0.95, $p = 0.00001$ with 100,000 permutations). Indeed, the number of species with complete empirical information for the ten considered traits was lower (207 species vs 301 in the original analysis). Given that the impact of considering or not root data from non-field conditions seems minimal, but excluding this data would result in the loss of around one-third of the species in the dataset with complete empirical observations, we have decided to keep the fine-root data from non-field conditions in the main analyses presented in the manuscript, while reporting

(in ED Table 2c) the main characteristics of the functional space obtained after excluding fine-root data that did not come from field observations.

Less importantly:

3. I found it hard to follow quite what was being reported in Figure 3. Is this species aggregation, is this species richness, is this species redundancy? (it seems different terms were used at different places). “SES” in caption of Figure 3 should perhaps be defined, to remind the reader, so they don’t have to dig deep down in Methods. To what extent should we expect these analyses to mirror the comparisons of dissimilarity (Fig 3)? That is, are the different trends in Figs 2b and 3b surprising, important or unimportant? In seemingly discussing this (Lines 193-7) the authors instead emphasise that climate drives trait variation both above- and below-ground, which indeed seems true, but not germane to the Figs 2b vs 3b discrepancy. Perhaps all these issues could be made a bit more clear?

R3: The SES values reported are the result of a null model in which the amount of functional space that a specific group (i.e. growth form, family, biome) occupies is expressed in relation to the average amount of space that a group with the same number of randomly-selected species is expected to occupy. Values of SES larger than 0 mean that the species in the considered group are more dispersed (i.e. occupy more space) than expected by chance, and vice versa. As such, both species “aggregation” and “redundancy” would be adequate ways of expressing the concept, with smaller SES values corresponding to groups in which species are more densely aggregated between them, and hence functionally more redundant. We understand that using both terms interchangeably can lead to confusion, and we used “redundancy” more consistently throughout the text in the new version of the manuscript. Most importantly, we have inverted the sign of the SES values, so that they better correspond to the notion of redundancy (i.e. after changing the sign, positive SES values indicate high redundancy, and negative SES values indicate low redundancy). We have also expanded the explanations that we give in the caption of Figure 3, as suggested.

Regarding the difference between dissimilarity and redundancy, whereas redundancy (i.e. -SES of functional richness) expresses a property of each group (i.e. within groups), dissimilarities reflect the differences between groups. In this case, the dissimilarity between any given pair of groups (e.g. between two biomes or two families) is estimated as one minus the overlap in the functional space between the groups. If two groups occupy a similar part of the functional space, then the dissimilarity between them should be small. In contrast, if the two groups occupy different regions of the functional space, the dissimilarity between them should be large. Note that these two properties (redundancy and

dissimilarity) are fundamentally different; for example, two groups can differ largely in their SES values (because one is composed of very redundant species and the other is composed of relatively different species) but occupy the same portion of the functional space, in which case dissimilarity will be low. Therefore, the trends that we report in Fig. 2b and 3b are conveying different (but complementary) messages: while in Figure 2b we show that the dissimilarity among biomes aboveground and belowground is positively correlated (i.e. that biomes that occupy different areas of the aboveground plane also occupy different areas of the fine-root plane), in Fig 3b we show that biomes that have redundant species in terms of their aboveground traits tend to have less redundant species in terms of fine-root traits and vice versa. In this regard, it seems particularly interesting that the relationship between redundancy in aboveground and fine-root traits is fundamentally different between families and biomes. We have added new panels to Fig. 3 to better show the influence of climate on these differences.

4. How best to describe the fact that there's one centre of data density in the multivariate analysis of root traits (Fig 1b). On lines 26-28 the authors write "...the diversity of syndromes on belowground plane is considerably lower, pointing towards a single optimal belowground strategy that is strongly selected across growth forms, families and biomes." On face value this statement makes little sense. The phrase "a single, optimal strategy" suggests that traits values converge so strongly that there is little or no meaningful variation. Clearly, that is not what is being reported. Or, put another way, what is this single "strategy"? – to take up water and nutrients from the soil?

Later (lines 2013), this result is reported in a more nuanced manner "Overall, these results are consistent with the idea that a relatively small number of trait syndromes are extremely prevalent, whereas many others, while viable, are rare". This feels like a better choice of words!

R4: We agree with the referee's point here, and have modified the text, removing the reference to an "optimal" strategy in fine-roots and focusing instead on the large differences in the prevalence of different suites of traits.

I also pondered the use of the word "rare" for a while (finally figuring it's ok), but still I was frustrated by the fact that there was no way to easily gauge how much variation there was in each root trait -- Figure ED1 has no axis tick marks or labels, which seems a bizarre omission.

R5: We have modified Fig. ED1 to include axis labels and tick marks.

Referee #2 (Remarks to the Author):

This is a most interesting manuscript that seeks to resolve variation in both above- and belowground plant traits worldwide, and specifically whether these two parts of plant functionality are linked. Such a potential link has been debated for some time but this is to my knowledge the first and best attempt to rigorously address the question.

The existence of a link between above- and belowground traits would reduce the dimensionality of current efforts to resolve global variation in plant functionality. Its absence would make the problem more difficult, or, at least, qualitatively different.

The general question posed is of fundamental importance for the rapidly emerging field of traits, plant function, and biome assembly. The overall analysis is thoughtful and important.

However, there are some potentially serious concerns which I address below. Perhaps most important is whether the argument – as presented – centers unnecessarily on a weaker part of the analysis?

Major issues:

1. Central message: It is not clear that the focus and central conclusion presented in the text and the title – lower diversity of trait syndromes below- than aboveground – is the most fundamental and potentially unbiased finding. First, this conclusion might be unnecessarily sensitive to the choice of specific traits considered in the analysis (addressed in #2, below). Second, the alternative and quantitatively strong conclusion “decoupling of the variation of above- and below-ground strategies” would seem of more fundamental significance and generality to the field. It also would seem less subject to concerns of selection bias.

Yes, the current emphasis on “diversity of trait syndromes” can be viewed as indirectly also communicating the more straight-forward above- vs. belowground decoupling message. But I fear that by centering the conclusions on the existence of a single additional dimension of trait variation above- vs. belowground, the central finding unnecessarily becomes sensitive to the biological differences introduced by the selection of traits, as described below.

A more rigorous way forward might be to first demonstrate as a central conclusion that, given the available global datasets, there is little to evidence of coupling between above- and belowground traits. This would be a new and significant finding of broad importance and interest to the field. The finding is well-supported by the quantitative analysis and less sensitive to selection bias. Parts of the text already successfully address this finding, including

statements such as: “incorporating fine-root traits into the global spectrum of plant form and function adds fundamentally non-redundant information”.

This can then second be followed by a more open discussion about: (i) the potential dimensionality of the above- vs. belowground trait space, and (ii) how the results may relate to the important ecological concepts of “dissimilarity” or “functional richness/redundancy”.

R6: We agree with the referee that the main message of the manuscript can be more strongly focused on the fact that we do not find any strong correlation between aboveground and fine-root traits, whereas the patterns of redundancy and dissimilarity should play a more secondary role. In accordance with this, we have modified several parts of the main text, including the title (now changed to “*Fine-root traits expand the global spectrum of plant form and function*”), the first paragraph (whose last sentence now reads: “Addition of fine-root traits increases the dimensionality of the GSPFF, highlighting the importance of considering belowground traits in the quest to define a global spectrum of whole-plant form and function”, lines 29-31), added different examples showing that the aboveground trait syndrome of a species doesn’t tell much about what its fine-root trait values are (e.g. lines 129-131, lines 133-138, lines 160-163), and discuss more clearly that our results do not support the plant economics spectrum hypothesis (lines 184-188, lines 232-234).

2. Above- vs. belowground dimensionality: The quantitative PCA analysis appears carefully done and is impressive overall. But it is not clear whether the current central conclusion – greater above- than belowground dimensionality – is caused by biased selection of above- vs. belowground traits.

My concern is that the selected traits appear to differ qualitatively, with the aboveground trait group containing a major dimension of biological variability that is not included in the belowground group. The aboveground dataset consists of traits that do not depend strongly upon the organismal plant size (e.g., leaf nitrogen) but also a second group that are strongly size-dependent (e.g., plant height). In contrast, the belowground group includes only the former (size-independent traits) and is agnostic about the second dimension of trait variation.

This would appear a natural consequence of the difficulty of measuring size-dependent belowground traits in nature – root system biomass, sum of fine root length per plant, or rooting dept demands substantial excavation, especially for large plants. This dimension of trait variation therefore is not available in global trait datasets.

But readers will still ask: If the equivalent size-dependent traits were available also for roots, then would the analysis show that also the

belowground trait space is organized in two dimensions (as the aboveground space)? And, if this is the case, then is the current focus of the manuscript on a dimensionality comparison misplaced, if not artifactual, in an otherwise important analysis?

And any such effect could likely cascade further into the inferences that extend to growth form (woody vs. herbaceous plants) or between-family differences. Inclusion of size-dependent traits only in the aboveground analysis risk the generation of statistical signals across any variables that correlate with size, including the statistical differences reported in the “functional space analysis” between woody vs. herbaceous plants (lines 126-135), and possibly between plant families (if they differ in stature; e.g., lines 135-137).

It would be helpful to see how the authors respond to these potential concerns, and whether they can address them in the text and perhaps also the quantitative analysis. Such an effort should also consider that some root traits – specifically the percent mycorrhizal colonization at a given root diameter (Fig. 1c in Ma et al., 2019, *Nature*) – have been shown to differ significantly between woody and herbaceous plant species, raising the possibility of an additional dimension of variation in belowground traits that were not considered in this analysis.

R7: Thank you for these important comments. Indeed, our aim in this manuscript is to incorporate fine-roots trait data into the global spectrum of plant form and function (as we make clearer now, including, among other things, a new title for the manuscript). We agree with the referee that the full dimensionality of the plant trait space is most likely higher than what we show here, since we have not considered all belowground traits that are likely to be important for plant biology. Therefore, the use of the term “belowground” to refer to the plane in the functional space that is related to fine-root traits was not optimal. In the new version of the manuscript, we have thoroughly revised the text to make clear that we are dealing with fine root traits, which are not the only relevant belowground traits. This topic was already acknowledged in a key part of the previous version of the manuscript (the last sentence of the main text: “Future inclusion of other belowground traits beyond fine-root traits, such as root architectural traits or mycorrhizal traits will further improve our understanding of the full strategy of plant species”); however, in the current version we are more straightforward about this point, particularly adding a new sentence right before the aforementioned one: “The belowground trait space is likely to have more dimensions beyond fine-root traits, partially independent or highly associated with those aboveground, but enough empirical data are not yet available to adequately test these ideas.” Below, we respond in more depth to each of the specific issues raised by the referee

LACK OF SIZE TRAITS BELOWGROUND: Considering the rewording we have done throughout the manuscript, the inclusion of size-related traits aboveground but not belowground becomes less relevant (since size-dependent traits are not relevant when discussing fine-root traits). However, we have attempted to collect data for traits related to the size of the root system. The GRooT database includes whole-root system traits as well, of which root mass fraction (root-shoot ratio), lateral spread and maximum rooting depth can be considered to be related to root size and have data for >1000 species (Table R4).

Table R4. *Number of species including data for root traits related to the size of the root system.*

Trait	Units	Acronym	No. of obs.	No of sp.
Root mass fraction	g/g	rmf	15,475	1,317
Lateral spread*	cm/y	ls	1,353	1,329
Maximum rooting depth	m	mrd	2,656	1,051

* All lateral spread observations included in GRooT come from the same source (the CLOPLA database)

However, as rightly pointed out by the referee (and summarized in the table above), the availability of size-related root traits is actually quite low. For obvious reasons, it does not make sense to use data from pots for root size traits, so we removed those, losing most of the root mass fraction data. There were only seven species (five of them grasses, none woody) with empirical data for all the root traits (the four fine-root traits plus the three size-related traits). If we select only one of the size-related traits (plus the four fine-root ones), then 44 species are left in the case of root mass fraction, 39 species for lateral spread, and 75 species for maximum rooting depth. These numbers are before accounting for species for which there is information for aboveground traits. If we include the aboveground traits, then we get:

- 7 species with all 13 traits (aboveground + fine-root + root size)
- 40 species with the 10 original traits + rmf
- 35 species with the 10 original traits + ls
- 62 species with the 10 original traits + mrd

Obviously, this low data availability precludes us from including this trait in the main analyses. However, we still explored the possibility raised by the referee that including root size traits might increase the dimensionality of the

belowground part of the space. For this, we used the full database including the 1,719 species with at least one aboveground and one belowground trait measured (as reported in the manuscript and shown as “full dataset” in ED Fig. 1). There were mrd data (the root-size trait with most data) for 270 of these species. In a procedure analogous to the one explained in R1 above (and in Supplementary Methods 2 in the new version of the manuscript), we estimated the correlation between mrd and the other ten traits considering all observations that have empirical information for the considered pair of traits. The correlation matrix revealed that mrd is weakly associated with the fine-root traits (Pearson correlations are 0.07 with root diameter, 0.04 with root tissue density, 0.03 with root nitrogen, -0.19 with specific root length), intermediately correlated to leaf traits (0.22 with leaf area, -0.09 with leaf nitrogen, -0.27 with specific leaf area) and more strongly correlated with size traits: plant height (0.54), specific stem density (0.47) and seed mass (0.49).

We then performed an eigenanalysis (singular value decomposition) on the pairwise correlation matrix. The eigenvalues suggested that adding root size does not change the dimensionality of our space, with only the first four principal components (which accounted for 73% of the total variation) having eigenvalues > 1 (the fifth eigenvalue was 0.90). Maximum rooting depth loaded most strongly on the first component, following the same direction as the aboveground size-related traits (see Fig. R2).

The fact that belowground size correlates with aboveground size is not surprising, and in line with more detailed assessments of biomass allocation patterns (Enquist & Niklas 2002; Niklas 2005). Given the low availability of mrd data, whose inclusion would dramatically reduce the number of species that we are able to map onto the functional space, we prefer not to include these results in the manuscript. Instead, in addition to the aforementioned rewording of the text to make clear that we only consider fine-root traits, we have included the aforementioned sentence in the discussion that acknowledges the possibility that root systems can have more dimensions that remain to be explored in the future when considerably more data becomes available.

