TRY – a global database of plant traits

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Abstract

Plant traits – the morphological, anatomical, physiological, biochemical, and phenological characteristics of plants and their organs – determine how primary producers respond to environmental factors, affect other trophic levels, influence ecosystem processes and services, and provide a link from species richness to ecosystem functional diversity. Trait data thus represent the raw material for a wide range of research from evolutionary biology, community and functional ecology to biogeography. Here we present the global database initiative named TRY, which has united a wide range of the plant trait research community worldwide and gained an unprecedented buy-in of trait data: so far 93 trait databases have been contributed. The data repository currently contains almost three million trait entries for 69,000 out of the world's 300,000 plant species, with a focus on 52 groups of traits characterising the vegetative and regeneration stages of the plant life cycle, including growth, dispersal, establishment and persistence. A first data analysis shows that most plant traits are approximately log-normally distributed, with widely differing ranges of variation across traits. Most trait variation is between species (interspecific), but significant intraspecific variation is also documented, up to 40% of the overall variation. Plant functional types (PFTs), as commonly used in vegetation models, capture a substantial fraction of the observed variation - but for several traits most variation occurs within PFTs, up to 75% of the overall variation. In the context of vegetation models these traits would better be represented by state variables rather than fixed parameter values. The improved availability of plant trait data in the unified global database is expected to support a paradigm shift from species to trait-based ecology, offer new opportunities for synthetic plant trait research and enable a

more realistic and empirically grounded representation of terrestrial vegetation in Earth system models.

Introduction

Plant traits - morphological, anatomical, biochemical, physiological or phenological features measurable at the individual level (Violle et al. 2007) - reflect the outcome of evolutionary and community assembly processes responding to abiotic and biotic environmental constraints (Valladares et al. 2007). Traits and trait syndromes (consistent associations of plant traits) determine how primary producers respond to environmental factors, affect other trophic levels, and influence ecosystem processes and services (Aerts and Chapin 2000, Grime 2001, Lavorel and Garnier 2002, Díaz et al. 2004, Grime 2006, Garnier and Navas in press.). In addition, they provide a link from species richness to functional diversity in ecosystems (Díaz et al. 2007). A focus on traits and trait syndromes therefore provides a promising basis for a more quantitative and predictive ecology and global change science (McGill et al. 2006, Westoby and Wright 2006).

Plant trait data have been used in studies ranging from comparative plant ecology (Grime 1974, Givnish 1988, Peat and Fitter 1994, Grime et al. 1997) and functional ecology (Grime 1977, Reich et al. 1997, Wright et al. 2004) to community ecology (Shipley et al. 2006, Kraft et al. 2008), trait evolution (Moles et al. 2005a), phylogeny reconstruction (Lens et al. 2007), metabolic scaling theory (Enquist et al. 2007), palaeobiology (Royer et al. 2007), biogeochemistry (Garnier et al. 2004, Cornwell et al. 2008), disturbance ecology (Wirth 2005, Paula and Pausas 2008), plant migration and invasion ecology (Schurr et al. 2005), conservation biology (Ozinga et al. 2009, Römermann et al. 2009) and plant geography (Swenson and Weiser 2010). Access to trait data for a large number of species allows testing levels of phylogenetic conservatism, a promising principle in ecology and evolutionary biology (Wiens et al.

2010). Plant trait data have been used for the estimation of parameter values in vegetation models, but only in a few cases based on systematic analyses of trait spectra (White et al. 2000, Kattge et al. 2009, Wirth and Lichstein 2009, Ziehn et al. accepted). Recently plant trait data have been used for the validation of a global vegetation model as well (Zaehle and Friend 2010).

While there have been initiatives to compile data sets at regional scale for a range of traits (e.g. LEDA[1], BiolFlor[2], EcoFlora[3], BROT[4]) or at global scale focusing on a small number of traits (e.g. GlopNet[5], SID[6]), a unified initiative to compile data for a large set of relevant plant traits at the global scale was lacking. As a consequence studies on trait variation so far have either been focussed on the local to regional scale including a range of different traits (e.g. Baraloto et al. 2010), while studies on global scale were restricted on individual aspects of plant functioning, e.g. the leaf economic spectrum (Wright et al. 2004), the evolution of seed mass (Moles et al. 2005 a,b) or the characterisation of the wood economic spectrum (Chave et al. 2009). Only few analyses on global scale have combined traits from different functional aspects, but for a limited number of plant species (e.g. Diaz et al. 2004).

In 2007, the TRY[7] initiative started compiling plant trait data from the different aspects of plant functioning on global scale to make the data available in a consistent format through one single portal. Based on a broad acceptance in the plant trait community (so far 93 trait databases have been contributed, Table 1), TRY has accomplished an unprecedented coverage of trait data and is now working towards a

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[1] LEDA - Life History Traits of the Northwest European Flora: http://www.leda-traitbase.org
[2] BiolFlor – Trait Database of the German Flora: http://www.ufz.de/biolflor
[3] EcoFlora - The Ecological Flora of the British Isles: www.ecoflora.co.uk
[4] BROT – Plant Trait Database for Mediterranean Basin Species: http://www.uv.es/jgpausas/brot.htm
[5] GlopNet – Global Plant Trait Network: http://www.bio.mq.edu.au/~iwright/glopian.htm
[6] SID - Seed Information Database: data.kew.org/sid/
[7] TRY – Not an acronym, rather an expression of sentiment: http://www.try-db.org

communal global repository for plant trait data. The new database initiative is expected to contribute to a more realistic and empirically based representation of plant functional diversity on global scale supporting the assessment and modelling of climate change impacts on biogeochemical fluxes and terrestrial biodiversity (McMahon et al. in press).

For several traits the data coverage in the TRY database is sufficient to quantify the relative amount of intra- and interspecific variation, as well as variation within and between different functional groups. Thus the dataset allows to examine two basic tenets of comparative ecology and vegetation modelling, which, due to lack of data, had not been quantified so far:

(1) On the global scale the aggregation of plant trait data at the species level captures the majority of trait variation. This central assumption of plant comparative ecology implies that, while there is variation within species, this variation is smaller than the differences between species (Garnier et al. 2001, Keddy et al. 2002, Westoby et al. 2002, Shipley 2007). This is the basic assumption for using average trait values of species to calculate indices of functional diversity (Petchey and Gaston 2006, de Bello et al. 2010, Schleuter et al. 2010), to identify ecologically important dimensions of trait variation (Westoby 1998), or to determine the spatial variation of plant traits (Swenson and Enquist 2007, Swenson and Weiser 2010).

