Globl Plant Spectrum

Term Paper - Modern concept in macroecology and Biogeography - Uni Göttingen

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Contents

Abstract

Aim: The global diversity of plant forms and functioning is endless, but still restricted to relatively few combinations of traits. Hence, the study of the traits spectrum provides interesting insights about plant strategies and related constraints. Díaz et. al (2016) were the first to analyze the global spectrum of plants' traits, however they used a limited number of traits. Our work extended their analysis by adding new traits related to root functioning and plant life forms.

Major taxa studied: Our analysis focuses on vascular plants on a global scale.

Methods: For the analysis, three datasets with different traits were used: leaf form and functioning, root form and functioning, and growth and life forms of plants. The datasets were analyzed independently and as a joined dataset by using Principal Component Analyses (PCA) and Principal Coordinate Analyses (PCoA). Additionally, the variation of traits for trees and non-trees was analyzed separately.

Results: Our results are consistent with the findings from Díaz et al. (2016). Plant traits distribute along two main axes, one connected to the plant height and the other to the leaf economic spectrum. Additional traits did not alter the distribution of traits considerably. This remains valid also when analyzing trees and non-trees separately.

Main conclusions: The results show that the leaf economic spectrum and the height are the main traits that are driving plant variation. Moreover, this study supports the hypothesis that root traits and leaf/plant traits are closely connected. Future studies should aim for an improved coverage of trait data and distribution data of plant species.

1   Introduction

The diversity of plants is characterized by a big variety of traits which allow for a wide range of possible trait constellations. However, there are only relatively few trait combinations that are actually present (Díaz et al. 2016). This leads to the scientific question of understanding how the actual traits are distributed and what their variation is. Specifically, by building a global spectrum of plant traits it is possible to understand which are the more successful combinations of traits, which are the traits that can explain the majority of the variation and to have a reference of the trait distribution that can be used to compare plants.

In 2016, Díaz et al. published the first global analysis of vascular plant variation based on several trait combinations. Their data set included vascular plant species of numerous plant families and of a wide geographical distribution. The analysis investigated six different plant traits related to plant form and functioning: plant height, stem specific density, lead area, leaf mass per area, nitrogen content per unit leaf mass, and diaspore mass. Two key dimensions emerged from the analysis which explained almost three-quarters of the variation: the overall size of plants and the size of plant organs (e.g. seeds), and the leaf structure (e.g. nitrogen content, mass per area). The results show that the trait space that was occupied by the analyzed species is strongly restricted compared to the total possible number of trait variations.

From this, the question arises whether the inclusion of a wider range of traits would alter the results. Overall, it is important to note that the traits included in the analysis of Díaz et al. (2016) solely focused on plant/leaf forms and functions and thereby neglected, for example, traits based on life form or root form and functioning. To explore if the inclusion of further traits can result in a different outcome of the analysis, we applied a similar methodology from Díaz et al. (2016), but with addition of other traits.

The traits used in the analysis originate from the combination of three datasets. The first dataset is the TRY dataset (Kattge et al. 2020), which includes the continuous traits used in the previous study by Diaz et al. Additionally, the GIFT (Global Inventory of Floras and Traits) dataset (Weigelt, König, and Kreft 2020) was used, as it provides an extensive coverage of categorical traits. Categorical traits are traits based on explicit values that cannot be described by continuous variables (e.g. photosynthetic pathway). Finally, also the GRooT (Global Root traits) dataset (Guerrero-Ramírez et al. 2021) was included in order to explore plant diversity at the root level and understand how this might be related to leaf traits. Subsequently, the datasets will be merged together in order to be able to analyze a complete spectrum. However, the datasets

have a high percentage of missing data and the overlap between species may not be optimal, hence obtaining a merged dataset with a sufficient number of species and traits can be challenging.

The aim of this study is to explore the traits spectrum of vascular plants, and in particular, how a spectrum obtained by the inclusion of several new traits can be compared to the global spectrum presented by Díaz et al. (2016). In their study, Díaz et al. hypothesize that adding more traits will not significantly change the overall spectrum. However we would expect that the trait distribution might occupy more space in the trait spectrum and that the two main axes of height and leaf structure will explain less of the total variation.

2 Methods

2.1 Data and data preparation

Three datasets of species' traits were used for the analysis: TRY dataset (Kattge et al. 2020), GRooT dataset (Guerrero-Ramírez et al. 2021) and GIFT dataset (Weigelt, König, and Kreft 2020). These datasets consist of species names and the respective trait values. The species included in the datasets are globally distributed and represent a sufficient selection of vascular plants of different growth forms and geographical origins. The TRY dataset mainly covers traits related to plant functioning and plant form, the GIFT dataset consists of similar traits but has additional traits based on life form and growth form. The GRoot dataset includes traits related to root form and functioning. In a first step, the data availability in each dataset was determined in order to identify the traits with high percentages of data coverage. Unfortunately, all three datasets have a high amount of missing data as can be seen in Figure 1, as an example of the missing data in the GRooT database.

Table 1 gives an overview over the traits that were selected for the subsequent analysis. These traits were selected according to the data coverage and biological significance. The amount of data available was a key aspect in deciding which traits to select. To facilitate this process for the combined dataset the total number of rows with non-missing data was calculated for each pair of traits (extended figure 8). This allowed the identification of the trait combination which resulted in the highest amount of data available after the merge.