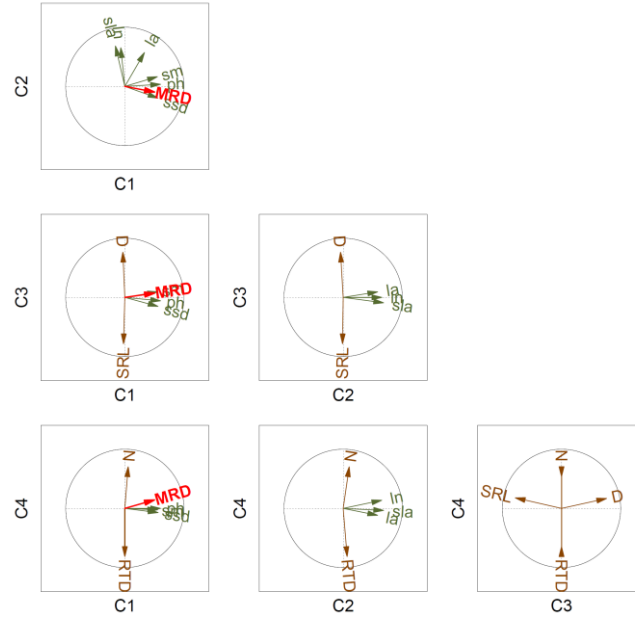


Fig. R2. Functional space defined by an eigenanalysis (followed by varimax rotation) of the correlation matrix between traits in the full dataset (1,719 species) after adding maximum root depth (MRD). Aboveground traits are shown in green colour, fine-root traits in brown, and MRD in red. Each panel shows a combination of two of the four components that define the full plant spectrum. Only those traits that had a loading of at least 0.4 in any of the represented components are shown to improve visualization.

POTENTIAL EFFECT OF SIZE ON RESULTS: Given the lack of size-related traits belowground, and understanding the referee's concern about their potential effects on patterns, we also performed a different estimation of the functional space after excluding the size-related traits aboveground (traits strongly related to the first component: plant height, specific stem density and seed mass). We used the same procedure as in the main analysis: estimation of the dimensionality of the space using Horn's parallel analysis, and PCA followed by varimax rotation of the retained components. By only keeping leaf and fine-root traits, we checked the robustness of the functional space to the removal of size-related traits. The space generated this way had three non-redundant dimensions that clearly corresponded to the three dimensions of the main space (built with ten traits), except, naturally, the size dimension. The first dimension corresponded to the leaf traits, the second represented the root-diameter-specific root length trade-off, and the third was the root economics dimension that confronts root nitrogen with root tissue density (Table R5).

Table R5. Loadings (eigenvectors) of the traits in a varimax-rotated PCA performed after excluding size-related traits ($n = 301$ species)

	C1	C2	C3
%Variance	25.7	25.2	20.2
la	0.50	-0.08	-0.30
ln	0.60	-0.02	0.29
sla	0.60	0.11	0.15
SRL	0.00	0.70	0.13
D	-0.01	-0.70	0.18
RTD	0.01	0.03	-0.62
N	0.14	-0.01	0.60

We think that this complementary analysis clearly shows that the orthogonality between leaf and fine-root traits is maintained even when size traits are not considered and is hence not an artefact of considering size only aboveground. In any case, given that our goal was to add fine-root traits to the GSPFF, we have decided to keep the full set of traits in the analyses (i.e. including size).

EFFECT OF SIZE-RELATED TRAITS ON PATTERNS OF DIFFERENTIATION: We understand the referee’s comment stating that the fact that the aboveground plane includes size-related traits—which are indeed very much associated with differences between woody and herbaceous species and differences between families—, could strongly influence these comparisons. We think this issue is fundamentally solved by not referring anymore to “belowground” diversity as we did in the previous version of the manuscript, but rather to diversity in the fine-root plane. We still think it is interesting to compare the patterns between the two planes that compose the defined space (the aboveground plane and the fine-root plane), since it yields novel information about the global organization of species in the functional space, and the distinction between the selected aboveground traits and fine-root traits is still meaningful. In any case, to make the comparison as fair as possible and clarify to which degree the results are a result of the sole effect of size, we have added a complementary set of PERMANOVA analyses in addition to the original ones that were based on the position of species on the two considered planes (aboveground vs fine-roots). These new PERMANOVA analyses are based on the individual components of the space, as well as on individual traits. This way, fine-root axes (C3 and C4) and traits, and leaf economics spectrum axis (C2) and traits can be compared after removing the dominant effect of size.

Indeed, we found that the variation explained by groups (woody vs herbaceous, families, biomes) was highest in the first component, which corresponds to plant size (59% of the variance in species position in C1 is explained by

woodiness, 73% by family, 19% by biome). After that, the differences between groups are higher in the second component than in any of the fine-root related components in all cases (Fig. R3, which we added also to the new version of the manuscript as ED Fig. 7). We repeated the same analyses also considering individual traits as a response variable, and the message was the same: the variation explained by groups is always higher for size-related traits, followed by leaf traits, and fine-root traits are the ones where differentiation is smallest. We think that these results provide support to the notion that differentiation is higher aboveground than in the fine-root plane, even without considering size. Although we still keep the main focus of this section of the manuscript at the differences and decoupling between the two planes, we now briefly discuss these findings (lines 150-153).

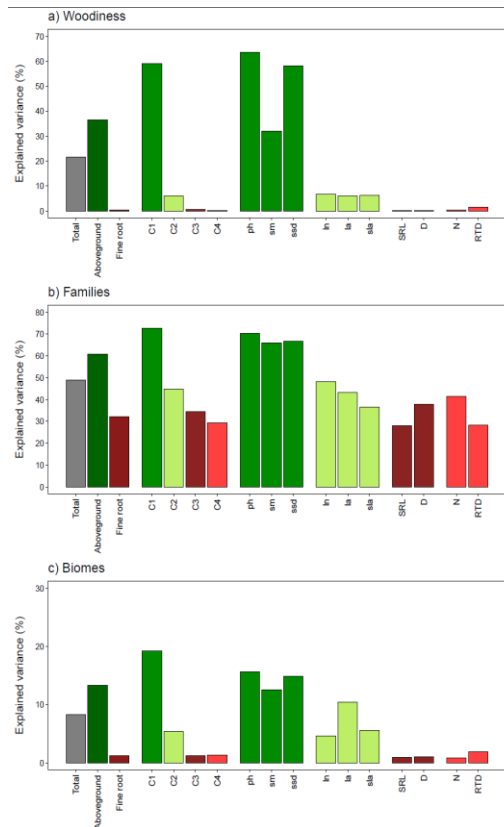


Fig. R3. Proportion of variance explained in PERMANOVA analyses by differences among groups (a: differences between woody vs herbaceous species, b: differences between families, c: differences between biomes) in the functional space considering different scales: four-dimensional space (total), aboveground and fine-roots plane, the individual components of the trait space, and the individual traits.

MYCORRHIZAL COLONIZATION: We agree with the reviewer about the importance of adding data of plant mycorrhizal colonization for a given root

diameter into our analyses (as shown in Ma *et al.*, 2018). However, after checking the availability of mycorrhizal colonization data in different databases, we do not deem this inclusion viable at the moment, due to three main reasons:

- First, in contrast with the data used in Ma *et al.* (2018), which was based on three papers using clearly comparable methods, there is no consistency in the collection of mycorrhizal colonization data. Indeed, this is the case for one of the latest databases on plant species mycorrhizal traits, the FungalRoot database (Soudzilovskaia *et al.* 2020). As it has been discussed in the root trait literature, the root diameter and branch hierarchy can strongly determine the presence of mycorrhizal fungal colonization. In particular, distal root-orders (thinner roots) generally perform soil resource mobilisation and uptake with the frequent support of mycorrhizal fungi, while more proximal root orders (thicker and longer-lived) are generally mycorrhiza-independent, performing transport and storage functions (Guo *et al.* 2008; Rewald *et al.* 2011; Ma *et al.* 2018). Further, the diversity of data origin and methodologies historically used and compiled in FungalRoot for the mycorrhizal fungal colonization estimation (for instance, more than 7 different approaches were described for arbuscular mycorrhizal plants) may add another conspicuous layer of potential bias. All these factors result in a very high degree of within-species variation in mycorrhizal fungal colonization, which makes this trait not reliable for inclusion in global analyses like the one we perform here. To show this, we estimated the proportion of the total variability in this trait in the FungalRoot dataset (considering only the subset of plant species with at least 10 measurements of mycorrhizal fungal colonization; $n = 53$ species) that is due to differences between species. For this, we used an intercept-only linear mixed model with species as a random factor, following Messier *et al.* (2010). These analyses revealed that only 19% of the total variance is due to differences between species (Fig. R4), while 81% is due to differences within species (and measurement error). This is a clear handicap for mycorrhizal colonization analyses since it is very difficult to discriminate species based on this trait (Shipley *et al.* 2016). Our case clearly differs from the Ma *et al.* (2018) database, where all measurements were made at a fixed root diameter or on the same root branch order (first-order roots), and carried out following a compatible protocol by approximately the same team in the same region, so that the differences between species are likely to be much higher.

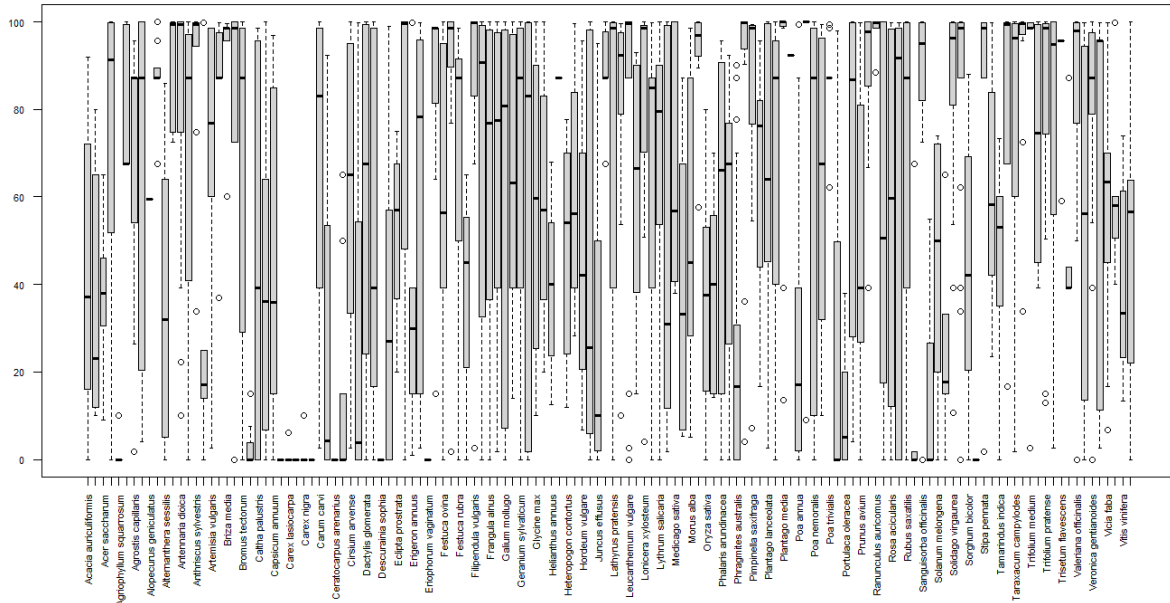


Fig. R4. Distribution of mycorrhizal fungal colonization values (%) for the species with at least 10 measurements for this trait in the FungalRoot database. Note the large amount of variation within species in this trait (the variance due to differences between species was 265, whereas the residual variance was 1060). Performing the same analysis after processing the response variable following the same steps as in Bergmann *et al.* 2020 (i.e. scaling colonization values to the range of 0 to 1 followed by arcsine square root transformation, plus accounting for study design and publication using a mixed model) yielded similar proportions of within- and between-species variation (80% and 20%, respectively).

- Second, and probably largely overlooked, is the lack of a consistent measure for comparing the root colonization in different mycorrhizal types. The nature of different mycorrhizal types (arbuscular: AM, ecto: EcM, ericoid, and orchid, among the most common ones) comprise the association of very different fungal and plant taxa. These taxonomically contrasting mycorrhizal types develop very different associations in functional and ecological terms (Smith & Read 2008). This precludes the use of a single meaningful measure for a proper comparison among different mycorrhizal types. This is particularly relevant when performing comparisons between woody and herbaceous species in terms of mycorrhizal fungal colonization, because while woody plants can be EcM or AM, herbaceous plants are AM, with a few exceptions.
- Third, appropriate data is not available for a representative number of plant species in our study. Ma *et al.* (2018) included 137 species with a

strong representation of woody plants (but with information for 27 herbaceous species, only), and matching our dataset in only 50 species. Similarly, the updated GRooT database (Guerrero-Ramírez et al., 2020), which is most likely also affected by the problems explained in the first point, comprises only 199 species included in our database, and also shows a strong bias towards woody plants (with 140 woody species and 59 non-woody species).

For completeness, we repeated the eigenanalysis as explained in **R1** including mycorrhizal colonization data from the GRooT database, obtaining virtually the same result reported in Bergmann *et al.* (2020) (i.e. mycorrhizal colonization goes parallel to root diameter). Due to the abovementioned reasons, we have decided not to include these analyses in the manuscript; reliable analyses on root-size traits and mycorrhiza remain for future studies when more comparable high-quality data becomes available.

3. Redundancy and dissimilarity: The last 1/3 of manuscript offers a very interesting analysis of “redundancy” and “dissimilarity” patterns in the above- and belowground trait space. The analysis evaluates the distribution of species traits relate spatially within the PCA scaling analysis, either in 2 dimensions (above- and belowground plane analyzed separately) or 3- dimensions (total dataset analyzed).

This analysis offers some really interesting patterns by itself and when compared against climate/biome dissimilarity. The quantitative approach is described well in the methods section. However, the main text treatment of this analysis reads relatively abstract despite the long-standing importance of the “redundancy” and “dissimilarity” terms within the field of ecology.