(2) On the global scale basic plant functional classifications capture a sufficiently important fraction of trait variation to represent functional diversity. This assumption is implicit in today’s dynamic global vegetation models (DGVMs), used to assess the response of ecosystem processes and composition to CO_2 and climate changes. Due to computational constraints and lack of detailed information these models have been

developed to represent the functional diversity of >300,000 documented plant species on Earth with a small number (5-20) of basic plant functional types (PFTs, e.g. Woodward and Cramer 1996, Sitch et al. 2003). This approach has been successful so far, but limits are becoming obvious and challenge the use of such models in a prognostic mode, e.g. in the context of Earth system models (Lavorel et al. 2008, McMahon et al., in press).

This article first introduces the TRY initiative and presents a summary of data coverage with respect to different traits and regions. For a range of traits we characterise general statistical properties of the trait density distributions, a prerequisite for statistical analyses, and provide mean values and ranges of variation. For ten traits that are central to leading dimensions of plant strategy we then quantify trait variation with respect to species and plant functional type and thus examine the two tenets mentioned above. Finally we demonstrate how trait variation within PFT is currently represented in the context of global vegetation models.

Material and Methods

Types of data compiled

The TRY data compilation focuses on 52 groups of traits characterising the vegetative and regeneration stages of plant life cycle, including growth, reproduction, dispersal, establishment and persistence (Table 2). These groups of traits were collectively agreed to be the most relevant for plant life-history strategies, vegetation modelling, and global change responses on the basis of existing shortlists (Grime et al. 1997, Weiher et al. 1999, Lavorel and Garnier 2002, Cornelissen et al. 2003b, Díaz et al. 2004, Kleyer et al. 2008) and wide consultation with vegetation modellers and plant ecologists. They include plant traits *sensu stricto*, but also ‘performances’ (*sensu* Violle et al. 2007), such as drought tolerance or phenology.

Quantitative traits vary within species as a consequence of genetic variation (among genotypes within a population/species) and phenotypic plasticity. Ancillary information is necessary to understand and quantify this variation. The TRY dataset contains information about the location (e.g. geographical coordinates, soil characteristics), environmental conditions during plant growth (e.g. climate of natural environment, or experimental treatment), and information about measurement methods and conditions (e.g. temperature during respiration or photosynthesis measurements). Ancillary data also include primary references.

By preference individual measurements are compiled in the database, like single respiration measurements or the wood density of a specific individual tree. The dataset therefore includes multiple measurements for the same trait, species and site. For some traits, e.g. leaf longevity, such data are only rarely available on single individuals (e.g. Reich et al. 2004), and data are expressed per species per site instead. Different measurements on the same plant (resp. organ) are linked to form observations that are hierarchically nested. The database structure ensures that (1) the direct relationship between traits and ancillary data and between different traits that have been measured on the same plant (resp. organ) is maintained and (2) conditions (e.g. at the stand level) can be associated with the individual measurements (Kattge et al. 2010). The structure is consistent with the Extensible Observation Ontology (OBOE; Madin et al. 2008), which has been proposed as a general basis for the integration of different data streams in ecology.

The TRY dataset combines several pre-existing databases based on a wide range of primary data sources, which include trait data from plants grown in natural environments and under experimental conditions, obtained by a range of scientists with different methods. Trait variation in the TRY dataset therefore reflects natural and potential variation on the basis of individual measurements at the level of single organs, and variation due to different measurement methods and measurement error (random and bias).

Data treatment in the context of the TRY database

The TRY database has been developed as a Data Warehouse (Fig. 1) to combine data from different sources and make them available for analyses in a consistent format (Kattge et al. 2010). The Data Warehouse provides routines for data extraction, import, cleaning and export. Original species names are complemented by taxonomically accepted names, based on a checklist developed by IPNI[8] and TROPICOS[9], which had been made publicly available on the TaxonScrubber website by the SALVIAS[10] initiative (Boyle 2006). Trait entries and ancillary data are standardized and errors are corrected after consent from data contributors. Finally, outliers and duplicate trait entries are identified and marked (for method of outlier detection see S1). The cleaned and complemented data are moved to the data repository, whence they are released on request.

Selection of data and statistical methods in the context of this analysis

For the analyses in the context of this manuscript we have chosen traits with sufficient coverage from different aspects of plant functioning. The data were standardized,

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[8] IPNI – The International Plant Names Index: http://www.ipni.org

[9] TROPICOS - Missouri Botanical Garden: http://www.tropicos.org

[10] SALVIAS – Analysis of Local Vegetation Inventories Across Sites: http://www.salvias.net

checked for errors and duplicates excluded. Maximum photosynthetic rates and stomatal conductance were filtered for temperature (15-30°C), light (PAR >500μmolm^2 s^{-1}), and atmospheric CO_2 concentration during measurements (300-400ppm); data for respiration were filtered for temperature (15-30°C)[11]. Statistical properties of density distributions of trait data were characterised by skewness and kurtosis on the original scale and after log-transformation. The Jarque-Bera test was applied to assess departure from normality (Bera and Jarque 1980). Finally outliers were identified (see supplementary material, S1). The subsequent analyses are based on standardized trait values, excluding outliers and duplicates.

PFTs were defined similar to those used in global vegetation models (e.g. Woodward and Cramer 1996, Sitch et al. 2003; see Table 5), based on standardized tables for the qualitative traits 'plant growth form', 'leaf type', 'leaf phenology type', 'photosynthetic pathway', and 'woodiness'[12].