Table 1: Traits used in the analysis with description. The traits are divided in the different dataset of origin.

| Trait name	Trait abbreviation	Unit/Values
TRY		
Adult plant height	*H*	m
Stem specific density	*SSD*	mg mm-3
Leaf mass per area	*LMA*	g m-2
Leaf Area	*LA*	mm2
N content per unit leaf mass	*N*	mg g-1
Diaspore mass	*SM*	mg
GRooT		
Root tissue density	*R_TD*	g cm-3
Mean root diameter	*R_diam*	mm
Specific root length	*SRL*	m g-1
Root nitrogen concentration	*R_N*	mg g-1
GIFT		
Parasite	*parasite*	facultative / independent / obligatory
Growth form	*growth_form*	herb / shrub / tree / other
Life form	*life_form*	chamaephyte / cryptophyte / hemicryptophyte / phanerophyte / therophyte
Lifecycle	*lifecycle*	annual / biennial
Photosynthetic pathway	*phot_path*	C3 / C4 / CAM
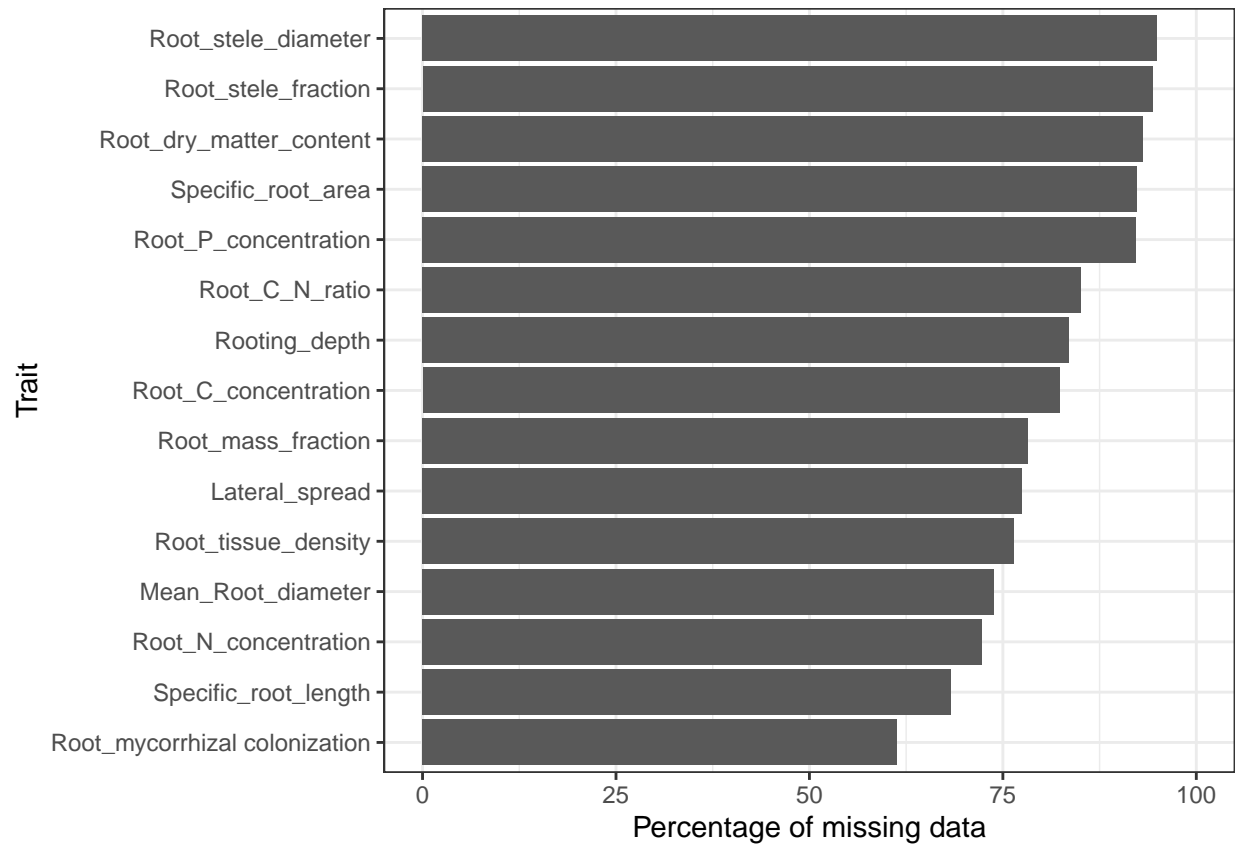
Figure 1: Percentage of species where trait data is missing for the entire GRooT dataset. Only the 15 most common traits are shown.

For some species, the datasets had different names, hence, in order to best compare the three different datasets, the species nomenclature was harmonized. This was done using the taxonstand R package (Cayuela et al. 2012), which uses The Plant Index database ("Home — the Plant List" 2021). Only the TRY and GRooT dataset were updated as the GIFT dataset already uses The Plant Index nomenclature.

The datasets were visually checked for outliers and extreme values were removed (as can be seen in Figure 2) . In particular for the TRY datasets the leaf area (LA) and seed mass (SM) traits had some extreme values that were removed. All the continuous variables were then normalized and transformed with a log10, in order to obtain a distribution more similar to a normal distribution.
The three datasets were merged using the species names, then the traits of interest were selected and the species with missing data removed.
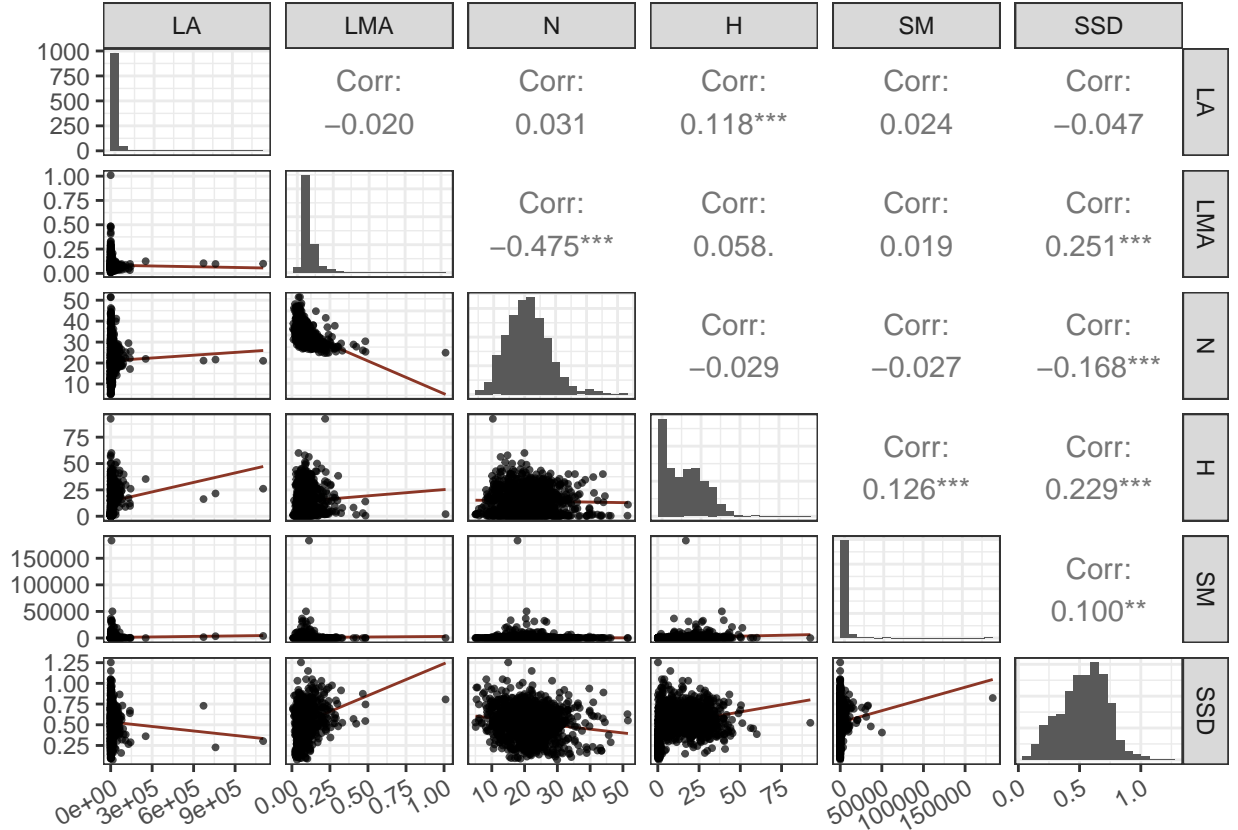