A reader of the main text gets the sense that what is presented is an analysis of clouds of points and their distances or overlap. And this, of course, is the case, but underlying these points are real-world biological species and traits that are distributed across biomes. I would welcome a bit more effort to bring in biological realism, to the degree possible. Beyond the natural question of whether the woody vs. herbaceous distinction (discussed above) drives the major results are issues such as: “what are the most dissimilar species pairs, and what biological characteristics appear to drive these differences?” Or, “what is the biological reason for why herbaceous species display greater redundancy belowground than woody species?” You get the idea.

R8: We have improved the degree of biological realism in the redundancy/dissimilarity analysis. In particular, we now provide more examples regarding the position of different widely-known species (lines 137-139) and clades on the different planes (lines 142-144), strengthening the links to previous results (lines 157-160) and bringing new explanations for the main

patterns observed, such as the higher redundancy of herbaceous vs woody species in the fine-root plane (lines 170-183).

4. Relation to previous work: The trait literature is vast, and it would be difficult to properly represent all previous findings and ideas. And it is understandable that comparisons are done against recent publications that have used the same fine root datasets.

The treatment could benefit, however, from comparing the ideas and results against recent similar studies. One such study (Ma et al. 2019) looked at a global dataset of 369 species with additional root traits based on first-order roots only (instead of root orders 1-3 combined). Using a two-dimensional PCA analysis similar to the present study, Ma et al. inferred “root trait organization that is functionally decoupled from the leaf economic spectrum” but based on a different set of reasoning than the present study (with emphasis on the functional role of nitrogen vs. structural traits in roots vs. leaves).

The study also observed a different organization of belowground traits than the present study. Of particular importance is the finding “that woody and herbaceous plants occupy different parts of the SRL versus root diameter relationship” and that woody and herbaceous plants differ in the pattern of mycorrhizal colonization (Fig. 1c) and in root tissue density (Fig. 1d).

This difference in findings ought to be addressed in a revised version, since the existence of a woody vs. herbaceous plants difference in root traits might introduce a second dimension of variability, analogous to what is observed aboveground. If so, the dimensional comparison may not be fundamentally different.

R9: As explained in **R7** above, unfortunately, we do not think that the available data on mycorrhizal colonization allows us to make any meaningful comparison with the results from Ma et al. (2018) in terms of the differences in mycorrhizal colonization patterns between woody and herbaceous species (due to the low ability of this trait to discriminate between species, and to the difference in the prevailing mycorrhizal type between woody and herbaceous species). Regarding the differentiation between woody and herbaceous species in other fine-root traits, we also have not found such a pattern in the fine-root plane or any of the components related to it. Rather, as we describe in the manuscript, the differences in the fine-root plane between these two growth forms are minimal. We do not know exactly where these differences stem from, although the dataset from Ma et al. (2018) includes a much smaller proportion of herbaceous species—in addition to the manuscript, the “Author Correction” to that paper (<https://www.nature.com/articles/s41586-019-1214-3>) provides extra information showing the low number of herbaceous species considered.

Moreover, the few herbaceous species considered in Ma et al. (2018) are also restricted to two particular biomes (“Desert” and “Grassland”), whereas other biomes (“Boreal”, “Temperate”, “Subtropical”, “Tropical”) include almost exclusively woody species (see ED Fig. 3 in Ma et al. 2018). Our dataset is much more balanced both in terms of herbaceous and woody species (which are almost equally represented) and in terms of the distribution of herbaceous species across biomes. The result of almost no segregation between woody and herbaceous species in terms of their fine-root traits that we describe is similar to the one described in Bergmann et al. (2020) (see Table S4 in that paper). We now mention the different findings between our manuscript and Ma et al.’s, including a reference to the unbalanced dataset used there, as well as the similarity to Bergmann et al.’s results in the main text of our manuscript (lines 133-137).

In addition, we have added a new set of analyses exploring the relationship between species redundancy at different levels (in the aboveground and belowground planes and in the total four-dimensional space) and productivity (lines 200-211 and Fig. 3c-e). We found that high productivity aboveground is linked to high aboveground redundancy at the biome level, and the opposite pattern for fine-root traits, which is in agreement with the pattern of lower root trait variability in biomes with higher seasonality reported by Ma et al. (2018).

5. Summary: This is a potentially exceptional contribution that addresses fundamental questions about the global organization of plant traits. The dataset is strong and this is the first effort to explicitly combine above and below-ground trait data, derived symmetrically from each species, and then exposed to rigorous quantitative analysis.

However, the focus may have been placed on a weaker part of the analysis, rather than the quantitatively more powerful comparison of above vs. below-ground trait organization, as well as issues of biological redundancy and dissimilarity. If appropriately revised, the manuscript has great potential to move this field forward through a creative and new analysis.

Referee #3 (Remarks to the Author):

Vascular plant trait diversity is globally higher above- than belowground
Carmona et al.

In this manuscript, the authors combined the global spectrum of plant form and function (GSPFF), representing the functional space aboveground and the root economic space (RES) representing the functional space belowground. The combination of above and belowground functional spaces is a fundamental step towards understanding whole-plant strategies, with this

study providing interesting new insights. For instance, the authors found that above and belowground functional spaces are not analogous to each other, with the belowground space providing additional information regarding plant form and function. Further, the authors provide evidence of whole-plant coordination based on their analysis of dissimilarity and redundancy among families and biomes. Overall, I find the integration of above and belowground functional spaces a priority. In addition, the authors used robust statistical analysis accompanied by a clear explanation, the code and the data. However, I am concerned that the paper's main conclusion, i.e., that vascular plant trait diversity is globally higher above- than belowground (as stated by the title, the abstract and the conclusion), may be misleading.

As the authors stated clearly in the introduction, the aboveground functional space included traits associated with plant size, aboveground organs, and the leaf economic spectrum while the belowground space reflects fine roots; as the authors stated fine roots are equivalent to leaves due to their role in resource acquisition. The authors tested species aggregation in above and belowground spaces, finding higher aggregation when compared with null models for above and belowground spaces. For aboveground, species were clustered in two hotspots associated mostly with plant size (i.e. plant height, specific stem density, and seed mass, with a bimodal distribution separating herbaceous and trees) as shown in Díaz et al 2016. For belowground, species were clustered in one hotspot as observed in Bergmann et al 2020. Based on species aggregation and further comparisons between dissimilarity between families and biomes and PERMANOVAs, the authors conclude that vascular plant trait diversity is globally higher above than belowground. Yet, for this study, the belowground space is limited to fine roots (which will be more comparable to the leaf economic spectrum). Therefore, it is difficult to know if there is higher plant trait diversity above than belowground or if this reflects that relevant traits belowground are missing in the analysis (with this point only briefly mentioned in lines 229 - 231).

For example, strong influence of plant size included aboveground and the absence of potential analogous traits belowground could explain differences in dissimilarities between above and belowground. The authors mentioned that “21% of the family pairs presented higher dissimilarities below- than aboveground. These cases mostly belonged to pairs of families including almost exclusively herbaceous species or woody species” (lines 141 – 143); this could highlight how differences in term of plant trait diversity above and belowground may be associated with plant size and to a lesser extent to more diverse strategies in nutrient acquisition when comparing leaf and fine-roots (as mentioned in lines 220 – 222). Therefore, for me, to make a statement as the “Vascular plant trait diversity is globally higher above- than

belowground”, it would be required to include belowground traits which could be analogous to plant size aboveground and/or traits which represent the root system. In contrast, the authors could clearly state that, i.e., “many species with the same fine-root syndrome display contrasting aboveground traits” (as mentioned in lines 129 - 130), which maybe be less impactful but more accurate.

R10: We agree with the referee that our choice of words for describing the fine-root plane as a “belowground” plane was generalising too much. We have now modified the manuscript to refer consistently to a “fine-root plane”, which we think solves most of the problems of interpretation raised. We have shifted the focus of the manuscript (including title) from the differences in diversity between the two planes to the fact that adding fine-root traits greatly expands the global spectrum of plant form and function by adding fundamentally independent dimensions. In addition, and as explained in **R7** above, we have now explored: 1) the potential effect of incorporating size traits belowground, which does not seem to add any new dimension of variation, 2) the invariance in the relationship between leaf and fine-root traits to the removal of the traits most strongly associated to the first component of the functional space, 3) the patterns of differentiation between groups (woody vs herbaceous, families and biomes) in the individual dimensions of the functional space and in the individual traits, which show that, even after removing the dominant effect of size, differentiation in leaf traits is generally higher than in root traits. We think that all these changes have led to more balanced interpretation and discussion of our results, and overall improved the quality of the manuscript.

Referee #4 (Remarks to the Author):

The aim of the manuscript is to link the global spectrum of plant form and function (GSPFF) to the root economic space (RES) taking advantage of the recently published database on global fine root traits. After decades of functional trait research which primarily focused on the aboveground plant organs more recent advances in belowground trait analysis widened the perspective of the field. Numerous recent papers search to understand belowground trait correlations and their relationship to ecosystem functioning and there is strong interest in the question of if and how above and belowground organs align and how these functional relationships can be expressed using plant traits. It is within this light that the submitted manuscript offers a very timely analysis with importance to a broad scientific field. There have been other attempts to the same question (which are referenced) but none so far with as large a dataset as the offered manuscript. Given the large and global representation of species, this enables the authors for the first time to also draw conclusions on the distribution of various

groups of plants (families, biomes) in total trait space. In addition to this general fit to the scope of the Journal, the manuscript is very clear and well written and overall good to follow. Statistical analyses appear technically sound to the best of my knowledge though I do not agree with some of the decisions in the analysis procedure or at least think there is room for better reasoning in some cases (see below). However, the overall approach is valid, the quality of data is very good and the presentation of results is of very high quality.

Despite this overall praise to the authors, I do have two points of major critique I would like to bring forth. First, I am not convinced the main or one of the main conclusions of the paper that “functional trait differentiation is consistently lower belowground than aboveground” is true. I think the paper is inherently written from an aboveground perspective while claiming a fair comparison of above and belowground traits. Yet aboveground the full spectrum of traits representing also growth form and most importantly size is considered in the analysis and compared with what belowground would only account for the leaf economics space – the fine root traits or a selection thereof. In the very last sentence of the paper it is concluded that more root traits need to be taken into account to further evaluate above- belowground trait variation and correlation but the remainder of the paper is giving the impression of equal comparison of the above and belowground plant compartments. The GSPFF includes growth form as stated by the name and this is via traits of seed mass and plant height while belowground only traits concerning economic space are included in the analysis. As stated in line 40 of the paper – “fine roots are functionally comparable to leaves” – not stems or tree trunks or seed mass or leaf size. I believe that including more and inherently different traits aboveground than belowground does not allow a “fair” comparison of the importance of root to the GSPFF and as such that the conclusions drawn from the paper when it comes to roots being less variable or explaining less variance in the data, are not sound and perhaps even partly wrong. I realize my own perspective might not be neutral on this ground, given that I am more of a root ecologist myself. Yet, being familiar with the larger part of multivariate trait analysis presented I am also aware that the number and identity of traits included in the analysis might have a large effect and in this manuscript this effect is totally dominated by plant height, seed and leaf area which is why the first axes mainly separates woody and non-woody plants while belowground this option is not available given the selected traits. With this I do not want to indicate that the analysis is not sound, I only suggest that the conclusions are better tuned to the results presented.

R11: We thank the referee for this comment, which concurs with the opinions of referees #2 and #3 above. As explained in the responses to these referees (which can be found in **R7** and **R10** within this letter), we have removed the references to a “belowground plane” and we now just mention a “fine-root plane”. We agree that this provides a much more balanced and fair comparison between the two planes. In particular, we have repeated the PERMANOVA analyses considering each axis of the space individually (rather than considering the two axes that constitute each plane), as well as individual traits. As correctly predicted by referee #4, size (and size-related individual traits) is the main driver of differentiation in the aboveground dataset, but there is still substantively higher differentiation in the leaf-related axis (and individual traits) than in either of the fine-root axes (and corresponding traits). We now discuss these new results, which are in line with previous observations (Liu *et al.* 2010), in the main text (lines 150-153) and have included a new figure (ED Fig. 7, corresponding with Fig. R3 in this letter) presenting them.

My second point of criticism is the large number of inferences drawn from the imputed dataset and the additional species put in the original PCA without changing the trait axes (which had been calculated based on the 301 species with full trait coverage). Basically, from line 120 onwards in the main text all further discussion is based on the imputed dataset of 1218 species. I think it is an interesting aspect of the manuscript to look at the distribution of different groups of species in the trait space. I also think that this aspect of the paper does need a critical mass of species which is higher than 300. However, to impute the data you do use phylogenetic information and the imputed dataset contains 54 more families than the dataset with full information. Still you project all additional 917 species on the same functional space created with the complete dataset of only 301 species (line 125) rather than calculate a second PCA based on the imputed data. All the following conclusions are based on this procedure of which I am not fully convinced.

R12: Thank you for pointing this out. In our manuscript we are describing, for the first time, a global pattern of functional traits combining those included in the original GSPFF with fine-root traits. Because of this, we considered that the most conservative way to do this was to use only those species with complete empirical trait measurements for all traits (301 species). This is what we do in the first half of the manuscript, where we describe the shape of the space, the relationships between traits in this space, and the general patterns of aggregation of species within it. As the referee points out, we did not think that 301 species were enough to further explore the patterns of the different groups. We opted to follow this most conservative approach by keeping the space built considering only complete information and projecting on it the species with imputed information. We understand the referee’s concern

regarding the creation of a second PCA based on the imputed dataset (1218 species), and we have performed such a procedure in the new version of the manuscript. The dissimilarity and redundancy results we report in the new version of the manuscript correspond to this new PCA built using the set of 1,218 species, as suggested by the referee. Note, however, that only minimal changes have occurred with respect to the results in the original version of the manuscript, and none of them affect in any way any of the conclusions. This is because the two functional spaces created in that way are practically identical, both in terms of the loadings of traits in the components (see Fig. R1b vs d in the context of **R1** above and the new ED Table 2) and in terms of the relative position of species within the space (Procrustes correlation = 0.996; $p = 0.00001$ with 100,000 permutations).