The evaluation of the two tenets of comparative ecology and vegetation modelling focuses on ten traits that are central to leading dimensions of trait variation or that are physiologically relevant and closely related to parameters used in vegetation modelling (Westoby et al. 2002, Wright et al. 2004): plant height, seed mass, specific leaf area (one-sided leaf area per leaf dry mass, *SLA*), leaf longevity, leaf nitrogen content per leaf dry mass (N_m) and per leaf area (N_a), leaf phosphorus content per leaf dry mass (P_m) and maximum photosynthetic rate per leaf area ($Amax_a$), per leaf dry

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[11] A temperature range for respiration from 15-30°C will add variability to trait values. Nevertheless, an immediate response of respiration to temperature is balanced by an opposite adaptation of basal respiration rates to long-term temperature changes. More detailed analyses will have to take short and long term impact of temperature on both scales into account. With respect to photosynthetic rates the problem is similar, but less severe.

[12] Description of qualitative traits used for PFT classification: plant growth form: grass, herb, climber, shrub, tree; leaf type: needle-leaved, broadleaved; leaf phenology type: deciduous, evergreen; photosynthetic pathway: C3, C4, CAM; woodiness: woody, non-woody.

mass ($Amax_m$) and per leaf nitrogen content ($Amax_N$)[13]. For each of the ten traits we quantified variation across species and PFTs in three ways: (1) Differences between mean values of species and PFTs were tested, based on one-way ANOVA. (2) Variation within species, in terms of standard deviation (SD), was compared to variation between species (same for PFTs). (3) The fraction of variance explained by species and PFT was calculated[14].

We observed large variation in SD within species if the number of observations per species was small (see funnel plot in S1). With an increasing number of observations, SD within species approached an average, trait specific level. To avoid confounding effects due to cases with very few observations per species, only species with at least five trait entries were used in statistical analyses (with exception of leaf longevity, where two entries per species were taken as the minimum number because species with multiple entries were very rare). The number of measurements per PFT was sufficient in all cases. Statistical analyses were done in R (R Development Core Team 2009).

Results

Data coverage in the TRY database

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[13] Specific relevance of the ten selected traits: plant height: vegetation carbon storage capacity; seed mass: plant regeneration strategy; leaf longevity: trade-off between leaf carbon investment and gain; SLA: link of light capture (area based) and plant growth (mass based); leaf N and P content: link of carbon and respective nutrient cycle; photosynthetic rates expressed per leaf area, dry mass and N-content: link of carbon gain to light capture, growth and nutrient cycle. Although we realize the relevance of traits related to plant water relations, we did not feel comfortable to include traits such as maximum stomatal conductance or leaf water potential into the analyses for the lack of sufficient coverage for a substantial number of species.

[14] Explained variance (R^2) was calculated as one minus the residual sum of squares divided by the total sum of squares.

As of 31.03.2011 the TRY data repository contains 2.88 million trait entries for 69,000 plant species, accompanied by 3.0 million ancillary data entries[15]. About 2.8 million of the trait entries have been measured in natural environment, less then 100.000 in experimental conditions (e.g. glasshouse, climate or open top chambers). About 2.3 million trait entries are for quantitative traits, while 0.6 million entries are for qualitative traits (Table 2). Qualitative traits, like plant growth form, are often treated as distinct and invariant within species (even though in some cases they are more variable than studies suggest, e.g. flower colour or dispersal mode), and they are often used as covariates in analyses, as when comparing evergreen vs. deciduous (Wright et al. 2005) or resprouting vs. non-resprouting plants (Pausas et al. 2004). The qualitative traits with the highest species coverage in the TRY dataset are the five traits used for PFT classification and leaf compoundness: woodiness (44,000 species), plant growth form (40,000), leaf compoundness (35,000), leaf type (34,000), photosynthetic pathway (32,000) and leaf phenology type (16,000); followed by N-fixation capacity (11,000) and dispersal syndrome (10,000). Resprouting capacity is noted for 3,000 species[16].

The quantitative traits with the highest species coverage are seed size (27,000 species), plant height (18,000), leaf size (17,000), wood density (12,000), SLA (9,000), plant longevity (8,000), leaf nitrogen content (7,000), and leaf phosphorus content (5,000). Leaf photosynthetic capacity is characterised for more than 2,000 species. Some of these traits are represented by a substantial number of entries per species, e.g. *SLA* has on average 10 entries per species, leaf N, P and photosynthetic

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[15] Not all data from the databases listed in Table 1 and summarized in Table 2 could be used in the subsequent analyses, because some recently contributed datasets were still being checked and cleaned in the data staging area (see Fig. 1).

[16] Description of qualitative traits: Plant dispersal syndrome: dispersed by wind, water, animal; N-fixation capacity: able/not able to fix atmospheric N_2; leaf compoundness: simple versus compound, resprouting capacity: able/not able to resprout.

capacity have about 8 resp. 5 entries per species, with a maximum of 1470 entries for leaf nitrogen per dry mass (N_m) for *Pinus sylvestris*.

About 40% of the trait entries (1.3 million) are geo-referenced, allowing trait entries to be related to ancillary information from external databases such as climate, soil, or biome type. Although latitude and longitude are often recorded with high precision, the accuracy is unknown. The geo-referenced entries are associated with 8502 individual measurement sites, with sites in 746 of the 4200 2x2° land grid cells of e.g. a typical climate model (Fig. 2). Europe has the highest density of measurements, and there is good coverage of some other regions, but there are obvious gaps in boreal regions, the tropics, northern and central Africa, parts of South America, southern and western Asia. In tropical South America, the sites fall in relatively few grid cells, but there are high numbers of entries per cell. This is an effect of systematic sampling efforts by long-term projects such as LBA[17] or RAINFOR[18]. For two individual traits the spatial coverage is shown in Figure 3. Here we additionally provide coverage in climate space, identifying biomes for which we lack data (e.g. temperate rainforests). More information about data coverage of individual traits is available on the website of the TRY initiative (http://www.try-db.org).