Figure 2: Pair plot with all the traits in the TRY dataset *before* normalization and outlier removal. It is possible to see extreme values numerous traits. Red line in scatter plot are a linear regression.

2.2   Trait spectrum analysis

To analyze the multidimensional spectrum, a PCA (Principal Component Analysis) (Wold, Esbensen, and Geladi 1987) was conducted with the selected species and traits from the TRY dataset. For this, the function `cmdscale` from the RBase package `stats` was used (R Core Team, 2021). The distance matrix was then computed as euclidean distance with the function `dist`, also from the RBase package stats. This analysis step was executed in order to determine whether it is feasible to obtain similar results to the ones that Díaz et al. (2016) reported. However, it has to be noted that the dataset from Díaz et al. is not public, hence the version of TRY dataset used in our analysis may not be exactly the same.

The PCA analysis is applicable only to continuous variables, however the GIFT dataset includes only categorical traits. Therefore, a new analysis approach was needed to analyze the data. A principal coordinate analysis (PCoA) was performed, using the Gower distance to calculate the distance matrix (Gower 1971),

as it works with both categorical and continuous variables. The gower distance was computed using the `gower.dist` from the `StatMatch` R Package (D'Orazio 2020). The PCoA was then calculated using the `cmdscale` scale function, as for the PCA.

The results of the PCoA/PCA analysis were plotted with the first two axes, as they explained a sufficient amount of the total variation. The function `envfit`, from the R package `vegan` (Oksanen et al. 2020), was used to fit the traits onto the PCoA points. Continuous variables were represented as vectors, while for categorical variables the centroid of each trait value was visualized.

In an extra step, the merged dataset was divided into two datasets based on the growth form: one dataset included all species of the growth form tree, the second one all species with growth forms different to tree, according to the GIFT dataset. This approach was done, as the results indicated a strong influence of the plant height on the variation explained by the PCoA. Hence, the dataset was split to exclude the influence of the height. After dividing the merged dataset, the PCoA analysis as described before was computed again, using the gower distance and the `cmdscale` function.

3   Results

3.1   Trait plant spectrum TRY dataset

For the TRY dataset the principal component analysis (PCA) was performed (Figure 3). After the removal of missing values the dataset contained 1028 species and 6 traits.

The results of the multivariate analysis are very similar to the results obtained by Díaz et. al. There are two couples of traits that can explain the majority of the variation in the plant spectrum. The first one is the height (H) and the seed mass (SM), which roughly correspond to the first PCA axis. These two traits are correlated to each other, as shown by the r^2 ($r^2 = 0.61$). The second main axis of variation is connected to the traits Leaf Mass Area (LMA) and Nitrogen (N), which are negatively correlated ($r^2 = -0.60$) and almost opposite in the PCA plot. Almost 70 % of the total variation is explained by the first two PCA axes.
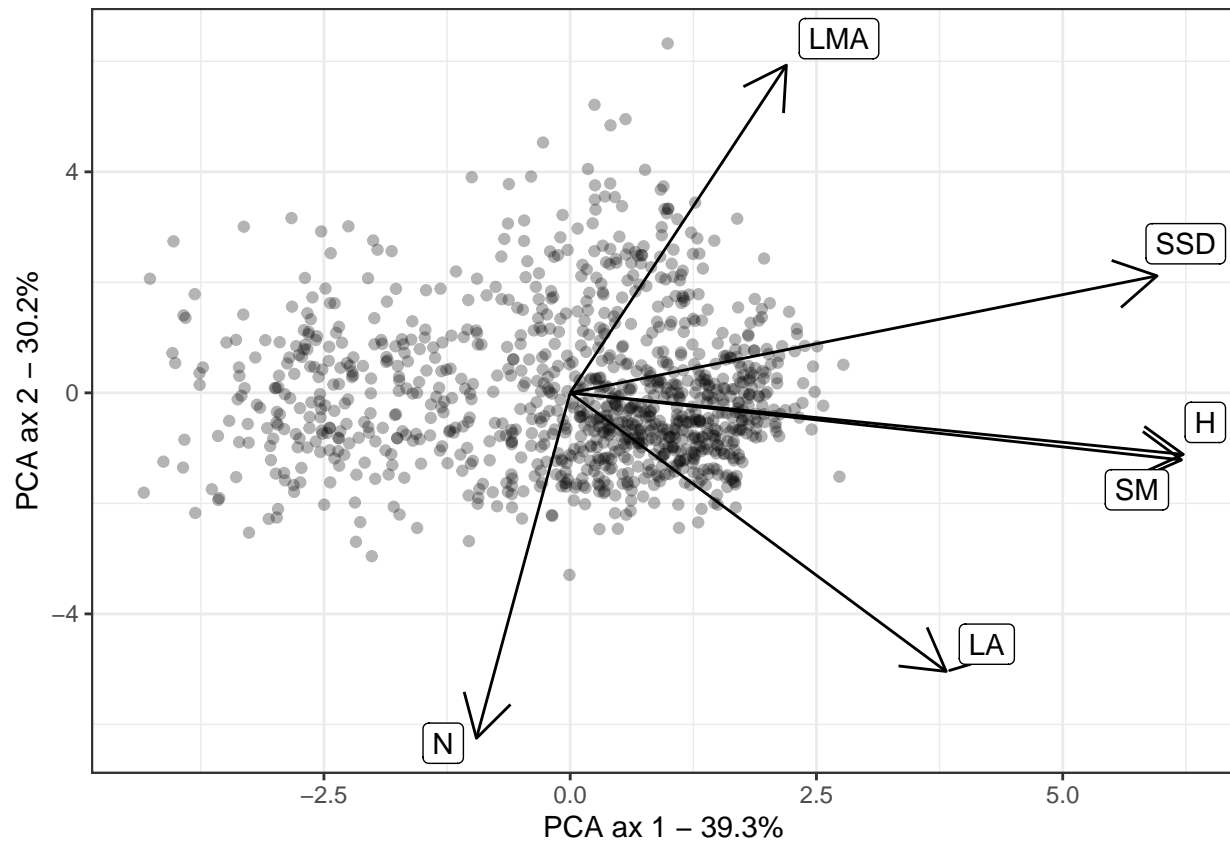