Further comments:

- Line 71: Varimax rotation is not without criticism in the community. I am not saying I would advise not to use it as in this case but I think a good justification beyond just “where traits are best related to axes” would be recommendable. This is especially important as you later map species positions in your so called trait planes. I am sure you are fully aware of this discussion and also guess that there has been a discussion in the group of authors about this point, but rotated PCA axes are strictly speaking not orthogonal which does have important implications for your conclusions. I recommend to give your line of thought more justification including perhaps also the original PCA for reference.

R13: We decided to make a varimax rotation after a thorough exploration of the dataset. This exploration is described in great detail in **R1** above. We have now included these explanations in the manuscript (Supplementary Methods 2: Exploration of the structure of the functional space), along with the characteristics of the original PCAs for the different subsets of species considered (ED Table 2), as requested. In essence, our results using a non-rotated PCA already show that the functional space is organised in the two planes that we present in the manuscript; however, the varimax rotated solutions are not only easier to interpret, but also less subject to particularities of the considered dataset. We checked that the new axes are orthogonal to each other (the correlation between the position of species in either of the four axes is zero), so we do not think this potential problem has any impact on our conclusions.

- I do wonder why the authors did not use phylogenetically corrected data for the analysis. They do use phylogenetic information for the imputed data but not the main analysis. Why not? Non-phylogenetic data might exaggerate the

result of the main PCA were most variance on the first axis explains the divergence between herbaceous species and angiosperm trees.

R14: We did not use phylogenetically corrected trait data because our main aim was to show fundamental (global) patterns and potential differences in the aboveground and fine root trait space of plants from an ecological rather than an evolutionary angle. Trait variation is the result of the interplay between phylogeny and ecological selection (Westoby *et al.* 1995) and we did not want to dismiss the ecological relevance of traits because of their potential association with phylogeny (Westoby *et al.* 1995; Díaz *et al.* 2007). We understand that the question for phylogenetic corrections in functional trait analyses is widely discussed, but considering our main aim, we think it is not justified (de Bello *et al.* 2015, 2017). Applying phylogenetic correction implies an *a priori* assumption that present-day trait variations might be more a consequence of phylogenetic relatedness rather than a continuous (eco-)evolutionary selection, which is not the focus of our paper. For example, following the example provided by the referee, we think that in our case, the functional differentiation between herbaceous species and angiosperm trees is a feature of our dataset, rather than an artefact that needs correction. With this, we do not intend to undermine the use of phylogenetic corrections; we think that they are not needed in cases like the present manuscript.

- Line 87 ff: It is not entirely clear from this paragraph which subset of species (301, imputed data set or other) was mapped and analysed here. The methods refer to the 301 for observed which should be mentioned also in the figure legend for clarity.

R15: Yes, it refers to the 301 species with complete empirical information. We have clarified this in the text.

- Line 113: which traits have been dropped?

R16: All traits had some non-zero loading on all axes so that all traits that are not shown in a plot (because they do not reach the required minimum loading in any of the represented axes) are dropped. We now include a table (ED Table 2) with all loadings, and we refer to it in the figure caption for more details.

- Line 122ff: The imputed dataset is a critical issue for me. Extended table 1 states the number of species per trait from which data needed to be imputed. From that table it is hard to see how only 15.4 % of data was imputed overall given that e.g. for root N more than 30% of trait info was missing. Please explain.

R17: What we meant in that table is that 15.4% of the records were imputed, not that 15.4% of the observations (i.e. species) were imputed. As pointed by the referee, some traits are more complete than others (e.g. specific root length

was missing for 4.5% of the species that we kept for the imputed dataset, whereas root nitrogen concentration was missing for 34%). On average, 15.4% of all observations were missing (i.e. 15.4% of the cells in the species x trait data contained missing values). Specifically, the table contained 10,305 records with trait measurements and 1,875 records that were missing. We have modified the text to highlight this.

In addition to this, we now provide a much deeper assessment of the performance of the imputation procedure. One critical aspect that has to be considered here is that our goal with the imputation was not to retrieve the values of species for all individual traits, but rather the position of the species in a functional space that is produced by combining several traits. Although there is literature comparing the performance of imputation procedures and the effects of biases in trait information when imputing individual traits, we are not aware of any paper considering the performance of imputing trait values to predict the position of species in a functional space (in this case a PCA). Following Carmona et al. (2021), we have now performed an extensive simulation exercise, creating artificial missing values for the 301 species with complete trait information (see line 425 and Supplementary Methods 1: Reliability of the imputation procedure). In short, we randomly selected 10 species with incomplete information and superimposed their patterns of missing trait values to 10 randomly-selected species from a subset of species with complete empirical information. By doing this, we reproduced a pattern of missing values consistent with the one in the original dataset, attaining a trait matrix that is identical to the one in which we performed the original imputation procedure, except for 10 randomly-selected species with complete empirical information to which we added artificial missing values. We then performed the phylogenetically-informed imputation procedure in this dataset, as described in Methods. Then, we used the imputed traits to project species onto the functional space based on the full dataset (with 1,218 species, as described in **R12**). Note that we did not estimate a new PCA because the goal here is to estimate how reliably we are retrieving the position of species for which we have artificially created missing data in exactly the same functional space. Finally, we compared the position of the 10 randomly-selected species in the different dimensions of the trait space without removing data (real position of the species) and after artificial removal and imputation of trait information. We estimated the performance of the imputation by means of the normalized root mean square error (NRMSE), which expresses the average distance between real and imputed positions of species as a proportion of the range of values of species in the corresponding dimension. We repeated this procedure 3010 times, to achieve 100 estimations for each of the species with complete empirical trait information, and attained an estimation of the average NRMSE value across repetitions for each of the dimensions of the functional space.

Our results show that the accuracy of the imputations is very high. This means that even in the cases in which some traits are missing for a given species (consider also that we limited the number of missing traits that were allowed to 50%, separately for the aboveground and the fine-root traits), along with its position in the phylogeny, the imputation procedure allows us to estimate the position of the species in the functional space with high accuracy. In short, our simulations show that the normalised mean square error (the mean square error in relation to the range of values of the corresponding dimension of the functional space) for each dimension is:

Component 1: 0.005 (0.5% of the range)

Component 2: 0.006 (0.6%)

Component 3: 0.005 (0.5%)

Component 4: 0.034 (3.4%)

On average, the imputation procedure retrieves the real position of a species with an error of less than 1% of the range of trait values for the first three components and 3.4% for the fourth component. For comparison, NMRSE values reported in Penone *et al.* (2014)—the most cited paper dealing with the accuracy of the imputation of missing data in trait databases while considering phylogenetic information—were always higher than 0.06 (6% of the range), even in the most benign of their scenarios (10% of missing data).

In addition, and attending to the previous comments by referee #4 (see comments for **R12**), we examined to what degree the imputation accuracy worsens for species without confamilial counterparts (for which the phylogenetic eigenvectors might not be so helpful). Indeed, imputation accuracy tended to be better for families with a higher number of species (see Fig. R5 below). However, this decrease in performance was low, and even in the case of species that are the only representative of their family, the average imputation error remained very low.

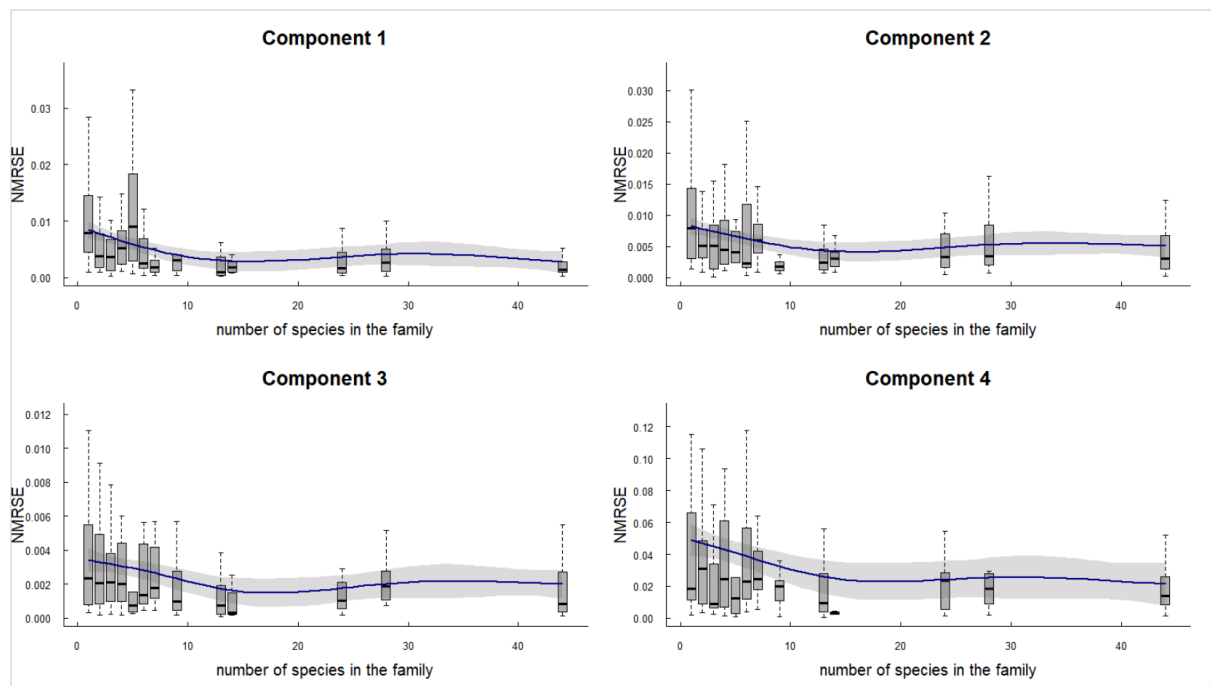


Fig. R5. Mean error (NRMSE) of the imputation procedure as a function of the number of species in the family of the imputed species. For each species, we used the average NRMSE across 100 simulated values. To explore the relationship between NRMSE and the number of species in the family, we fitted generalized additive models (mean \pm 2 SE represented). Note that, although imputation accuracy increases with the number of species within the family of the imputed species, the imputation is very accurate even for species without any confamilial counterpart.

- Line 129 ff: this is the type of conclusion I am referring to above. I am not convinced this is true.

R18: As explained above, we now refer exclusively to a “fine-root” rather than a “belowground” plane. We think that this change solves the issue. The section now reads as: “We examined the patterns of functional differentiation among groups of species and found that fine-root traits were more similar than aboveground traits when comparing herbaceous and woody species, different families or biomes. This is in line with the observation of a single functional hotspot in the fine-root plane but two hotspots aboveground, meaning that species with similar fine-root syndromes can display contrasting aboveground traits.”

- Line 217: “ we found that plants differentiate preferentially in the above- rather than in the belowground part of this functional trait space” while before in most cases the correct relation between GSPFF and fine root traits

is mentioned, this sentence is much more general. See my first major comment.

R19: We have modified the sentence and now refer to the fine-root part of the functional space, rather than the belowground part.

• Line 339: did you at some point calculate species mean trait values? I did not see this mentioned.

R20: Yes; we explain how we did this in lines 344-348

• Line 377: Why did you use phylogenetic information here but not use phylogenetically corrected data?

R21: We included phylogenetic information in our imputation process to increase the accuracy of imputations by complementing information of traits partly based on phylogenetic relatedness of species. However, as we stated in more detail in **R14** above, we don't consider this phylogenetic relatedness a bias that needs correction and we do not want to dismiss the ecological relevance of traits because of their potential association with phylogeny.

• Line 414: It appears that the examination of the belowground plane is a repetition of the Bergmann et al. paper. Why would you exactly repeat that here? To show they were correct of that those results can be reproduced? Seems strange to me.

R22: We had three main aims in mind when we decided to replicate the analyses from the Diaz et al. (2016) and Bergmann et al. (2020) papers. First, we wanted to show that we can reproduce those results with our data. This is particularly important with the aboveground data, since we used a different version of the TRY database than the one used in Diaz et al. Although we used exactly the same data as in Bergmann et al (2020), hence our complete dataset for fine-root trait includes 748 species, we repeated the analysis for completeness. Second, we also wanted to explore what is the dimensionality of the functional spaces built considering only aboveground and fine-root traits using consistent methods (Bergmann et al. 2020 does not report what were their criteria to define the dimensionality of the fine-root trait space). Note that formally defining the dimensionality of the individual spaces (both are two-dimensional) is key for our results, since we show that the dimensionality of the space when considering all the traits together is four. Finally, we wanted to explore what is the correspondence of species positions in these two independently estimated spaces. While it is clear that the functional space based on the combined aboveground and fine-root traits is four, we think that showing that there is a very weak correlation between the positions of species in the only-aboveground and only-fine-roots spaces reinforces the main message of the manuscript, i.e. that adding fine-root traits to the GSPFF

incorporates fundamentally non-redundant information. We have modified the text in the methods section to make these points clearer (lines 457-477).

- Line 484: Did I understand correctly that you mapped the imputed data onto the original trait space (300 species) and calculated dissimilarities based on these matrices?

R23: Yes, that is what we did. As explained above, we initially considered that it was more correct to use only the species with complete empirical information to describe the functional space and then project the species with imputed information onto that space. However, we have modified this analysis now, so that we use the imputed species also in the estimation of the PCA for 1218 species. Results are virtually unchanged.

- Extended Data Fig 1: While this figure nicely shows the difference between the shared species and the full dataset, it does not show the difference between the imputed (on which a large part of the manuscript is based) and the full dataset. Distribution of data for plant height differs clearly for subset and full set. Subset height is more dichotomous than full set?

R24: Good point, thank you. Now, we have added information about the relationships in the imputed dataset, instead of the full dataset. Still, height differs between the complete and imputed dataset because woody species tend to be better documented than non-woody species. This is a pervasive feature when considering vascular plant data beyond traits (e.g. conservation status is better studied for woody than herbaceous species), as can be seen in the bivariate probabilistic plots in ED Fig. 4 (complete information) and ED Fig. 6 (imputed information).

- Figure 2b – enlarge writing in the graph.