General pattern of trait variation: test for normality

For 52 traits the coverage of database entries was sufficient to quantify general pattern of density distributions in terms of skewness and kurtosis, and to apply the Jarque-Bera test for normality (Table 3). On the original scale all traits but one are positively skewed, indicating distributions tailed to high values. After log-transformation the

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[17] LBA – The Large Scale Biosphere-Atmosphere Experiment in Amazonia: http://www.lba.inpa.gov.br/lba

[18] RAINFOR – Amazon Forest Inventory Network: http://www.geog.leeds.ac.uk/projects/rainfor

distributions of 20 traits are still positively skewed, while 32 traits show slightly negative skewness. For 49 of the 52 traits the Jarque-Bera test indicates an improvement of normality by log-transformation of trait values - only for three traits normality was deteriorated (leaf phenolics, tannins and carbon content per dry mass; Table 3). The distribution of leaf phenolics and tannins content per dry mass is in between normal and log-normal: positively skewed on the original scale, negatively skewed on log-scale. Leaf carbon content per dry mass has a theoretical range from zero to 1000mg/g. The mean value, about 476mg/g, is in the centre of the theoretical range, and the variation of trait values is small (Table 4).

Nevertheless, according to the Jarque-Bera test, also on a logarithmic scale all traits show some degree of deviation from normal distributions (indicated by small p-values, Table 3). Seed mass, for example, is still positively skewed after log-transformation (Table 3). This is due to substantial differences in the number of database entries and seed masses between grasses/herbs, shrubs and trees (Figure 4a). Maximum plant height in the TRY database has a strong negative kurtosis after log-transformation (Table 3). This is due to a bimodal distribution: one peak for herbs/grass and one for trees (Fig. 4b). The number of height entries for shrubs is comparatively small – which may be due to a small number or abundance of shrub species *in situ* (i.e. a real pattern) but is more likely due to a relative ‘under-sampling’ of shrubs (i.e. an artefact of data collection). Within the growth forms herbs/grass and shrubs, height distribution is approximately log-normal. For trees the distribution is skewed to low values, because there are mechanical constrictions to grow taller than 100 m. The distribution of *SLA* after log-transformation is negatively skewed with positive kurtosis (Table 3) - an imprint of needle-leaved trees and shrubs besides the majority of broadleaved plants (Figure 4c). The distribution of leaf nitrogen content per dry mass after log-transformation has small skewness, but negative kurtosis (Table 3) - the data are less concentrated around the mean than normal (Fig. 4d). In several cases, sample size is sufficient to characterise the distribution at different levels of aggregation, down to the species level. Again we find approximately log-normal distributions (e.g. *SLA* and N_m for *Pinus sylvestris*; Fig. 4c,d).

Ranges of trait variation

There are large differences in variation across traits (Table 4). The standard deviation (SD, expressed on a logarithmic scale[19]) ranges from 0.03 for leaf carbon content per dry mass (resp. about 8% on the original scale) to 1.08 for seed mass (resp. -95% and +1100% on the original scale). Leaf carbon content per dry mass, stem density and leaf density show the lowest variation, followed by the concentration of macro-nutrients (nitrogen, phosphorus), fluxes and conductance (photosynthesis, stomatal conductance, respiration), the concentration of micro-nutrients (e.g. aluminium, manganese, sodium), traits related to length (plant height, plant and leaf longevity), and traits related to leaf area. Mass-related traits show the highest variation (seed mass, leaf dry mass, N and P content of the whole leaf - in contrast to concentration per leaf dry mass or per leaf area). The observations reveal a general tendency towards higher variation with increasing trait dimensionality (length < area < mass; for more information see S3).

Tenet 1: Aggregation at the species level represents the major fraction of trait variation

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[19] Note two characteristics of SD on the logarithmic scale: (1) it corresponds to an asymmetric distribution on the original scale: small range to low values, large range to high values; (2) it can be compared directly across traits. For more information see supplementary material S2.

There is substantial intraspecific variation for each of the ten selected traits (Table 5): for single species the standard deviation is above 0.3 on logarithmic scale, e.g. SD=0.34 for maximum plant height of *Phyllota phyllicoides* (-55 and +121% on the original scale), but based on only six observations, and SD=0.32 in case of *Dodonaea viscosa* (n = 26). The SD of N_m for *Poa pratensis* is 0.17 (n = 63), which is almost equal to the range of all data reported for this trait, but this is an exceptional case. The trait and species with the most observations is nitrogen content per dry mass for *Pinus sylvestris* with 1470 entries (SD = 0.088, -18% and +22%). The variation in this species spans almost half the overall variation observed for this trait (SD=0.18), covering the overall mean (Figure 4d). For several trait-species combinations the number of measurements is high enough for detailed analyses of the variation within species (e.g. on an environmental gradient).

The mean SD at the species-level is highest for plant height (0.18) and lowest for leaf longevity (0.03, but few observations per species, Table 5). For all ten traits the mean SD within species is smaller than the SD between species mean values (Table 5). Based on ANOVA, mean trait values are significantly different between species: at the global scale 60-98% of trait variance occurs interspecific (between species, Fig. 5). Nevertheless, for three traits (P_m, N_a, $Amax_a$) almost 40% of the variance occurs intraspecific (within species, Fig.5).

Tenet 2: Basic PFTs capture a sufficiently important fraction of trait variation to represent functional diversity

For all ten traits, the PFT mean values are significantly different between PFTs (Table 5). Four traits show larger variation between PFT mean values than within PFTs (plant height, seed mass, leaf longevity, $Amax_m$), two traits show similar variation between PFT means and within PFTs (*SLA*, $Amax_N$). As a consequence, more than 60% of the observed variance occurs between PFTs for plant height and leaf longevity, and about 40% of the variation occurs between PFTs for seed mass, *SLA*, $Amax_m$ *and* $Amax_N$ (Fig. 5). The high fraction of explained variance for these six traits reflects the definition of PFTs based on the closely related qualitative traits: plant growth form, leaf phenology (evergreen/deciduous), leaf type (needle-leaved/broadleaved) and photosynthetic pathway (C3/C4). For theses traits plant functional types, such as those commonly used in vegetation models capture a considerable fraction of observed variation with relevant internal consistency. However, for certain traits the majority of variation occurs within PFTs: four traits show smaller variation between than within PFTs, causing substantial overlap across PFTs (N_m, N_a, P_m, $Amax_a$). In these cases only about 20-30% of the variance is explained by PFT, and about 70-80% of variation occurs within PFTs.