Figure 3: PCA for TRY dataset. Axes 1 and 2 with the amount of variation explained. Arrows represent continous traits

3.2   Plant trait spectrum of root traits

The GRooT dataset required more pre-processing, as many traits are missing for the majority of the species (Figure 1). Therefore, only 4 traits were selected:

- Root tissue density (R_TD)
- Mean root diameter (R_diam)
- Specific root length (SRL)
- Root Nitrogen concentration (R_N)

Even though the trait "Root mycorrhizal colonization" showed the lowest percentage of missing data, it was not included in the data analysis as this trait was of minor importance and by removing it, it was possible to

include more species in the analysis. The PCA analysis was performed with 824 species and 4 traits (Figure 4). The four traits can be divided into two couples. The specific root length is highly correlated with the first PCA axis and opposed to the mean root diameter. Conversely, the root nitrogen concentration is opposed to the root tissue density and more correlated with the second PCA axis. The first two axes explain more than 75% of the total variation.
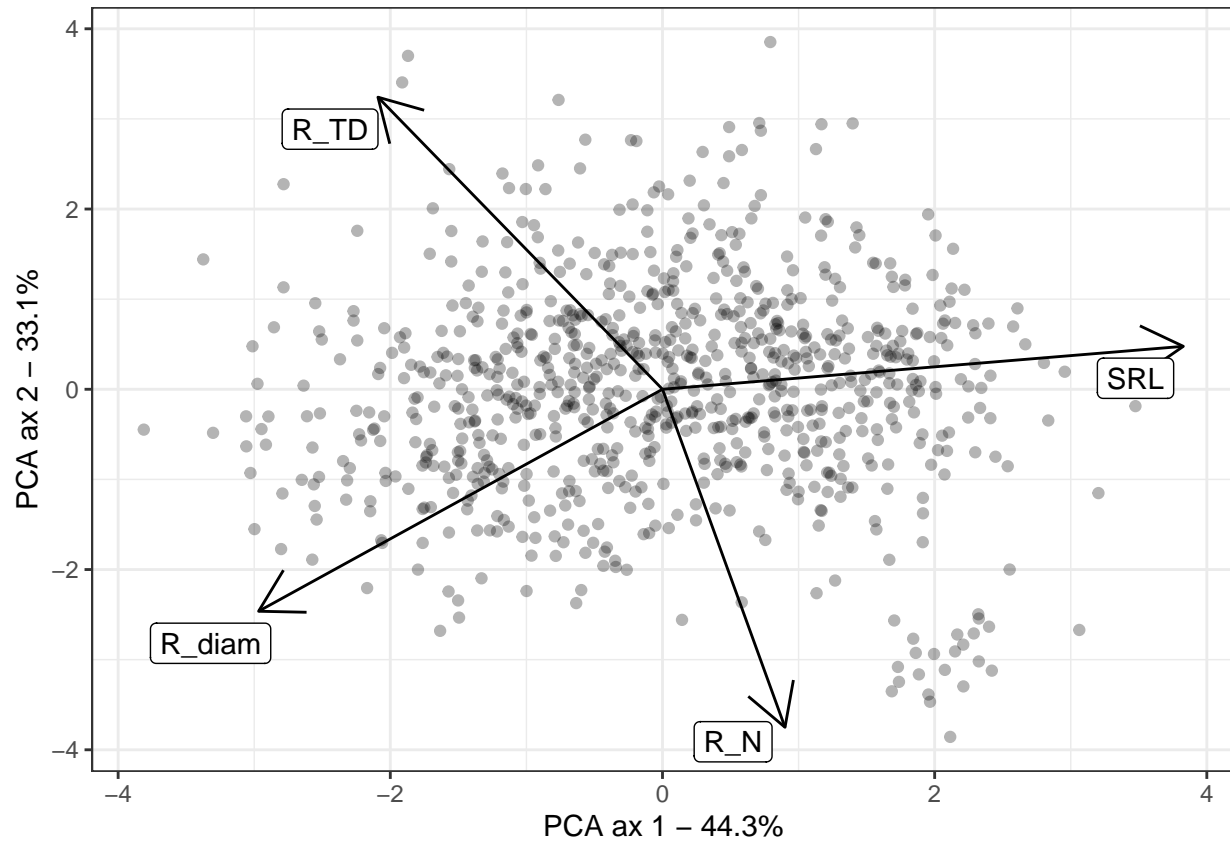

Figure 4: PCA for GRooT dataset. Axes 1 and 2 with the amount of variation explained. Arrows represent continous traits

3.3   Plant trait spectrum of leaf, root and plant traits

Based on the data availability, the following continuous traits from the TRY and GRooT dataset were used for the joined analysis:

- Specific root length (SRL)
- Root nitrogen concentration (R_N)
- Mean root diameter (R_diam)
- Leaf mass area (LMA)
- Leaf nitrogen concentration (N)
- Plant height (H)
- Seed mass (SM)

In comparison to the single analysis of the datasets, as described before, the joined analysis did not include the leaf area, the specific stem density and the root tissue density anymore, as the data limitation of these traits severely reduced the number of species that could be included in the analysis. Figure 5 shows the correlation between the analyzed traits and the distribution of the data points. It becomes clear that plant height is negatively correlated with the root length and the seed mass and positively correlated with the root diameter of plants. Furthermore, the figure shows that root diameter and root length are negatively correlated.