R25: Done

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Reviewer Reports on the First Revision:

Referee #1 (Remarks to the Author):

This fresh version is excellent. It is very clearly written, and addresses the concerns I had on the previous version. The response letter (or extended essay!) is also very good. I look forward to when journals adopt the policy of routinely publishing these also.

Here are two exceedingly minor comments:

L71. "The first two dimensions (C1 and C2) were mostly related to aboveground traits..."
It might be more clear here to call these "components" rather than "dimensions", in line with naming them "C1" and "C2".

L82. "The fact that four dimensions are required to adequately capture non-redundant trait variation, as found in the present study, suggests that aboveground and fine-root trait syndromes involve traits that are not necessarily analogous to each other"

To this I would add that the aboveground and fine-root trait sets are also therefore not clearly correlated (and *also* not analogous to each other).

Referee #2 (Remarks to the Author):

This still is a potentially most interesting manuscript that seeks to resolve variation in both above- and belowground plant traits worldwide, and specifically whether these two parts of plant functionality are linked.

The re-organization has helped focus the manuscript on the most rigorous result, that is also of broad interest among ecologists: the lack of a clear coupling (correlation) between above- and belowground traits. This removes from central stage the potential bias(es) inherent in the selection of the different traits. The emphasis is now on the strongest result.

The revised title seems ok, though it is a bit indirect with respect to the central message/result. It does not communicate to a reader what is new, or what the major finding(s) are.

The introduction is improved and now set up the central question of the degree of covariation between above- and below-ground traits, and relates this to specific (and differing) hypotheses in the literature. This is followed by an interesting analysis and strongly argued results that compare above and below-ground trait dimensions. This reads effective, save a few minor issues that I note in my detailed comments below.

However, starting with "occupational space analysis" on line 120 the manuscript runs into serious problems. I was surprised that the authors have not sought to address in a convincing manner fundamental concern raised by three of four referees, and which the authors themselves agreed with in their response: that there may be selection bias among the traits, so that the belowground traits do not necessarily display the same extent of variation as the aboveground traits.

The proposed solution – changing a word choice (from "below-ground" to "fine root") — so as to restrict the scope of analysis — is not the answer. The issue remains abundantly clear to a reader: The main text immediately states (lines 34-37) that a major dimension of aboveground trait organization is caused by plant size (and introduces the woody vs. herbaceous comparison). The text then goes on to show this graphically across PCA axis 1 in Fig. 1. And yet the size issue, the tree vs. herbaceous issue, and the potential effect(s) introduced by biased trait selection are never addressed in any nuanced form in the text.

I must admit I am a bit surprised as to how these concerns were addressed in the response to referees. The referees received an agreement and thorough-thorough and detailed sets of new analyses, but the issues were essentially not acknowledged or addressed in the main text.

The apparent argument that "there is not enough data for us to analyze" is not sufficient here – the issues are self-evident, rooted in: (i) the fundamental difference between the types (size dependent vs. independent) of above vs. below-ground traits compared, (ii) published indications that mycorrhizal colonization may differ between woody and herbaceous species, raising the possibility of bimodal trait organization also belowground; and (iii) except for root N, the remaining root traits (diameter, specific root length and root tissue density) are all mathematically related ($SRL = 4 / (\pi \times D^2 \times RTD)$) – which means that they have a limited ability to vary independently. It is therefore entirely unclear whether adding a trait not related to these three traits (e.g., root phosphorus, root branching intensity, etc.) will or will not increase the overall variance of belowground traits.

Similarly, to suddenly restrict the analysis to only sub-components of the dataset (e.g., comparing only size-independent traits) does not **alone** answer the question. It needs to be accompanied by a thoughtful discussion that addresses the above issues.

Conclusions such as "We found that plants differentiate preferentially in the aboveground rather than in the fine root part of this functional trait space" do not seem warranted, given these concerns.

I had hoped that the revised manuscript would simply acknowledge these issues, and bring them into the discussion of the occupational space analysis, while backing off on some of the very strong and definite claims that the issues compromise. Examples would be short sentences such as: "This analysis points to the need for data also on size-dependent belowground traits, which, in turn may ultimately allow us to compare the true extent of differentiation in both above- and belowground traits." And, "Inclusion of mycorrhizal traits may add differentiation in the belowground trait dimension, as indicated by a possible bimodal pattern in mycorrhizal colonization between woody and herbaceous species (Ma et al.)." Etc.

I'm not sure what went wrong, and perhaps I am misunderstanding the intent of the revision, but my impression is that the issues were dealt with abstractly (and at great detail) in the response to reviewers, but I cannot find them sufficiently internalized in the main text.

I would propose the following: 1) Maintain the central focus and initial analysis of above- vs. below correlation; 2) Revise the ensuing space analysis, so that the results are offered in a more nuanced discussion about trait selection and potential biases; 3) Shorten and greatly simplify the end part of the space/diversity analysis, which now has grown in detail and analysis so that it is difficult for a reader to follow and to understand the central message; and 4) Back off on strong statements and conclusions that may be subject to trait selection bias.

The following minor comments may help conceptually sharpen the introduction:

1. Line 33 – spell out GSPFF.
2. Line 33 -- "in six key ABOVEGROUND traits".
3. Line 38 -- "how SPECIFIC BELOWGROUND traits relate to the GSPFF".
4. Line 40 -- "cycling, thus considerably contributing to stabilizing organic matter in soils" does not follow. "AND CONTRIBUTES to stabilizing ..."

Referee #3 (Remarks to the Author):

The manuscript by Carmona et al., makes a great contribution towards our understanding of whole-plant form and function by integrating the largest databases available on plant functional traits. The authors found that four dimensions are needed to capture the variability in plant form and function, with this finding having fundamental repercussions in our understanding of plant functional ecology. As an additional step, the authors explored the influence of growth form, families, and biomes on the plant spectrum (either as a whole or by including only aboveground or fine root spaces). In the current version, the authors provide additional analysis and a more careful interpretation of their results.

The authors did a great job providing a global spectrum of whole-plant form and function and assessing how robust this spectrum is (either testing the influence of the number of species included, i.e., full empirical versus imputed datasets, or by the influence of the varimax rotation). In addition, new analyses can contribute towards a biological understanding of the whole-plant form and function spectrum. My main suggestion regarding their main finding is to provide a 1) holistic interpretation, i.e., whole-plant form and function instead of above versus fine-roots, and 2) an explanation in biological terms. The authors show for the first time the whole-plant form and function spectrum. But because the Results and Discussion are presented as above versus fine-roots, their findings sounds as confirmatory analysis of Díaz et al., 2016 and Bergmann et al., 2020, instead of providing an integrative perspective in which plants are recognized as a whole, instead of a sum of independent organs. For instance, what do the four dimensions mean in terms of whole-plant syndromes? Is it possible to provide a couple of examples of species representing these syndromes? What do these mean in terms of plant strategies?

Based on reviewers' comments, the authors explored the influence of belowground size traits, specifically, maximum rooting depth (mrd), in the whole-plant spectrum. Yet, due to lower coverage, the authors decided not to include the analysis in the manuscript but mention that "the belowground trait space is likely to have more dimensions beyond fine-root traits, partially independently or associated with those aboveground but not enough empirical data are currently available to adequately test these ideas" (lines 245 – 247). From my perspective, despite mrd cannot be included directly on the space, the analysis presented in the response #7 can contribute to elucidate whole-plant form and function. Particularly, mrd loaded strongly on the first component, following the same direction as the aboveground size related traits (Fig R2). While this is not surprising, it is an indication that the size component, it is not exclusively driven by aboveground but it may be a whole-plant component. Therefore, the aggregation in two functional hotspots observed aboveground can be also observed belowground, as shown when the size axis is combined with the components related to fine-roots (C3 and C4, Extended Data Figure 4 and 6). My suggestion will be to include the analysis and Fig R2 in the supplementary information and, discuss potential repercussions for a holistic interpretation of the whole-plant spectrum.

The authors went further, performing a set of impressive analyses assessing the influence woodiness, families and biomes on the whole-plant form and function spectrum (as well as in their components separately). While understanding matches and mismatches between aboveground and fine-roots can provide a deeper understanding of the whole-plant spectrum, an explicit inclusion of the total space (assessed for the functional redundancy patterns and the variance explained in the Permanova) will provide the integrative approach which is still missing for this second part.

My last suggestion is to recognize the limitations. The authors are using the largest databases available as well as imputation to maximize the number of species used in the second set of analyses. The used databases contain the most complete data available now, but they also have gaps (e.g., under-representation of hyperdiverse families), with these gaps amplified by using only the species for which above and fine-root traits are available. Therefore, it would be to recognize the limitations when assessing within and among family variation.

Similarly, in the response # 14, the authors explain the importance of both, phylogeny and ecological selection, when understanding global functional patterns. This is not my area of

expertise and I apologize if this does not make sense but I wonder if the ecological aspect associated with biomes could be masked because a great proportion of the data used is imputed, giving higher weight to the phylogenetic aspect (in this regard, it would be great to see the number of cases with full empirical data for each biome on the extended Data Figure 2b, not only the number of the imputed dataset). Also, while null models control for number of species, it would be good to know which limitations in representing functional strategies, e.g., tropical rainforest represented by 94 species while temperate seasonal forest by 885 species, could influence our understanding about differences between biomes (also when comparing diversity coverage in relative terms).

Minor comment

Mutualist: As any collaboration, plant-fungal interactions are more complex. Thus, I will suggest not using this term to describe them.

Referee #4 (Remarks to the Author):

Being a review on a revised version I want to highlight the improved parts of the manuscript rather than give again an overall summary of results, originality and methods. In brief, the manuscript links the global spectrum of plant form and function (GSPFF) to the root economic space (RES) of fine root traits in a well written paper with sound statistical analyses and high quality, up to date presentation of results. The paper offers the potential to widen the perspective of trait based functional ecology and should attract interest of a broad readership.

I would like to congratulate the authors to this thorough and extremely detailed revision. 37 pages of rebuttal letter is – at least for me – a first. Importantly, however, it is not the amount of words but the content which is convincing. Compared to the previous version this revised form is substantially improved and now much more consistent in its presentation and discussion of the data provided. This is particularly true for the phrasing of sentences around the importance and differences of trait variability for roots related to the fact of unbalanced trait representation which has been criticized by 3 out of 4 reviewers (myself included). Extended figure 7 helps to highlight the points also brought up by the reviewers which are now also partly picked up in the paper itself. I think exploring this question in depth might need a second paper as perhaps also indicated by the length of the rebuttal to this point. There are quite a number of potential open questions raised here but the line of argument is now much clearer and more restricted to the fine root traits included. While I am still not convinced by all of the arguments brought forward in the rebuttal letter (see below), I value the overall logic and large amount of additional analyses to substantiate the authors position.

I think some of the additional data now provided in the revised version is indeed essential to properly judge the validity of the conclusions drawn in the manuscript. This is true e.g. for the full information on functional traits spaces now presented in extended data table 2. I am also pleased by the addition of the sensitivity analysis for the imputed dataset.

Overall, the revised version now is much more convincing and a highly valuable manuscript offering a valid and robust analysis of aboveground and fine root trait correlation using the largest global dataset available so far. The manuscript is of broad importance to the field of ecology and fits very well to the scope of the journal.

I have some minor comments I would still want to see fixed.

Minor comments:

Line 59: homogenize leaf and root n – either both content per unit mass or both concentration – measurements should be the same in both cases from my knowledge of the traits.

Line 110: All traits are depicted so mentioning of non - depicted traits in the figure legend is not necessary.

Line 117: should be root nitrogen concentration

Line 123: It is not clear at this point what you mean with 50% of the above and belowground traits – I would guess you refer to the 3 traits above and 2 traits below dataset? This is what you

name imputed dataset in table 1? I would think you should refer to extended data table 1 here?
Line 205: I struggled with this sentence and had to read it several times to follow. It would be easier to argue along the same lines as in the previous sentences - lower biomass aboveground >> reduced competition for light >> higher trait diversity. In contrast, low water availability and high seasonality leads to low biomass belowground BUT reduced trait diversity.

Line 222: not clear what is meant with "opposite of functional richness SES"

Line 516: "of" the observed values

The varimax rotation issue: I very much appreciate the presentation of PCA data with and without varimax rotation in the rebuttal and the extended data of the paper in this new version. I think this helps the reader to judge the differences. The authors claim those are minor, I disagree with this general statement. While true for the full and imputed dataset, I see clear and important differences between rotated and not-rotated PCA in the complete dataset. Without rotation the collaboration root traits load on PC 2. With varimax they load on PC3. As the PCA of this complete dataset is the most conservative of the paper and thus forms the basis for the conclusions. In the manuscripts and the rebuttal the authors discuss that in all cases (of different datasets) the PCAs reveal four dimensions and discuss in detail how the "fundamental structure" is reflected in the same way. There is also mentioning that leaf traits load differently, yet none about the differences for the root traits let alone that fine root traits in the unrotated version explain a larger part of the overall variance. I think this should be added to the discussion. Other than that I respect the decision of using varimax with the information provided. In the rebuttal it reads "As a result, the simple structure revealed in the eigenanalysis of the full dataset was somewhat "hidden" in the complete dataset" – this seems like a positive description of what I explained above.

Author Rebuttals to First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

This fresh version is excellent. It is very clearly written, and addresses the concerns I had on the previous version. The response letter (or extended essay!) is also very good. I look forward to when journals adopt the policy of routinely publishing these also.

We are happy that the reviewer liked the last version of the manuscript. We are very grateful for the reviewer's valuable comments.

Here are two exceedingly minor comments:

L71. "The first two dimensions (C1 and C2) were mostly related to aboveground traits..."

It might be more clear here to call these "components" rather than "dimensions", in line with naming them "C1" and "C2".

Done.

L82. "The fact that four dimensions are required to adequately capture non-redundant trait variation, as found in the present study, suggests that aboveground and fine-root trait syndromes involve traits that are not necessarily analogous to each other"

To this I would add that the aboveground and fine-root trait sets are also therefore not clearly correlated (and *also* not analogous to each other).

Although we understand the reviewer's point, we have preferred to leave the sentence unchanged. In that particular part of the text, we refer to the biological patterns, and what matters is whether the traits are analogous—that is, they perform similar “general functions”—the correlation is a secondary aspect there. Further, there is always some degree of correlation between pairs of variables: we think that mentioning the lack of correlation here could leave to interpretation problems.