Representation of trait variation in the context of global vegetation models

To demonstrate how the observed trait variation is represented in global vegetation models, we first compare observed trait ranges of *SLA* to parameter values for *SLA* used in 12 global vegetation models; then we compare observed trait ranges of N_m to state-variables of nitrogen concentration calculated within the dynamic global vegetation model O-CN (Zaehle and Friend 2010).

Some vegetation models separate PFTs along climatic gradients into biomes, for which they assign different parameter values. A rough analysis of *SLA* along the latitudinal gradient (as a proxy for climate) indicates no major impact on *SLA* within PFT (Fig. 6), and we further jointly analyse *SLA* data by PFT. However, the range of observed trait values for *SLA* per PFT is remarkably large, except for the PFT ‘needle-leaved deciduous trees' (Fig. 6, 7). The parameter values from most of the 12 models match moderately high density of *SLA* observations, but most are clearly different from the mean, and some parameter values are at the low ends of probabilities, surprisingly far off the mean value of observations.

The range of observed trait values for N_m per PFT is also high (Fig. 8), except for the PFT 'needle-leaved evergreen trees'. Modelled state-variables are in most cases within the range of frequently observed trait values - model values for the PFT 'needle-leaved evergreen trees' match the observed distribution almost perfectly. Nevertheless, there are considerable differences between modelled and observed distributions: the modelled state-variables are approximately normally distributed on the original scale, while the observed trait values are log-normally distributed; the range of modelled values is substantially smaller than the range of observations; and the highest densities are shifted. Apart from possible deficiencies of the O-CN model, the deviation between observed and modelled distributions may be due to inconsistencies between compiled traits and modelled state-variables: trait entries in the database are not abundance-weighted with respect to natural occurrence, and they represent the variation of single measurements, while the model produces "community"' measures. The distribution of observed data presented here is therefore likely wider than the abundance-weighted leaf nitrogen content of communities in a given model grid cell.

Discussion

The TRY initiative and the current status of data coverage

The TRY initiative has been developed as a Data Warehouse to integrate different trait databases. Nevertheless, TRY does not aim to replace existing databases, but rather provides a complementary way to access these data consistently with other trait data - it facilitates synergistic use of different trait databases. Compared to a Meta Database approach, which would link a network of separate databases, the integrated database (Data Warehouse) provides the opportunity to standardize traits, add ancillary data, provide accepted species names, and to identify outliers and duplicate entries. A disadvantage of the Data Warehouse approach is that some of the databases contributing to TRY are continuously being developed (see Table 2). However, these contributions to TRY are regularly updated.

The list of traits in the TRY database is not fixed, and it is anticipated that additional types of data will be added to the database in the future. Examples include sap-flow measurements, which are fluxes based on which trait values can be calculated, just as photosynthesis measurements can be used to determine parameter values of the Farquhar model (Farquhar et al. 1980), and leaf venation, which has recently been defined in a consistent way and appears to be correlated with other leaf functional traits (Sack and Frole 2006, Brodribb et al. 2007, Blonder et al. 2011). Ancillary data, contributed with the trait data, may include images. There is also room for expansion of the phylogenetic range of the data incorporated in the database. There is currently little information on non-vascular autotrophic cryptogams in TRY (i.e. bryophytes and lichens), despite their diversity in species, functions and ecosystem effects, and the growing number of trait measurements being made on species within these groups.

The qualitative traits with greatest coverage (more than 30,000 species for woodiness, plant growth form, leaf compoundness, leaf type, photosynthetic pathway) represent about 10% of the estimated number of vascular plant species on land. The quantitative traits with most coverage (5,000-20,000 species for e.g. seed mass, plant height, wood density, leaf size, leaf nitrogen content, *SLA*) approach 5% of named plant species. Although it represents a limited set of species (5-10%), most probably it includes the most abundant (dominant) species. The high number of characterised species opens up the possibility of identifying the evolutionary branch-points at which large divergences in trait values occurred. Such analyses will improve our understanding of trait evolution at both temporal and spatial scales. They highlight the importance of including trait data for autotrophs representing very different branches of the Tree of Life (Cornelissen et al. 2007, Lang et al. 2009) in the TRY database.

For some traits, we know that many more data exist, which could potentially be added to the database. Nevertheless, for some traits the lack of data reflects difficulties in data collection. Table 2 shows some traits where species coverage is thin, most probably because the measurements are currently difficult or laborious. Root measurements fall into this category. Rooting depth (or more exactly, maximum water extraction depth) is among the most influential plant traits in global vegetation models, yet we have estimates for only about 0.05% of the vascular plant species. Data for other root traits is even scarcer. However, many above ground traits correlate with below ground traits (see Kerkhoff et al. 2006), so the data in TRY do give some indication about below ground traits. Apart from this, root traits are focus of current studies (Paula and Pausas 2011). Anatomical traits also have weak coverage in general. Quantifying anatomy from microscopic cross-sections is a slow and painstaking work and there is currently no consensus on which are the most valuable variables to quantify in leaf sections, apart from standard variables such as tissue thicknesses and cell sizes, which show important correlations with physiological function, growth form and climate (Givnish 1988, Sack and Frole 2006, Markesteijn et al. 2007, Dunbar-Co et al. 2009, Hao et al. 2010). An exception is wood anatomy, where TRY contains conduit densities and sizes for many species (about 7000 and 3000 species, respectively). Finally, allometric or architectural relationships that describe relative biomass allocation to leaves, stems, and roots through the ontogeny of individual plants are presently scattered across 72 different traits, each with low coverage. These traits are essential for global vegetation models and this is an area where progress in streamlining data collection is needed.

Many trait data compiled in the database were not necessarily collected according to similar or standard protocols. Indeed many fields of plant physiology and ecology lack consensus definitions and protocols for key measurements. However, progress is being made as well towards *a posteriori* data consolidation (e.g. Onoda et al. 2011), as towards standardizing trait definitions and measurement protocols, e.g. via a common plant trait Thesaurus[20], and a handbook and website[21] of standard definitions and protocols (Cornelissen et al. 2003b, Sack et al. 2010).