It is however noticeable that the data points related to the plant height are not normally distributed, even after normalizing the data. This might be due to the removal of missing data and, subsequently, the removal of species from the data set.
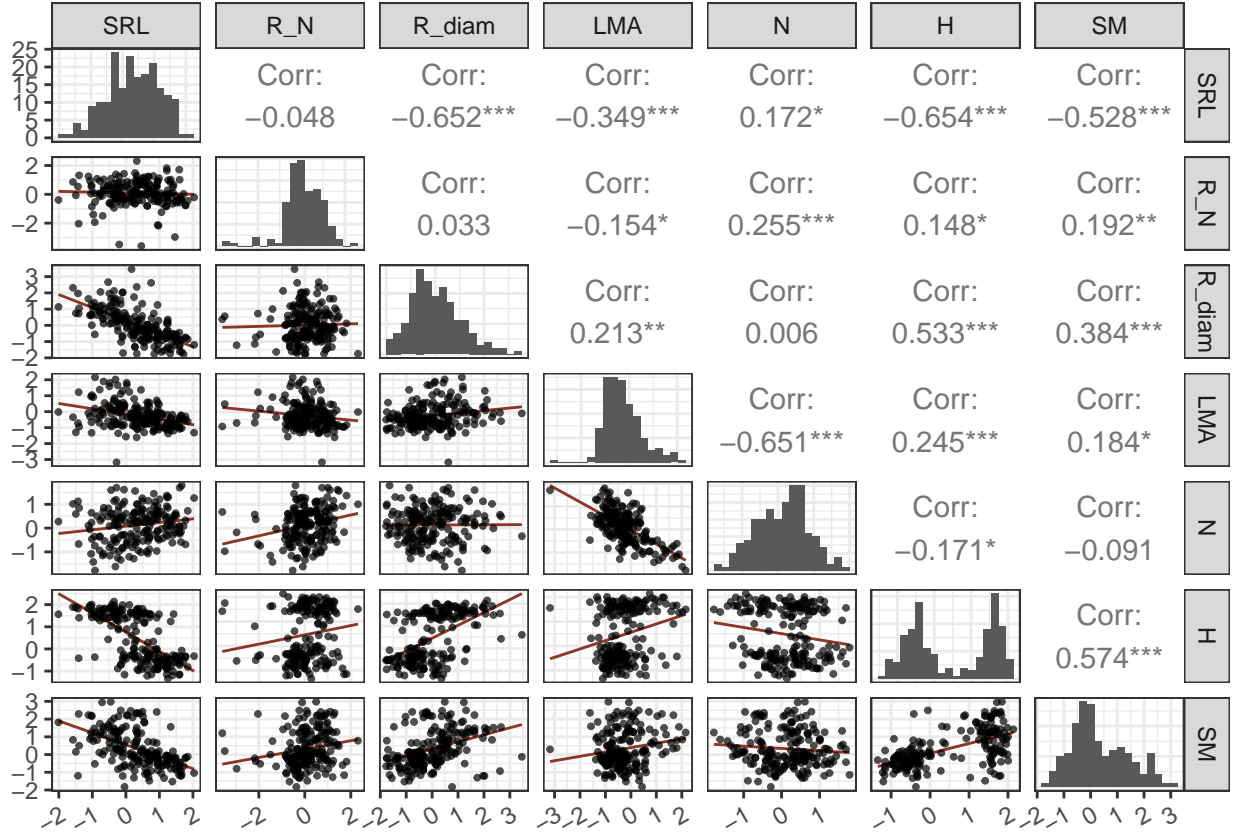

Figure 5: Pair plot with all the continous trait used in the analysis from the TRY and GRooT dataset after normalization and outliers removal. Red line in scatter plot are a linear regression line.

For the categorical traits that were included in the GIFT data set, the following traits were selected for the analysis:

- Parasite
- Growth form
- Lifecycle
- Life form
- Photosynthetic pathway

A detailed description of the individual traits can be found in Table 1. The merged data table of all three datasets consists of 193 species and 12 different traits.

For the joined dataset a Principal Coordinate Analysis (PCoA) was performed. The first axis of the PCoA explains about 60% of the variation and, as can be seen in Figure 6, is mainly related to the plant height and the seed mass. The second axis accounts for about 15% of the variation and is connected to the leaf mass area and leaf nitrogen concentration.

In accordance with the results shown in Figure 6, the PCoA indicates the positive correlation of plant height, seed mass and root diameter and the negative correlation of these traits with root length. The distribution of the categorical traits shows that high growing plants belong to the life form 'tree' and the growth form 'phanerophyte' and that for low growing plants the traits can be distinguished for plants with smaller leaves and higher nitrogen concentration and plants with bigger leaves and lower nitrogen concentration. The latter