Referee #2 (Remarks to the Author):

This still is a potentially most interesting manuscript that seeks to resolve variation in both above- and belowground plant traits worldwide, and specifically whether these two parts of plant functionality are linked.

The re-organization has helped focus the manuscript on the most rigorous result, that is also of broad interest among ecologists: the lack of a clear coupling (correlation) between above- and belowground traits. This removes from central stage the potential bias(es) inherent in the selection of the different traits. The emphasis is now on the strongest result.

We thank the reviewer for the comments. Below, we provide detailed responses to all of the raised issues.

The revised title seems ok, though it is a bit indirect with respect to the central message/result. It does not communicate to a reader what is new, or what the major finding(s) are.

We have modified the title, which now is “Fine-root traits in the global spectrum of plant form and function”. We think it is a more parsimonious and compact title, which informs about the main topic and the general novelty (combining GSPFF and RES) of the paper.

The introduction is improved and now set up the central question of the degree of covariation between above- and below-ground traits, and relates this to specific (and differing) hypotheses in the literature. This is followed by an interesting analysis and strongly argued results that compare above and below-ground trait dimensions. This reads effective, save a few minor issues that I note in my detailed comments below.

However, starting with “occupational space analysis” on line 120 the manuscript runs into serious problems. I was surprised that the authors have not sought to address in a convincing manner fundamental concern raised by three of four referees, and which the authors themselves agreed with in their response: that there may be selection bias among the traits, so that the belowground traits do not necessarily display the same extent of variation as the aboveground traits.

The proposed solution – changing a word choice (from “below-ground” to “fine root”) — so as to restrict the scope of analysis — is not the answer. The issue remains abundantly clear

to a reader: The main text immediately states (lines 34-37) that a major dimension of aboveground trait organization is caused by plant size (and introduces the woody vs. herbaceous comparison). The text then goes on to show this graphically across PCA axis 1 in Fig. 1. And yet the size issue, the tree vs. herbaceous issue, and the potential effect(s) introduced by biased trait selection are never addressed in any nuanced form in the text.

I must admit I am a bit surprised as to how these concerns were addressed in the response to referees. The referees received an agreement and thorough-thorough and detailed sets of new analyses, but the issues were essentially not acknowledged or addressed in the main text.

The apparent argument that “there is not enough data for us to analyze” is not sufficient here – the issues are self-evident, rooted in: (i) the fundamental difference between the types (size dependent vs. independent) of above vs. below-ground traits compared, (ii) published indications that mycorrhizal colonization may differ between woody and herbaceous species, raising the possibility of bimodal trait organization also belowground; and (iii) except for root N, the remaining root traits (diameter, specific root length and root tissue density) are all mathematically related ($SRL = 4 / (\pi \times D^2 \times RTD)$) – which means that they have a limited ability to vary independently. It is therefore entirely unclear whether adding a trait not related to these three traits (e.g., root phosphorus, root branching intensity, etc.) will or will not increase the overall variance of belowground traits.

We understand the reviewer’s concerns here, although we do not fully agree with the criticism. In our previous response and the previous version of the manuscript, we strived to make it much clearer that the belowground traits we are analysing are exclusively fine-root traits, and that these do not indicate, by any means, all the dimensions of belowground plant variation. In other words, we are not comparing aboveground vs belowground trait variation but rather aboveground vs fine-root trait variation. On the other hand, the reviewer is right in pointing out that it is possible that some aspects of belowground trait variation (but not, to the best of our knowledge, of fine-root trait variation) are contained in the first component. In our previous response, we did our best to find data to clarify this aspect, and as we argued there, we did not think such data is of sufficient quality and for enough species to justify including root size in the main analyses, so we restricted those analyses to the response letter. We still consider that there is not enough data to merit including this variable in our analyses, but we now discuss (based on strong published evidence relating aboveground and belowground biomass [Enquist & Niklas, 2002; Niklas, 2005]) the possibility that the size of the belowground part of the plant is indeed correlated with the first component, which could then be interpreted as a whole-plant size component (lines 223-228).

Regarding mycorrhizal colonization, we also tried hard to find the best available information for that trait. As we argued in the previous response letter, this trait is probably too labile to be considered as a reliable trait to show interspecific differences in global datasets: only 19% of the total variance in mycorrhizal colonization in the FungalRoot dataset (Soudzilovskaia et al., 2020) is due to differences between species, while 81% is due to differences within species. Effectively this means that (i) a lot of measurements per species would be needed to have an accurate estimation of the mean value of any given species; such data are not available, and (ii) even so, these mean values are probably not a very good indicator of the relationship between colonization intensity and the other root traits (because for any given value of root diameter, colonization intensity can vary widely). This is

not surprising, since the available information from databases includes roots from different orders (as we discussed in the previous letter) measured with different methods which might yield not fully comparable results, and under a diverse array of environments, soil conditions, and mycorrhizal fungi species. This is why we argued in the letter that only the approach followed by Ma et al (2018), i.e. measuring mycorrhizal colonization in situ in uniform conditions and comparable methods, could be considered valid. In the previous version of the manuscript we tried to acknowledge the point of the inclusion of mycorrhizal traits by including it in a key part of the paper (the last sentence of the main text); we have now expanded this discussion, as suggested by the reviewer.

Regarding the third argument of the reviewer (how could the inclusion of different belowground traits affect the conclusions), we think that the plane we present here should be robust to the addition of other fine-root traits. We have not included such traits because there is not enough data availability. However, published evidence suggests that the fine-root space is most likely two-dimensional, and that the main trends of variation are indeed well represented by the traits we chose. Ma et al. (2018) showed (in their ED Fig. 1) a PCA that very much corresponds with the fine-root plane of our manuscript. Interestingly, they included more traits than we did (for a smaller group of species), but these extra traits are correlated with the traits we present; for example, root length and mycorrhizal colonization are positively correlated with root diameter, and root carbon is in the same dimension of variation as root N (Ma et al. 2018 ED Fig. 1). Bergmann et al (2020) also showed that considering other traits does not change the main message (fine-root trait space as a plane; see Fig. 2E in that paper): root life span is positively correlated to root tissue density, mycorrhizal colonization is again positively correlated to root diameter, as is cortex fraction. None of these papers examined the correlation of root phosphorus, as suggested by the reviewer. We collected information on root P from GRooT, and processed the trait data in the same way as the other fine-root traits included in our analyses. GRooT includes root P information for 231 of the 1719 species from our full dataset (i.e species with at least one trait with empirical information both in the TRY and GRooT datasets), but only for 82 species from our complete dataset (301 species with full information for the 10 traits that form the GSPFF and the RES). While this precludes including root P in the manuscript, we were still able to estimate the matrix of correlation between pairs of traits and perform the subsequent eigenanalysis, as we did with maximum rooting depth. Eigenvalues suggested that the dimensionality of the space was still four (the eigenvalue of the fifth component being 0.89), and root P loaded most strongly on the fourth component of this space, following the same direction as root N (which is the trait that had the strongest pairwise correlation with root P, Pearson = 0.47). The other mentioned trait (root branching intensity) is an architectural trait, which we are not including in our analyses (and for which there is even less information available in the GRooT dataset); however, we mention that including architectural traits in the picture would be important (lines 230-232).

Similarly, to suddenly restrict the analysis to only sub-components of the dataset (e.g., comparing only size-independent traits) does not *alone* answer the question. It needs to be accompanied by a thoughtful discussion that addresses the above issues.

Conclusions such as “We found that plants differentiate preferentially in the aboveground rather than in the fine root part of this functional trait space” do not seem warranted, given these concerns.

We apologize if our message was not clear enough. We should stress once more that due to the data availability we addressed only fine-root traits, which do not represent the whole diversity of belowground traits. Nevertheless, we believe that our results and conclusions are solidly anchored on the empirical evidence. We found that the fine-root part of the space is a plane, which is in agreement not only with Bergmann et al. (2020), who used the same source of root data as us, but also with Ma et al. (2018) using different data. Most importantly, we show that it remains a plane when the correlations with aboveground traits are included, which is one of the main findings in our manuscript. Further, the fundamental characteristics of this plane (in terms of how each trait loads on each component) are consistent between these two previous papers and our results. This strongly suggests that the plane we are considering is indeed representative of variation in fine-root traits (which is indeed a subset of belowground traits, but in response to the referee’s valuable advice in the first round we have carefully removed our claims about belowground diversity in general). We then show that differentiation between groups of plants (herbaceous vs woody, families and biomes) are always larger in the aboveground plane than in the fine-root plane. We think this conclusion is one of the main novel results from our manuscript, we think it is supported by the data and analyses we present, and we carefully interpreted it in the context of fine roots only.

Importantly, this message cannot be generalized to belowground trait diversity overall. To make this clearer, we have now modified the last paragraph of the main text to show that (i) we have only selected a subset of belowground traits (namely, fine-root traits), (ii) results could differ if other belowground traits had been analysed, and (iii) this includes the strong possibility that the two functional hotspots could be present belowground too, but not in fine roots (lines 226-228).

I had hoped that the revised manuscript would simply acknowledge these issues, and bring them into the discussion of the occupational space analysis, while backing off on some of the very strong and definite claims that the issues compromise. Examples would be short sentences such as: “This analysis points to the need for data also on size-dependent belowground traits, which, in turn may ultimately allow us to compare the true extent of differentiation in both above- and belowground traits.” And, “Inclusion of mycorrhizal traits may add differentiation in the belowground trait dimension, as indicated by a possible bimodal pattern in mycorrhizal colonization between woody and herbaceous species (Ma et al.).” Etc.

Thank you for these suggestions. We have included sentences similar to the ones proposed by the reviewer:

“For example, previous assessments of biomass allocation patterns^{33,34} have shown that aboveground and belowground biomass are positively correlated, so that the size of the belowground system is likely to be associated with the first, size-related, component. This suggests that this dimension could be interpreted in terms of the size of the whole plant, and

thus the two functional hotspots observed in the aboveground space might be also observed in the belowground space. Also, inclusion of mycorrhizal traits^{18,35,36} may further modify the belowground trait dimensionality. However, not enough empirical data are currently available to adequately test these ideas.." (Lines 223-230)

I'm not sure what went wrong, and perhaps I am misunderstanding the intent of the revision, but my impression is that the issues were dealt with abstractly (and at great detail) in the response to reviewers, but I cannot find them sufficiently internalized in the main text.

I would propose the following: 1) Maintain the central focus and initial analysis of above- vs. below correlation; 2) Revise the ensuing space analysis, so that the results are offered in a more nuanced discussion about trait selection and potential biases; 3) Shorten and greatly simplify the end part of the space/diversity analysis, which now has grown in detail and analysis so that it is difficult for a reader to follow and to understand the central message; and 4) Back off on strong statements and conclusions that may be subject to trait selection bias.

We have modified our manuscript following these suggestions. In particular, we have included several instances (as stated in the previous responses) where we discuss the potential implications of adding other belowground traits not included here. However, as also argued above, we found that our conclusions about the differences in the patterns of occupation by species of the aboveground and fine-root planes of the space we describe, are sound. Originating the fine-root data we use, our results show consistent and robust structure of the space, which is also in agreement with the related literature, but future studies can indeed explore similar questions from a different focus.

The following minor comments may help conceptually sharpen the introduction:

1. Line 33 – spell out GSPFF.

Done.

2. Line 33 -- "in six key ABOVEGROUND traits".

Done.

3. Line 38 -- "how SPECIFIC BELOWGROUND traits relate to the GSPFF".

We haven't modified this part of the text. In the sentence we refer to fine-root traits, as we do in the rest of the manuscript. We would prefer to avoid this kind of overgeneralization, that stretches beyond the empirical evidence we have, as explained in previous paragraphs.

4. Line 40 -- "cycling, thus considerably contributing to stabilizing organic matter in soils" does not follow. "AND CONTRIBUTES to stabilizing ..."

Done.

Referee #3 (Remarks to the Author):

The manuscript by Carmona et al., makes a great contribution towards our understanding of whole-plant form and function by integrating the largest databases available on plant functional traits. The authors found that four dimensions are needed to capture the variability in plant form and function, with this finding having fundamental repercussions in our understanding of plant functional ecology. As an additional step, the authors explored the influence of growth form, families, and biomes on the plant spectrum (either as a whole or by including only aboveground or fine root spaces). In the current version, the authors provide additional analysis and a more careful interpretation of their results.

We are very grateful to the reviewer for their comments and positive opinion about our manuscript.

The authors did a great job providing a global spectrum of whole-plant form and function and assessing how robust this spectrum is (either testing the influence of the number of species included, i.e., full empirical versus imputed datasets, or by the influence of the varimax rotation). In addition, new analyses can contribute towards a biological understanding of the whole-plant form and function spectrum. My main suggestion regarding their main finding is to provide a 1) holistic interpretation, i.e., whole-plant form and function instead of above versus fine-roots, and 2) an explanation in biological terms. The authors show for the first time the whole-plant form and function spectrum. But because the Results and Discussion are presented as above versus fine-roots, their findings sounds as confirmatory analysis of Díaz et al., 2016 and Bergmann et al., 2020, instead of providing an integrative perspective in which plants are recognized as a whole, instead of a sum of independent organs. For instance, what do the four dimensions mean in terms of whole-plant syndromes? Is it possible to provide a couple of examples of species representing these syndromes? What do these mean in terms of plant strategies?

Thank you for these suggestions. We agree that considering the four-dimensional space opens new possibilities for differentiation among species that were not visible if the aboveground and fine-root planes are considered independently. Considering this, we have added new sections in the paper where we give examples of species that are similar in one of the planes, but differ in the other, and discuss some of these differences in terms of plant strategies (lines 85-97). Because of space constraints in the main text, there is a limit to the number of examples we can mention, so we have decided to include a new web application (Supplementary Application 1: <https://globaltrait.shinyapps.io/GlobalTraits>) to allow readers to explore the occupation of the space on their own (including a three dimensional visualization). We think that this application really shows how combining aboveground and fine-root traits improves our understanding of plant trait variation. At the same time, we are concerned that it is a too bold generalization to refer to whole-plant syndromes, since, as

rightly pointed out by reviewer #2, we do not include all aspects of plant trait variation, so that we think that the whole-plant interpretation is not possible at this point.