Information about the abiotic and biotic environment in combination with trait data is essential to allow an assessment of environmental constraints on the variation of plant traits (Fyllas et al. 2009, Meng et al. 2009, Ordoñez et al. 2009, Albert et al. 2010b, Poorter et al. 2010). Some of this information has been compiled in the TRY database. However, the information about soil, climate and vegetation structure at measurement sites is not well structured, because there is no general agreement on what kind of environmental information is most useful to report in addition to trait measurements. A consensus on these issues would greatly improve the usefulness of

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[20] Plant Trait Thesaurus: http://trait_ontology.cefe.cnrs.fr:8080/Thesauform/

[21] PrometheusWiki: http://prometheuswiki.publish.csiro.au/tiki-custom_home.php

ancillary environmental information. Geographic references should be a priority for non-experimental data.

The number of observations or species with data for all traits declines rapidly with an increasing number of traits: fewer species have data for each trait (see S3). In cases where multivariate analyses rely on completely sampled trait-species matrices, this issue poses a significant constraint on the number of traits and/or species that can be included. Gap filling techniques, e.g. hierarchical Bayesian approaches or filtering techniques (Shan and Banerjee 2008, Su and Khoshgoftaar 2009) offer a potential solution. On the other hand, simulation work in phylogenetics has shown that missing data are not by themselves problematic for phylogenetic reconstruction (Wiens 2003, 2005). Similar work could be done in trait-based ecology, and the emerging field of ecological informatics (Recknagel 2006) may help to identify representative trait combinations while taking incomplete information into account (e.g. Mezard 2007) .

General pattern and ranges of trait distribution

Based on the TRY dataset, we characterised two general patterns of trait density distributions: (1) plant traits are rather log-normal than normal distributed, and (2) the range of variation tends to increase with trait-dimensionality. Here the analysis did benefit from compiling large numbers of trait entries for several traits from different aspects of plant strategy. Based on the rich sampling we could quantify simple general rules for trait distributions and still identify deviations in the individual case. The approximately log-normal distributions confirm prior reports for individual traits (e.g. Wright et al. 2004) and are in agreement with general observations in biology (Kerkhoff and Enquist 2009), although we also observe deviation from log-normal distribution, e.g. as an imprint of plant growth form or leaf type. Being approximately log-normal distributed is most probably due to the fact that plant traits often have a lower bound of zero but no upper bound relevant for the data distribution. This log-normal distribution has several implications: (1) On the original scale relationships are to be expected multiplicative rather than additive (Kerkhoff and Enquist 2009, see as well S2). (2) Log- or log-log scaled plots are not sophisticated techniques to hide huge variation, but the appropriate presentation of the observed distributions (e.g. Wright et al. 2004). On the original scale bivariate plots of trait distributions are to be expected heteroscedastic (e.g. Kattge et al. 2009). (3) Trait related parameters and state-variables in vegetation models can be assumed log-normal distributed as well, e.g. Fig. 7 and 8 (Knorr and Kattge 2005). For more details see S2.

For several traits we quantified ranges of variation: overall variation, intra- and interspecific variation, and variation with respect to different functional groups. Most of the trait data compiled within the TRY database have been measured within natural environments and only a small fraction comes from experiments. Therefore the impact of experimental growth conditions on observed trait variation is probably small in most cases (see Figure 3) and the observed trait variation in the TRY database comprises primarily natural variation at the level of single organs, including variation due to different measurement methods and, of course, measurement errors. However, systematic sampling of trait variation at single locations is a relatively new approach (Albert et al. 2010a, Albert et al. 2010b, Baraloto et al. 2010, Hulshof and Swenson 2010, Jung et al. 2010b, Messier et al. 2010), and it may therefore be shown that trait variability under natural conditions is underestimated in the current data set.

Tenets revisited

The results presented here are a first step to illuminate two basic tenets of plant comparative ecology and vegetation modelling at a global scale: (1) The aggregation of trait data at the species level represents the major fraction of variation in trait values. At the same time, we have shown surprisingly high intraspecific variation - for some traits responsible for up to 40% of the overall variation (Table 5, Fig. 4, 5). This variation reflects genetic variation (among genotypes within a population/species) and phenotypic plasticity. Through the TRY initiative, a relevant amount of data is available to quantify and understand trait variation beyond aggregation on species level. The analysis presented here is only a first step to disentangle within and between species variability. It is expected that in combination with more detailed analyses the TRY database will support a paradigm shift from species to trait-based ecology.

(2) Basic plant functional types, such as those commonly used in vegetation models capture a considerable fraction of observed variation with relevant internal consistency. However, for certain traits the majority of variation occurs within PFTs – responsible for up to 75% of the overall variation (Table 5, Fig. 4, 5, 6, 7, 8). This variation reflects the adaptive capacity of vegetation to environmental constraints (Fyllas et al. 2009, Meng et al. 2009, Ordoñez et al. 2009, Albert et al. 2010b, Poorter et al. 2010) and it highlights the need for refined plant functional classifications for Earth system modeling. The current approach to vegetation modelling, using few basic PFTs and one single fixed parameter value per PFT (even if this value equals the global or regional mean) does not account for the rather wide range of observed values for related traits and thus does not account for the adaptive capacity of vegetation. A more empirically based representation of functional diversity is

expected to contribute to an improved prediction of biome boundary shifts in a changing environment.

There are new approaches in Earth system modelling to better account for the observed variability: suggesting more detailed PFTs, modelling variability within PFTs, or replacing PFTs by continuous trait spectra. In the context of this analysis we focused on a basic set of plant functional types. This schema is not immutable and there is not one given functional classification scheme. In fact, PFTs are very much chosen and defined along specific needs – and the availability of information. For example, the PFTs used in an individual based forest simulator (e.g. Chave 1999), are by necessity very different to those used for DGVMs. The TRY dataset will be as important for allowing the definition of new, more detailed PFTs as for parameterizing the existing ones. Some recent models represent trait-ranges as state variables along environmental gradients rather than as fixed parameter values. The O-CN model (Zaehle and Friend 2010) is an examples towards such a new generation of vegetation models, also the NCIM model (Esser et al. 2011), or in combination with an optimality approach the VOM model (Schymanski et al. 2009). Finally, functional diversity may be represented by model ensemble runs with continuous trait spectra and without PFT classification (Kleidon et al. 2009). However, compared to current vegetation models, these new approaches will be more flexible with respect to the adaptive capacity of vegetation. The TRY database is expected to contribute to these developments, which will provide a more realistic, empirically grounded representation of plants and ecosystems in Earth system models.