mainly belong to the growth form 'graminoid' and the life forms 'hemicryptophyte' and 'chamaephyte.' It is also noticeable that among the smaller plants, species with bigger leaves are mainly 'C4' plants, whereas 'C3' plants are shown to be of medium height and to have medium leaves. Concerning the life cycle of the plant species, the PCoA shows that medium high plants are mainly perennial plants, whereas smaller plants have a biennial and annual life cycle.
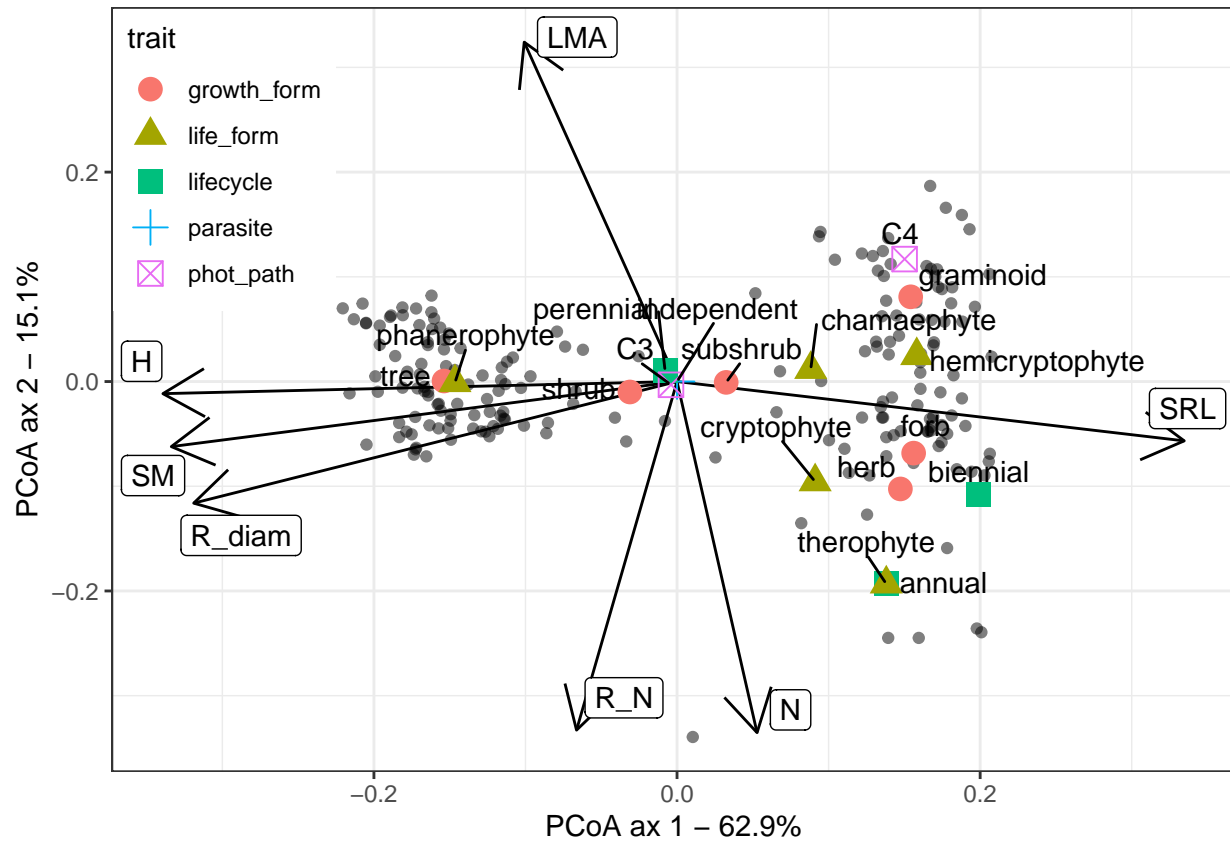

Figure 6: PCoA axes 1 and 2 with complete dataset with traits from TRY, GRooT and GIFT. Arrow represent continous traits while point different values of categorical traits.

3.4   Plant trait spectrum of trees and non-trees

After dividing the data set into 'trees' and 'non-trees,' the tree data table consisted of 91 species and the non-tree data table of 102 species. Then, a PCoA was conducted for both data tables. The two main axes and the influence of the individual traits can be seen in Figure 7. For both PCoAs, the first axis explains between 30-35% of the variation and the second axis accounts for around 25% of the variation. However, there are some differences in the influence of the traits noticeable. Overall, the tree species are more widely distributed than the non-tree species. Furthermore, the root nitrogen concentration seems to be positively correlated to the root length of tree species and negatively correlated to the root length of non-tree species.
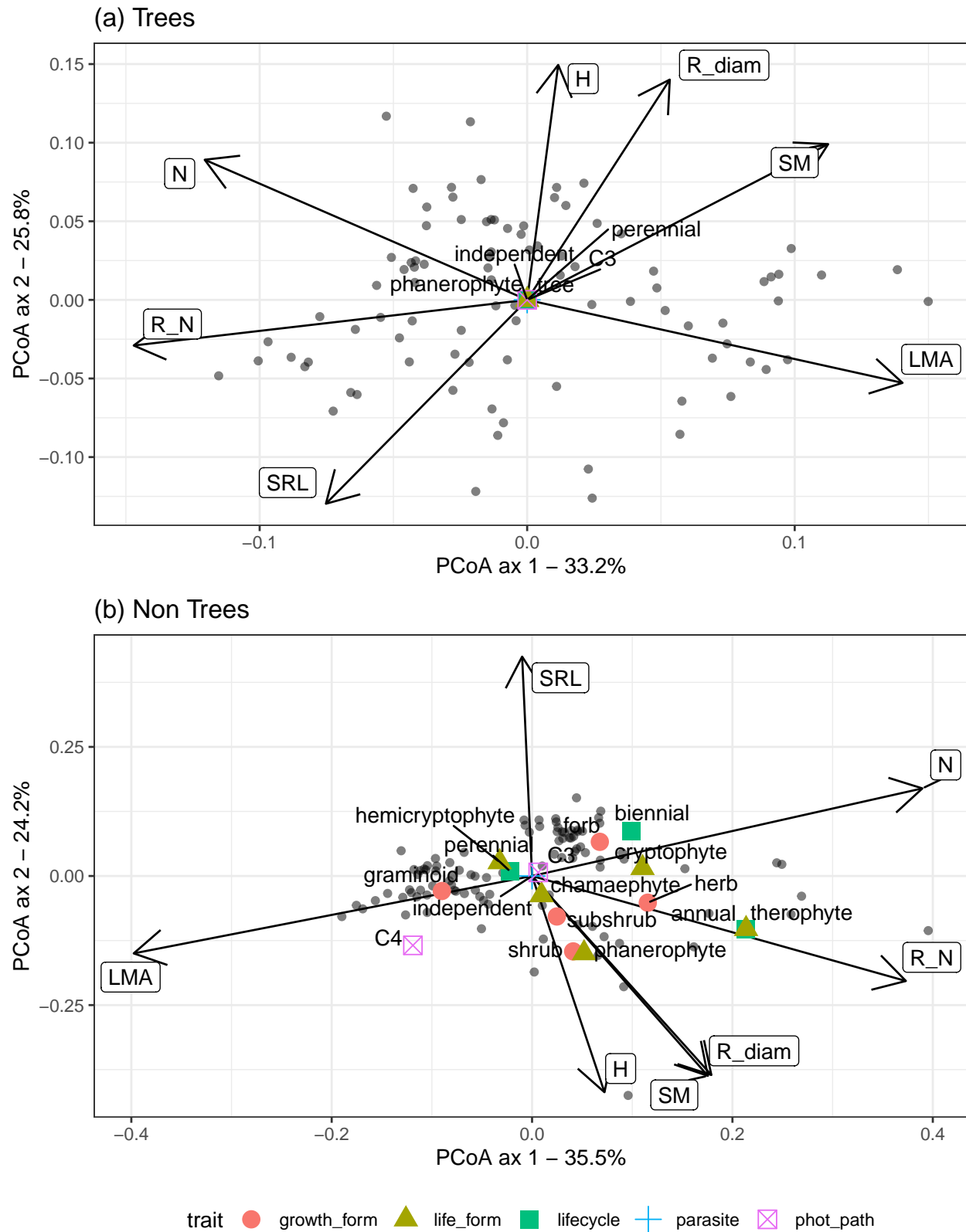
Figure 7: PCoA axes 1 and 2 with dataset divided between trees (a) and non trees (b). Arrow represent continous traits while point different values of categorical traits.