Based on reviewers' comments, the authors explored the influence of belowground size traits, specifically, maximum rooting depth (mrd), in the whole-plant spectrum. Yet, due to lower coverage, the authors decided not to include the analysis in the manuscript but mention that "the belowground trait space is likely to have more dimensions beyond fine-root traits, partially independently or associated with those aboveground but not enough empirical data are currently available to adequately test these ideas" (lines 245 – 247). From my perspective, despite mrd cannot be included directly on the space, the analysis presented in the response #7 can contribute to elucidate whole-plant form and function. Particularly, mrd loaded strongly on the first component, following the same direction as the aboveground size related traits (Fig R2). While this is not surprising, it is an indication that the size component, it is not exclusively driven by aboveground but it may be a whole-plant component. Therefore, the aggregation in two functional hotspots observed aboveground can be also observed belowground, as shown when the size axis is combined with the components related to fine-roots (C3 and C4, Extended Data Figure 4 and 6). My suggestion will be to include the analysis and Fig R2 in the supplementary information and, discuss potential repercussions for a holistic interpretation of the whole-plant spectrum.

Thank you for pointing this out. Yes, we agree that belowground diversity is indeed not fully captured by the traits we considered (which are size-independent fine-root traits), and also that the first component is very likely to be an indicator of the size of the whole-plant and its organs, not only aboveground but also belowground. We agree that this is not surprising, given the strong relationships between above- and belowground mass allocation. However, we still consider that there is not enough data to merit including this variable in our analyses; rather, we think this is one of the self-evident patterns mentioned by reviewer 2, because there is strong published evidence showing that aboveground and belowground biomass are strongly and positively correlated, particularly at the global scale [Enquist & Niklas, 2002; Niklas, 2005]). Therefore, we now discuss the possibility that the size of the belowground part of the plant is indeed correlated with the first component, which could then be interpreted as a whole-plant size component (lines 223-228)

The authors went further, performing a set of impressive analyses assessing the influence woodiness, families and biomes on the whole-plant form and function spectrum (as well as in their components separately). While understanding matches and mismatches between aboveground and fine-roots can provide a deeper understanding of the whole-plant spectrum, an explicit inclusion of the total space (assessed for the functional redundancy patterns and the variance explained in the Permanova) will provide the integrative approach which is still missing for this second part.

We have modified the text in different parts to better show the patterns of differentiation while considering the total four-dimensional space. In addition to the examples of species mentioned above, and to the inclusion of the web application, we now explain more clearly that specialised and generalist families in the total space appear so also in the individual

aboveground and fine-root planes (e.g. lines 185-190), and we better emphasize the significance of the fact that redundancy is higher when considering the total space (lines 157-160).

My last suggestion is to recognize the limitations. The authors are using the largest databases available as well as imputation to maximize the number of species used in the second set of analyses. The used databases contain the most complete data available now, but they also have gaps (e.g., under-representation of hyperdiverse families), with these gaps amplified by using only the species for which above and fine-root traits are available. Therefore, it would be to recognize the limitations when assessing within and among family variation.

We completely agree with this point. We now recognize this limitation more explicitly in the main text (lines 216-221):

“Understanding the covariation of above- and belowground traits will illuminate how evolution has shaped plant strategies to cope with biotic and abiotic environments. Such understanding will require filling the existing gaps in data: despite using the most complete data currently available, many families are absent from our assessment, and the representation of different biomes is uneven (Extended Data Fig. 2).”

Similarly, in the response # 14, the authors explain the importance of both, phylogeny and ecological selection, when understanding global functional patterns. This is not my area of expertise and I apologize if this does not make sense but I wonder if the ecological aspect associated with biomes could be masked because a great proportion of the data used is imputed, giving higher weight to the phylogenetic aspect (in this regard, it would be great to see the number of cases with full empirical data for each biome on the extended Data Figure 2b, not only the number of the imputed dataset). Also, while null models control for number of species, it would be good to know which limitations in representing functional strategies, e.g., tropical rainforest represented by 94 species while temperate seasonal forest by 885 species, could influence our understanding about differences between biomes (also when comparing diversity coverage in relative terms).

We have included the number of species from each biome in the complete dataset in the Extended Data Figure 2b, as suggested by the reviewer. Although redundancy results using our null model approach are by definition independent from species richness (they compare the amount of space occupied by some group with the expected amount of space occupied by a random group with the same number of species), the precision of the representation is not independent, so that when very few species are considered, the patterns can become unreliable. This is why we restricted comparisons among groups (in terms of overlap and redundancy) only to groups with at least 15 species, which we consider a reasonable limit and is in line with what is proposed in the literature (Blonder, Lamanna, Violle, & Enquist, 2014). In any case, to be sure that our redundancy analyses are robust to the use of imputed dataset, we have now performed the redundancy estimations considering only the species from the complete dataset. This reduces very much the number of families that can be reliably considered: even if we restrict the minimum number of species that a family or biome must have to be included in the analysis from 15 (as in the manuscript) to 10, we can

estimate redundancy only for 6 families, and the number of biomes drops to 9. The Pearson correlation between the redundancies for these biomes and families that can be estimated using both the complete and imputed dataset was 0.86, which suggests that our results using the imputed dataset are reliable. In any case, we now mention in the main text the fact that representation of different biomes is uneven (lines 218-221).

Minor comment

Mutualist: As any collaboration, plant-fungal interactions are more complex. Thus, I will suggest not using this term to describe them.

We have changed the wording, and now we say “plant-fungal interactions”.

Referee #4 (Remarks to the Author):

Being a review on a revised version I want to highlight the improved parts of the manuscript rather than give again an overall summary of results, originality and methods. In brief, the manuscript links the global spectrum of plant form and function (GSPFF) to the root economic space (RES) of fine root traits in a well written paper with sound statistical analyses and high quality, up to date presentation of results. The paper offers the potential to widen the perspective of trait based functional ecology and should attract interest of a broad readership.

I would like to congratulate the authors to this thorough and extremely detailed revision. 37 pages of rebuttal letter is – at least for me – a first. Importantly, however, it is not the amount of words but the content which is convincing. Compared to the previous version this revised form is substantially improved and now much more consistent in its presentation and discussion of the data provided. This is particularly true for the phrasing of sentences around the importance and differences of trait variability for roots related to the fact of unbalanced trait representation which has been criticized by 3 out of 4 reviewers (myself included). Extended figure 7 helps to highlight the points also brought up by the reviewers which are now also partly picked up in the paper itself. I think exploring this question in depth might need a second paper as perhaps also indicated by the length of the rebuttal to this point. There are quite a number of potential open questions raised here but the line of argument is now much clearer and more restricted to the fine root traits included. While I am still not convinced by all of the arguments brought forward in the rebuttal letter (see below), I value the overall logic and large amount of additional analyses to substantiate the authors position.

I think some of the additional data now provided in the revised version is indeed essential to properly judge the validity of the conclusions drawn in the manuscript. This is true e.g. for the full information on functional traits spaces now presented in extended data table 2. I am also pleased by the addition of the sensitivity analysis for the imputed dataset.

Overall, the revised version now is much more convincing and a highly valuable manuscript offering a valid and robust analysis of aboveground and fine root trait correlation using the largest global dataset available so far. The manuscript is of broad importance to the field of ecology and fits very well to the scope of the journal.

We are very grateful to the reviewer for their constructive reviews of our manuscript.

I have some minor comments I would still want to see fixed.

Minor comments:

Line 59: homogenize leaf and root n – either both content per unit mass or both concentration – measurements should be the same in both cases from my knowledge of the traits.

Done.

Line 110: All traits are depicted so mentioning of non - depicted traits in the figure legend is not necessary.

Done.

Line 117: should be root nitrogen concentration

Done.

Line 123: It is not clear at this point what you mean with 50% of the above and belowground traits – I would guess you refer to the 3 traits above and 2 traits below dataset? This is what you name imputed dataset in table 1? I would think you should refer to extended data table 1 here?

Yes, we meant that. We have modified the text accordingly.

Line 205: I struggled with this sentence and had to read it several times to follow. It would be easier to argue along the same lines as in the previous sentences - lower biomass aboveground >> reduced competition for light >> higher trait diversity. In contrast, low water availability and high seasonality leads to low biomass belowground BUT reduced trait diversity.

Done.

Line 222: not clear what is meant with “opposite of functional richness SES”

We have removed it from the figure caption, since the meaning of the term is better explained in Methods.

Line 516: “of” the observed values

Done.

The varimax rotation issue: I very much appreciate the presentation of PCA data with and without varimax rotation in the rebuttal and the extended data of the paper in this new version. I think this helps the reader to judge the differences. The authors claim those are minor, I disagree with this general statement. While true for the full and imputed dataset, I see clear and important differences between rotated and not-rotated PCA in the complete dataset. Without rotation the collaboration root traits load on PC 2. With varimax they load on PC3. As the PCA of this complete dataset is the most conservative of the paper and thus forms the basis for the conclusions. In the manuscripts and the rebuttal the authors discuss that in all cases (of different datasets) the PCAs reveal four dimensions and discuss in detail how the “fundamental structure” is reflected in the same way. There is also mentioning that leaf traits load differently, yet none about the differences for the root traits let alone that fine root traits in the unrotated version explain a larger part of the overall variance. I think this should be added to the discussion. Other than that I respect the decision of using varimax with the information provided. In the rebuttal it reads “As a result, the simple structure revealed in the eigenanalysis of the full dataset was somewhat “hidden” in the complete dataset” – this seems like a positive description of what I explained above.

We have included a sentence similar to the one proposed in the caption of Figure 1:

“Compared to the unrotated PCA, the varimax rotation retrieves the fundamental structure of trait variation in the dataset in a more interpretable and consistent way (i.e. less dependent on the specific subset of species considered; see Methods)”

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Reviewer Reports on the Second Revision:

Referee #2:

Remarks to the Author:

Review of Carmona et al.:

This is a strong manuscript that has been even further strengthened by the last set of revisions. Save for one notable exception, which I address below, the writing is clear, well-structured and thoughtfully delivered. It is an impressive effort and a first (but inherently limited) step towards formulating an understanding of whole-plant trait coordination (as eloquently noted by referee #3).

There are several improvements:

1. The slight change in the title is an improvement, in my estimation.
2. The first paragraph and start of the main text remain largely the same and read very well.
3. The initial discussion of the C1-C4 dimensions (starting on line 86) has been greatly improved. It now reads more straight-forward, less abstract, and makes use of the taxonomic comparisons (*Tsuga-Nothofagus* and *Pinus-Helianthus-Diaospyros*) previously presented later in the manuscript, to help the reader immediately visualize the key result. Very nice.
4. The occupational space analysis (starting on line 99) and the biome/NPP analysis (starting on line 145) have also been improved by additions of sentences that guide the reader to the main findings and interpretations. Again, nice, throughout.

I have only one remaining concern:

The last paragraph now addresses several of the issues that were previously presented only in the response to the reviewers. This is an important improvement that addresses potential concerns and nuances that will naturally occur to a thoughtful reader.

Despite this improvement, however, a reader will still not be sufficiently educated about the fundamentally important concern initially raised by three of the four reviewers: that the observed differences in above- vs. belowground dimensionality may be influenced by the inclusion of size-dependent traits above- but not belowground.

Yes, the new last paragraph text now explicitly addresses this (lines 222-229), but this comes way late in the presentation, much like a post-hoc addendum in response to reviews. I would think that a generalist reader must be informed about this issue at an earlier stage in the text, at the very point where the differences in dimensionality is first addressed – on line 111 or so. A reader deserves this information up-front as it will greatly help him/her interpret the overall findings and argument.

Following the sentence “By contrast, on the fine-root plane, species are mostly concentrated around a central hotspot...” I would suggest the insertion of a second sentence such as: “This difference may be related to the lack of extant and sufficient data on root traits that scale with

plant size (e.g., rooting depth or root system size; Niklas 2005), and that might contribute to variation along a size-dependent belowground dimension analogous to C1.”

Please note that I have no concerns whatsoever about the “robustness” of the author’s dataset or analysis. And, yes, the results as reported are very well supported empirically and by the quantitative/statistical analysis. I agree. But those are not my concerns.

Instead, my point is that a reader ought to be made aware of the underlying issue when the result is first presented. This will not detract from the quality or impact of the work. Instead, it will strengthen the manuscript by offering clarity and transparency to generalist readers (specialists will notice either way).

Minor comment: There is one section of the text that reads unclear, and that may be difficult for a generalist reader to follow. Lines 158-161 explains that redundancy was higher in the total dimensional space, followed by aboveground, and then belowground spaces. It may be difficult for a reader to understand how this translates into the conclusion that total and aboveground space tends to be “partitioned” (and thus non-redundant, in a reader’s eye) while fine-root space is “shared” (and this redundant, if redundancy means species with similar trait values). Please clarify.

Referee #3:

Remarks to the Author:

I really enjoyed reading the current version of the paper by Carmona et al, the authors did an excellent job improving the clarity and the biological interpretation. I was surprised that the authors developed a shiny app in response to the comments and I am happy they did it. The shiny app is a great tool for visualizing complex above and fine-root strategies simultaneously. I need to admit, I spend a considerable amount of time playing with this shiny app. I only have a couple of minor comments.

Minor comments

Lines 209 – 215: I suggest being careful with this statement: “Greater differentiation in aboveground trait syndromes may have emerged from larger variation in the experienced conditions and performed functions compared to fine roots, including competition for light, reproduction, less stable environmental conditions, and stronger and more heterogeneous effects of fire and large herbivores.”. For instance, while fine roots are not involved on the competition for light, they are involved in the acquisition of multiple resources (see Weemstra et al 2016), with root involved in resource competition and facilitation among plants as well as with microbial communities (e.g., Johnson et al, 2009 New Phytologist). Also, other relevant functions in which the plant belowground system is involved such as reproduction and responses to fire are not included because trait selection (see Klimešova et al 2019 Perspectives in Plant Ecology, Evolution and Systematics). Therefore, this statement, from my perspective, is based on an unequal comparison.