A unified database of plant traits in the context of global biogeography

The analyses presented here are only a first step to introduce the TRY data set. To better understand, separate, and quantify the different contributions to trait variation observed in TRY, more comprehensive analyses could be carried out, e.g. variance partitioning accounting for phylogeny and disentangling functional and regional influences or analysis of (co-)variance of plant traits along environmental gradients. An integrative exploration of ecological and biogeographical information in TRY is expected to substantially benefit from progress in the science of machine learning and pattern recognition (Mjolsness and DeCoste 2001). In principle, we are confronted with a similar challenge that genomics faced after large-scale DNA sequencing techniques had become available. Instead of thousands of sequences, our target is feature extraction and novelty detection in thousands of plant traits and ancillary information. Nonlinear relations among items and the treatment of redundancies in trait space have to be addressed. Nonlinear dimensionality reduction (Lee and Verleysen 2007) may shed light on the inherent structures of data compiled in TRY. Empirical inference of this kind is expected to stimulate and strengthen hypothesis driven research (Golub 2010, Weinberg 2010) towards a unified ecological assessment of plant traits and their role for the functioning of the terrestrial biosphere.

The representation of trait observations in a spatial or climate context in the TRY database is limited (Fig. 2, 3). This situation can be overcome using complementary data streams: trait information can be spatially expanded with comprehensive compilations of species occurrence data, e.g. from GBIF or herbarium sources. For SLA and leaf nitrogen content we provide an example for combining trait information with species occurrence data from the GBIF database and with climate reconstruction data derived from the CRU[22] database (Fig. 3). Given that the major fraction of variation is between species, the variation of species mean trait values may be used - but with caution - as a proxy for trait variation, as has already been done in recent studies at regional and continental scales (Swenson and Enquist 2007, Swenson and Weiser 2010). Ollinger et al. (2008) derived regional maps of leaf nitrogen content and maximum photosynthesis from trait information in combination with eddy covariance fluxes and remote sensing data. Based on these approaches and advanced spatial interpolation techniques (Shekhar et al. 2004), a unified global database of plant traits may permit spatial mapping of key plant traits at a global scale (Reich 2005).

The relationship between plant traits (organism-level) and ecosystem or land surface functional properties is crucial. Recent studies have built upon the eddy covariance network globally organized as FLUXNET[23] and inferred site specific ecosystem-level properties from the co-variation of meteorological drivers and ecosystem-atmosphere exchange of CO_2 and water (Baldocchi 2008). These include inherent water use efficiency (Reichstein et al. 2007, Beer et al. 2009), maximum canopy photosynthetic capacity (Ollinger et al. 2008), radiation use efficiency, and light response curve parameters (Lasslop et al. 2010). How species traits relate to these ecosystem-level characteristics has not been investigated, but should be possible via a combined analysis of FLUXNET and TRY data. For example, it is possible to test the hypothesized correlation between SLA, P, and N content of dominant species with radiation use efficiency and inherent water use efficiency at the ecosystem level (as implicit in Ollinger et al. 2008). Similarly, patterns of spatially interpolated global

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[22] CRU - Climate Research Unit at the University of East Anglia, UK: http://www.cru.uea.ac.uk

[23] FLUXNET - a network of regional networks coordinating observations from micrometeorological tower sites: http://www.fluxnet.ornl.gov

fields of biosphere-atmosphere exchange (Beer et al. 2010, Jung et al. 2010a) may be related to spatialized plant traits in order to detect a biotic imprint on the global carbon and water cycles. Such increased synthetic understanding of variation in plant traits is expected to support the development of a new generation of vegetation models with a better representation of vegetation structure and functional variation (Lavorel et al. 2008, Violle and Jiang 2009).

Conclusions and Perspectives

The TRY database provides unprecedented coverage of information on plant traits and will be a permanent communal repository of plant trait data. The first analyses presented here confirm two basic tenets of plant comparative ecology and vegetation modelling at global scale: (1) the aggregation of trait data at the species level represents the major fraction of variation and (2) plant functional types cover a relevant fraction of trait variation to represent functional diversity in the context of vegetation modelling. Nevertheless, at the same time these results reveal for several traits surprisingly high variation within species, as well as within PFTs - a finding, which poses a challenge to large-scale biogeography and vegetation modelling. In combination with improved (geo)-statistical methods and complementary data streams, the TRY database is expected to support a paradigm shift in ecology from being based on species to a focus on traits and trait syndromes. It also offers new opportunities for research in evolutionary biology, biogeography, and ecology. Finally, it allows the detection of the biotic imprint on global carbon and water cycles, and fosters a more realistic, empirically grounded representation of plants and ecosystems in Earth system models.

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Tables

Table 1: Databases currently contributing to the TRY database. Databases are separated whether they are at a final stage or still continuously developed, and whether they are or not public available as an electronic resource in the Internet. Databases that are already integrated databases, pooling a range of original databases (e.g. LEDA, GLOPNET) are highlighted by asterisks (*). Contributions are sorted alphabetically by principal contact person. A database can consist of several datasets (268 individual files have currently been imported to the TRY database). Most of the non-public databases contain unpublished besides published data.

Table 2: Summary of data coverage in the TRY data repository (31.03.2011) for the 52 groups of focus traits and one group lumping all other traits (53). Traits that address one plant characteristic but expressed differently are summarized in groups, e.g. the group “leaf nitrogen content“ consists of the three traits: leaf nitrogen content per dry mass, leaf nitrogen content per area and nitrogen content per leaf. In the case of respiration the database contains 105 related traits: different organs, different reference values (e.g. dry mass, area, volume, nitrogen) or characterizing the temperature dependence of respiration (e.g. Q_{10}). Specific information for each trait is available on the TRY website (http://www.try-db.org). Data sets: number of contributed datasets; Species: number of species characterised by at least one trait entry; Entries: number of trait entries; Geo-referenced, Location, Soil: number of trait entries geo-referenced by coordinates, resp. with information about location or soil. *: qualitative traits assumed to have low variability within species. Bold: qualitative traits standardized and made publicly available on the TRY website.