4 Discussion

Selecting the most important traits with the highest data availability was the first crucial step before starting the data analysis. To receive reliable results, it was necessary to filter the traits that influence the variation of plant species the most, but of which, in addition, data coverage was sufficient enough for a subsequent analysis. Therefore, traits with low data coverage were excluded from the analysis, as well as traits of minor importance (e.g. Root mycorrhizal colonization).

Compared to only the TRY dataset, in the final PCoA analysis several additional traits were included, but the results are still similar to the ones obtained with fewer traits (Figures 3 and 6). The results clearly show that there is a coordination between different traits. This aspect is important for plants as natural selection favours an optimal allocation of resources, where each trait follows the plant's overall strategy (Peter B. Reich 2014).

The variation of the leaf traits can be effectively summarized with one axis, the leaf economic spectrum (LES) (Poorter, Lambers, and Evans 2014; Wright et al. 2004, 2005). This spectrum has, on one side, species with quick turn around in leafs, high nutrient concentration and low mass per area. On the other side, there are plants with low turn around times, low nutrient concentration and high leaf mass area. This represents a range of strategies that plants use to allocate resources (Wright et al., 2004), going from fast growth but low persistence to slow growth but longevity of leaves. The economic spectrum is confirmed in our analysis, as the PCoA plots (Figures 3, 4, 6) show a clear LMA-N axis, which represents the leaf economic spectrum. Moreover, this axis explains a high amount of the total variation.

Root traits are also coordinated along a root economic spectrum (RES). The root economic spectrum is similar to the LES with fast productive species on one end having low root tissue density and high root nitrogen concentration, while slow persistent species with high root tissues density and low nitrogen content can be found on the other end. Roots, however, are less constrained than leaves and the relative importance of the RES is debated. Some authors propose to use the RES to summarize the whole root trait variation (Freschet et al. 2010; Peter B. Reich 2014), while others suggest that the root trait spectrum is actually more complex (Kong et al. 2019; Kramer-Walter et al. 2016). In particular Kramer-Walter et al. (2016) identify a second main axis of variation, independent from the RES, that is characterized by the specific root length and the root diameter. Our results (Figure 4) support this thesis, in fact the N-tissue density axis (RES) is roughly orthogonal to the root diameter - specific root length axis.

Adding categorical traits extended the traits that could be used for the analysis by characteristics based on categories rather than values and therefore enabled the inclusion of important traits such as life forms and growth forms. But, as can be seen in Figure 6, the categorical traits show some clear connections with the other traits. The variation of plant species that is explained by the categorical traits is, as well, distributed in the two main axes already identified by Díaz et al. (2016). Whereas the traits 'life form' and 'growth form' are, first of all, aligned with the plant height and then, for smaller plants, with the LES, the life cycle of plant species is mainly connected with the leaf economic spectrum.

As already identified by Díaz et al. (2016), plant height plays an important role in the variation of plant species. Adding additional traits did not lower this influence, but even increased the amount of variation that can be explained by the axis related to the plant height (Figure 6). While in the first analysis the axis representing the influence of height accounted for 39% of variation (Figure 3), in the analysis of the joined datasets the axis referring to the height explained more than 60% of variation.

Figure 6, similar to Figure 3, shows variation mainly into two axes. This indicates that below-ground traits, such as root diameter or root length, stand in close relation to above-ground traits. Previous studies identified similar correlations which led to the conclusion that plant strategies can be assumed to extend from leaf traits to root traits (Mokany and Ash 2008; P. B. Reich et al. 2003; Roumet, Urcelay, and Díaz 2006; Tjoelker et al. 2005; Withington et al. 2006). Anatomical constraints are among the main factors influencing the correlation of plant traits. For instance, tall plants are in need of a more stable stem and thicker roots in order to enable further growth. In contrast, smaller plants can invest in a faster growth, but are subsequently bound to a shorter life span (Kramer-Walter et al. 2016). However, in the literature there is not a definite agreement on the relationship between leaf traits and root traits (Mommer and Weemstra 2012). In our analysis, due to the

inclusion of the height, which was not considered in the previous literature, we obtained a good coordination between the root and the rest of the plant traits. The root diameter - specific root length axis is aligned with the height (Figure 6), while the root nitrogen distribution is similar to the leaf nitrogen content.

Another correlation that can be identified is the alignment of plant height and seed mass (Figure 3 and 6) which shows that tall plants tend to have bigger seeds and vice versa. This stands in contrast with the findings of P. B. Reich et al. (2003) who concluded that seed mass differences mainly occur within fixed height categories rather than between different heights.