Lines 227 – 229: The authors could link this hypothesis to their supplementary material if they want to include their preliminary results showed in the previous response (response #7, Fig R2). Another key reference regarding biomass allocation is Pooter et al 2011 New Phytologist.

The authors mention the discrepancies regarding the loadings of leaf-related traits in the supplementary information. Maybe to be transparent a sentence about this can be included in the main text too.

For consistency, it would be good to use plant-fungal interactions or collaboration for the

supplementary information too.

Finally, I am glad to see how the paper developed.

Referee #4:

Remarks to the Author:

The manuscript aims to link the global spectrum of plant form and function (GSPFF) to the root economics space (RES) using the largest trait dataset available to date. In the first part, the manuscript studies the covariation between aboveground and fine root traits and presents a very interesting analysis and discussion comparing trait dimensionality between the different plant parts. In the second part of the paper the authors analyse the aggregation of species and functional divergence in the aboveground and fine-root plains and study differences between growth forms, families and biomes. Though equally thoroughly analyzed and presented, this second part still only vaguely addresses the issue of the effect of differences in trait selection on trait variation (see below for details) except for a paragraph in the conclusions. Overall, the revised version again improved on an already very well written paper and offers a sound statistical analysis with high quality presentation of results. The second revision offers some more improvement on the introduction and the central line of argument in the first part of the paper but no fundamental changes as far as I can judge. I do like the inclusion of specific examples in the new text and also appreciate the app where readers could check individual species in trait space. All my comments from the previous version were well addressed and I am mostly happy with this version of the manuscript.

However, reading carefully through the second part of the manuscript again, I did notice that the overall tone of argument was in some places not corresponding to what had been said in the rebuttal letter and also does not really solve the concern brought forward by reviewer #2.

Specifically, this is true for the argument that using "fine-root traits" instead of "belowground traits" does solve all of the problems related to the strong difference in trait selection above and belowground. This is not the case as clearly pointed out by reviewer and the current revision does not fully solve that point. In fact, there are several parts giving the impression that the difference in trait selection is not acknowledged. I would like to specify this with examples:

(1) In lines 99-115 the differences in functional divergence between aboveground and fine-root traits are assessed but the concluding sentence (or the whole paragraph) does not mention the potential effect of trait selection differences. The problem of trait selection is clearly acknowledged in the rebuttal letter, where additional data provided some further insight, but in the paper – though present – is not always properly emphasized. In this specific example, rather than ending with a very diffuse sentence that "a relatively small number of trait syndromes is extremely prevalent, whereas many others, while viable, are rare" this differentiation should have been mentioned.

(2) There are a number of statements still generalizing the results as evidence for lower belowground trait variation compared to the aboveground variation. Again, using the word "fine-roots" might not change the perception of the reader unless repeatedly stated as such. It needs to be pointed out explicitly that with fine-roots no size related traits as aboveground are included. Statements like "general pattern of higher functional trait variation aboveground" (line 205) or "In addition we found that plants differentiate preferentially in the aboveground rather than the fine-root part of this functional traits space" do not help to clarify this fact. Rather I would suspect that these sentences will be cited in future as general statements of support for overall differences in trait variation above and belowground. I think in these sentences you have to clarify that size is included above but not below.

I do realize the problem of missing trait data and this is well pointed out in the conclusion part. Yet I think adding 1 or 2 half sentences on this fact earlier in the discussion might help the reader to put the results into a better perspective.

Minor comment:

In L133 – you cite Bergmann et al. 2020 as support for your finding that the suits of fine root

traits of woody and herbaceous species are virtually the same, yet in the Bergmann paper there was a significant difference between woody and non-woody traits (table S4 that paper) while the pattern of the RES did in fact look really similar between both. This is correctly referred to in lines 163 ff. Perhaps this is what you intend to say but I find it misleading. Clarify please.

In the suppl methods description after the formula to calculate orthogonality on page 3, delete either "estimated" or "averaged".

Author Rebuttals to Second Revision:

Referee #2:

Remarks to the Author:

Review of Carmona et al.:

This is a strong manuscript that has been even further strengthened by the last set of revisions. Save for one notable exception, which I address below, the writing is clear, well-structured and thoughtfully delivered. It is an impressive effort and a first (but inherently limited) step towards formulating an understanding of whole-plant trait coordination (as eloquently noted by referee #3).

Thank you for your kind comments, we are glad that you are satisfied with our revision.

There are several improvements:

1. The slight change in the title is an improvement, in my estimation.
2. The first paragraph and start of the main text remain largely the same and read very well.
3. The initial discussion of the C1-C4 dimensions (starting on line 86) has been greatly improved. It now reads more straight-forward, less abstract, and makes use of the taxonomic comparisons (*Tsuga-Nothofagus* and *Pinus-Helianthus-Diaospyros*) previously presented later in the manuscript, to help the reader immediately visualize the key result. Very nice.
4. The occupational space analysis (starting on line 99) and the biome/NPP analysis (starting on line 145) have also been improved by additions of sentences that guide the reader to the main findings and interpretations. Again, nice, throughout.

I have only one remaining concern:

The last paragraph now addresses several of the issues that were previously presented only in the response to the reviewers. This is an important improvement that addresses potential concerns and nuances that will naturally occur to a thoughtful reader.

Despite this improvement, however, a reader will still not be sufficiently educated about the fundamentally important concern initially raised by three of the four reviewers: that the observed differences in above- vs. belowground dimensionality may be influenced by the inclusion of size-dependent traits above- but not belowground.

Yes, the new last paragraph text now explicitly addresses this (lines 222-229), but this comes way late in the presentation, much like a post-hoc addendum in response to reviews. I would think that a

generalist reader must be informed about this issue at an earlier stage in the text, at the very point where the differences in dimensionality is first addressed – on line 111 or so. A reader deserves this information up-front as it will greatly help him/her interpret the overall findings and argument.

Following the sentence “By contrast, on the fine-root plane, species are mostly concentrated around a central hotspot...” I would suggest the insertion of a second sentence such as: “This difference may be related to the lack of extant and sufficient data on root traits that scale with plant size (e.g., rooting depth or root system size; Niklas 2005), and that might contribute to variation along a size-dependent belowground dimension analogous to C1.”

Please note that I have no concerns whatsoever about the “robustness” of the author’s dataset or analysis. And, yes, the results as reported are very well supported empirically and by the quantitative/statistical analysis. I agree. But those are not my concerns.

Instead, my point is that a reader ought to be made aware of the underlying issue when the result is first presented. This will not detract from the quality or impact of the work. Instead, it will strengthen the manuscript by offering clarity and transparency to generalist readers (specialists will notice either way).

We have now addressed this issue earlier in the text have added the suggested sentence in lines 116-118.

Minor comment: There is one section of the text that reads unclear, and that may be difficult for a generalist reader to follow. Lines 158-161 explains that redundancy was higher in the total dimensional space, followed by aboveground, and then belowground spaces. It may be difficult for a reader to understand how this translates into the conclusion that total and aboveground space tends to be “partitioned” (and thus non-redundant, in a reader’s eye) while fine-root space is “shared” (and this redundant, if redundancy means species with similar trait values). Please clarify.

We have clarified the meaning by adding a short explanation: “(i.e. the amount of variation among groups is relatively larger)”, line 165

Referee #3:

Remarks to the Author:

I really enjoyed reading the current version of the paper by Carmona et al, the authors did an excellent job improving the clarity and the biological interpretation. I was surprised that the authors developed a shiny app in response to the comments and I am happy they did it. The shiny app is a great tool for visualizing complex above and fine-root strategies simultaneously. I need to admit, I spend a considerable amount of time playing with this shiny app. I only have a couple of minor comments.

Thank you for your comments; we are very happy you liked the manuscript and the app.

Minor comments

Lines 209 – 215: I suggest being careful with this statement: “Greater differentiation in aboveground trait syndromes may have emerged from larger variation in the experienced conditions and performed

functions compared to fine roots, including competition for light, reproduction, less stable environmental conditions, and stronger and more heterogeneous effects of fire and large herbivores.”. For instance, while fine roots are not involved on the competition for light, they are involved in the acquisition of multiple resources (see Weemstra et al 2016), with root involved in resource competition and facilitation among plants as well as with microbial communities (e.g., Johnson et al, 2009 New Phytologist). Also, other relevant functions in which the plant belowground system is involved such as reproduction and responses to fire are not included because trait selection (see Klimešova et al 2019 Perspectives in Plant Ecology, Evolution and Systematics).

Therefore, this statement, from my perspective, is based on an unequal comparison.

We have modified the sentence, removing the reference to functions and simply leaving the reference to higher environmental variability and disturbances aboveground. The sentence now reads: “Greater differentiation in aboveground trait syndromes compared to fine roots may have emerged, for example, from less stable environmental conditions³², and stronger and more heterogeneous effects of fire and large herbivores³³ aboveground” (Lines 216-219)

Lines 227 – 229: The authors could link this hypothesis to their supplementary material if they want to include their preliminary results showed in the previous response (response #7, Fig R2). Another key reference regarding biomass allocation is Pooter et al 2011 New Phytologist.

We understand the referee’s point here. However, after careful consideration, we still would prefer not to include those results in this manuscript (including the supplementary materials), since they are based on a rather small sample size (270 species in total with maximum rooting depth data, but only 62 of them with data for the other 10 considered traits). We have added the suggested reference.

The authors mention the discrepancies regarding the loadings of leaf-related traits in the supplementary information. Maybe to be transparent a sentence about this can be included in the main text too.

We think that adding such a sentence would move the focus of the text to a very technical detail (small changes in the correlations between pairs of traits depending on the considered sample size) and have chosen not to include it; however, we would do so if the editor considers that such a sentence should be included.

For consistency, it would be good to use plant-fungal interactions or collaboration for the supplementary information too.

Done

Finally, I am glad to see how the paper developed.

Thank you again for all your comments and help to improve the manuscript.

Referee #4:**Remarks to the Author:**

The manuscript aims to link the global spectrum of plant form and function (GSPFF) to the root economics space (RES) using the largest trait dataset available to date. In the first part, the manuscript studies the covariation between aboveground and fine root traits and presents a very interesting analysis and discussion comparing trait dimensionality between the different plant parts. In the second part of the paper the authors analyse the aggregation of species and functional divergence in the aboveground and fine-root traits and study differences between growth forms, families and biomes. Though equally thoroughly analyzed and presented, this second part still only vaguely addresses the issue of the effect of differences in trait selection on trait variation (see below for details) except for a paragraph in the conclusions. Overall, the revised version again improved on an already very well written paper and offers a sound statistical analysis with high quality presentation of results. The second revision offers some more improvement on the introduction and the central line of argument in the first part of the paper but no fundamental changes as far as I can judge. I do like the inclusion of specific examples in the new text and also appreciate the app where readers could check individual species in trait space. All my comments from the previous version were well addressed and I am mostly happy with this version of the manuscript.

We are very glad that you liked our manuscript and thank you for your comments and suggestions.

However, reading carefully through the second part of the manuscript again, I did notice that the overall tone of argument was in some places not corresponding to what had been said in the rebuttal letter and also does not really solve the concern brought forward by reviewer #2. Specifically, this is true for the argument that using “fine-root traits” instead of “belowground traits” does solve all of the problems related to the strong difference in trait selection above and belowground. This is not the case as clearly pointed out by reviewer and the current revision does not fully solve that point. In fact, there are several parts giving the impression that the difference in trait selection is not acknowledged. I would like to specify this with examples:

(1) In lines 99-115 the differences in functional divergence between aboveground and fine-root traits are assessed but the concluding sentence (or the whole paragraph) does not mention the potential effect of trait selection differences. The problem of trait selection is clearly acknowledged in the rebuttal letter, where additional data provided some further insight, but in the paper – though present – is not always properly emphasized. In this specific example, rather than ending with a very diffuse sentence that “a relatively small number of trait syndromes is extremely prevalent, whereas many others, while viable, are rare” this differentiation should have been mentioned.

We have added the sentence proposed by Referee #2: “This difference may be related to the lack of sufficient data on root traits that scale with plant size (e.g., rooting depth or root system size²³) and might contribute to variation along a size-dependent belowground dimension analogous to C1”, which we think solves this issue.

(2) There are a number of statements still generalizing the results as evidence for lower belowground trait variation compared to the aboveground variation. Again, using the word “fine-roots” might not change the perception of the reader unless repeatedly stated as such. It needs to be pointed out explicitly that with fine-roots no size related traits as aboveground are included. Statements like “general pattern of higher functional trait variation aboveground” (line 205) or “In addition we found that plants differentiate preferentially in the aboveground rather than the fine-root part of this functional traits space” do not help to clarify this fact. Rather I would suspect that these sentences will be cited in future as general statements of support for overall differences in trait variation above and belowground. I think in these sentences you have to clarify that size is included above but not below.

I do realize the problem of missing trait data and this is well pointed out in the conclusion part. Yet I think adding 1 or 2 half sentences on this fact earlier in the discussion might help the reader to put the results into a better perspective.

We have modified the sentence in Line 205, to make even clearer that the result refers only to fine-root traits: “Combining the most comprehensive trait databases available, we found that incorporating fine-root traits into the global spectrum of plant form and function³ enriches it with non-redundant information, and exposes a general pattern of higher functional trait differentiation for aboveground than for fine-root traits.”.

Similarly, we have also modified the last paragraph to make it even more clear that our results might be modified when new traits considering other aspects of belowground functional variation are added.

Minor comment:

In L133 – you cite Bergmann et al. 2020 as support for your finding that the suits of fine root traits of woody and herbaceous species are virtually the same, yet in the Bergmann paper there was a significant difference between woody and non-woody traits (table S4 that paper) while the pattern of the RES did in fact look really similar between both. This is correctly referred to in lines 163 ff. Perhaps this is what you intend to say but I find it misleading. Clarify please.

Bergmann et al found a significant difference between woody and non-woody species in the RES, but with an R2 value of 0.007, which is comparable to what we report (0.004). We have modified the sentence to make this point clearer (Line 133-137).

In the suppl methods description after the formula to calculate orthogonality on page 3, delete either “estimated” or “averaged”.

Done.