Nevertheless, our findings have to be interpreted carefully as the data points for plant height showed a non-normal distribution (Figure 5), which indicates that the dataset used for the analysis might lack an overall representation of plant traits in some cases. More precisely, the distribution of height data points shows that the data set mainly covers tall and small plants and has an underrepresentation of medium sized plants.

In order to reduce the influence of height the dataset was divided into woody and non-woody plants and the PCoA performed separately (Figure 7). Interestingly, even in this scenario the trait spectrum is still characterized by two main axes: height and LES. However, their importance changes, as the LES is aligned with the first PCA axis while the height with the second one. Hence, the height explains less of the total variation but still remains a crucial trait. All the other traits remain connected to these two axes with the exception of the root nitrogen which is less coordinated with the leaf nitrogen content.

Despite the broad scale of the analysis, some limitations have to be noted and taken into account when interpreting the results. Firstly, data for the different traits in the data sets were severely limited due to a high amount of missing data. This led to a considerable reduction of available traits for the analysis. Additionally, as a consequence of the limited amount of included traits, the number of species that could be analyzed was reduced as well. Consequently, it has to be acknowledged that because of the limited data of traits and species, the distribution of the included species decreased which, for instance, can be directly seen in the distribution of data points for plant height. It becomes visible that because of the limited data points, a considerable fraction of species was left out in the analysis. Therefore, the results might not be suitable for globally applicable interpretations and conclusions, as they likely cannot be seen as representative on a global scale.

While the general idea of including numerous traits in the analysis promises a broader overview over the variation of plant characteristics, the results show that, in contrast to this idea, plant variation is still mainly influenced on two main axes. Additionally, the inclusion of further traits and the usage of multiple datasets limits the amount of species that can be included in the analysis and therefore decreases the reliability of the results.

5   Conclusion

This study supports the findings by Diaz et al. (2016) that global plant variation is mainly influenced by two main characteristics: the leaf economic spectrum which balances leaf construction costs against potential growth, and the size of the plant and its organs. Plant height, in particular, has been shown to have a considerable importance on the global variation of plants, even when including additional traits in the analysis. The inclusion of additional traits enabled the analysis of a broader range of possible influences on global plant variation and supports a better understanding of adaptations and trade-offs of plant species on a global scale. The results indicate that a global plant spectrum can be used to assess the distribution of plant species and the influence that traits have on it. Further research should focus on the availability and coverage of plant trait data and the geographical distribution of plant species. An improved data set might provide further insight into global plant variation and could lead to the emergence of alternative patterns. Furthermore, it might be beneficial to analyze plant variation with regard to different plant taxa to determine more concrete patterns of variation for related plant species. In this context, the division of plant species into, for example, conifer and deciduous species might be a reasonable approach.

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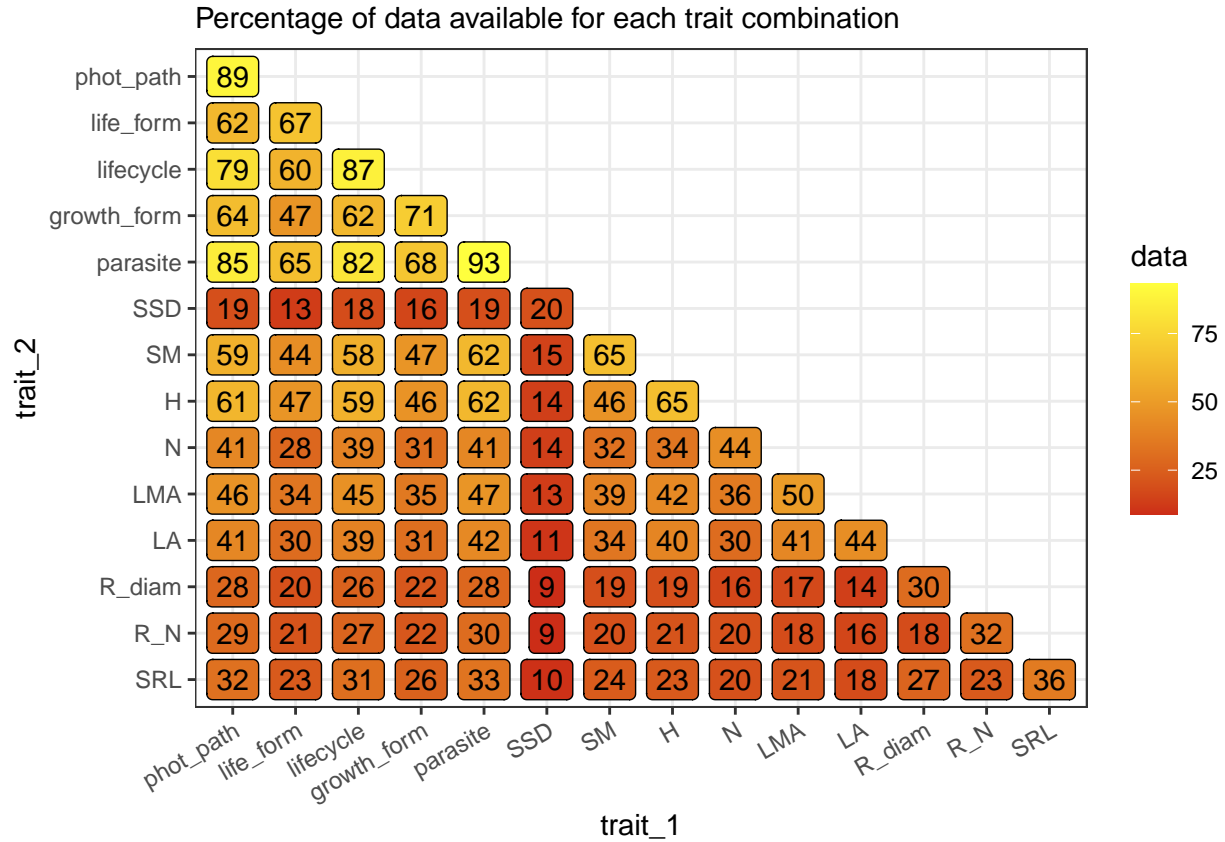
Extended figures

Figure 8: Percentage of data available for each pairwise trait combination. The data availability include only the two select traits at each time, hence it doesn't represents the combination of multiple traits.