Table 3: Statistical properties for the density distributions of 52 traits with substantial coverage and a test for deviation from normality, on the original scale and after log-transformation of trait values. Results based on dataset after excluding obvious errors, but before detection of outliers. Skewness: measure of the asymmetry of the density distribution (0 in case of normal distribution, <0: left-tailed distribution, >0 right tailed distribution); Kurtosis: measure of the "peakedness" of the density distribution (here presented as excess kurtosis: 0 in case of normal distribution, <0: wider peak around the mean, >0: a more acute peak around the mean); JB test: result of Jarque–Bera test for departure from normality (0 for normal distribution; >0 for deviation from normal distribution)**;** p-value: probability of obtaining a test statistic at least as extreme as the observed, assuming the null hypothesis, here the data are normal distributed, is true (on the original scale, resp. after log-transformation, >0.5 in case of normality accepted at 95% confidence); change of normality: difference between results of Jarque–Bera test on the original scale and after log-transformation of trait data (>0: improvement of normality by log-transformation, <0: deterioration of normality by log-transformation); RMSE: Root mean squared error; bold: traits for which we quantified the fraction of variance explained by species and PFT.

Table 4: Mean values and ranges for 52 traits with substantial coverage, based on individual trait entries, after exclusion of outliers and duplicates. Values for $Amax_N$ were calculated based on database entries for Amax and leaf N content per area resp. dry mass. Mean values have been calculated as arithmetic means on a logarithmic scale and retransformed to original scale. SD: standard deviation on log10-scale. Traits are sorted by decreasing SD. Bold: traits for which we quantified the fraction of variance explained by species and PFT (cf. Table 5, Fig. 5). *: Mean values for leaf

phenolics, tannins and carbon content were calculated on the original scale, the SD is, provided on log-scale, for comparability.

Table 5: Variation within and between species and within and between plant functional types (PFT). Light grey: standard deviation within group; dark grey: standard deviation between groups; n: number of entries; nsp, n/sp and n/PFT: number of species vs. number of mean number of entries per species and PFT, mean values: calculated as arithmetic mean on log-scale and retransformed to original scale, sign. p: significance level for difference between means for PFTs and species. Traits: Seed mass (mg), Plant height: maximum plant height (m), *LL*: leaf lifespan (month); *SLA*: specific leaf area (mm^2/mg); N_m: leaf nitrogen content per dry mass (mg/g); P_m: leaf phosphorus content per dry mass (mg/g); N_a: leaf nitrogen content per area (g/m^2), $Amax_a$: light saturated photosynthetic rate per leaf area (μmol /m^2/s), $Amax_m$: light saturated photosynthetic rate per dry mass (μmol/g/s), $Amax_N$: light saturated photosynthetic rate per leaf nitrogen content (μmol/g/s). SD is based on log10-transformed trait data, after exclusion of duplicates and outliers, including data derived under experimental growth conditions. Numbers in brackets along with names of plant functional types characterize the numbers of species attributed to the respective PFT. Plant species were selected to provide examples from different functional types and with entries for each of the ten traits.

Figures

Figure 1: The TRY process of data sharing. Researcher C contributes plant trait data to TRY (1) and becomes a member of the TRY consortium (2). The data are transferred to the Staging Area, where they are extracted and imported, dimensionally and taxonomically cleaned, checked for consistency against all other similar trait entries and complemented with covariates from external databases (3; Tax = taxonomic databases, IPNI/TROPICOS accessed via TaxonScrubber (Boyle 2006), Clim = climate databases, e.g. CRU, Geo = geographic databases). Cleaned and complemented data are transferred to the Data Repository (4). If researcher C wants to retain full ownership, the data are labelled accordingly. Otherwise they obtain the status ‘freely available within TRY’. Researcher C can request her/his own data – now cleaned and complemented – at any time (5). If she/he has contributed a minimum amount of data (currently >500 entries), she/he automatically is entitled to request data other than her/his own from TRY. In order to receive data she/he has to submit a short proposal explaining the project rationale and the data requirements to the TRY steering committee (6). Upon acceptance (7) the proposal is published on the Intranet of the TRY website (title on the public domain) and the data management automatically identifies the potential data contributors affected by the request. Researcher C then contacts the contributors who have to grant permission to use the data and to indicate whether they request co-authorship in turn (8). All this is handled via standard e-mails and forms. The permitted data are then provided to researcher C (9), who is entitled to carry out and publish the data analysis (10). To make trait data also available to vegetation modellers (e.g. modeller E) – one of the pioneering motivations of the TRY initiative – modellers are also allowed to directly submit

proposals (11) without prior data submission provided the data are to be used for model parameter estimation and evaluation. We encourage contributors to change the status of their data from ‘own’ to ‘free’ (12) as they have successfully contributed to publications. With consent of contributors this part of the database is being made publicly available without restriction. So far look-up tables for several qualitative traits (see Table 2) have been published on the website of the TRY initiative (http://www.try-db.org). Meta-data are also provided without restriction (13).

Figure 2: Data density of geo-referenced trait entries. Top: number of sites per 2x2° grid cell, bottom: number of trait entries per grid cell.

Figure 3: Data density for (a) SLA (1862 sites) and (b) leaf nitrogen content per dry mass (3458 sites), and data density in climate space: (c) *SLA* and (d) leaf nitrogen content per dry mass (N_m). Red: geo-referenced measurement sites in the TRY database, dark grey: distribution of entries in the GBIF database for species characterised by entries of leaf nitrogen content per dry mass in the TRY database, light grey: continental shape, respectively all entries in the GBIF database in climate space. Mean annual temperature and mean annual precipitation are based on CRU gridded climate data. Climate space overlaid by major biome types of the world following Whittaker et al. (1975); Tu: Tundra, BF: Boreal Forest, TeG: Temperate Grassland, TeDF: Temperate Deciduous Forest, TeRF: Temperate Rain Forest, TrDF: Tropical Deciduous Forest, TrRF: Tropical Rain Forest, Sa: Savanna, De: Desert. Biome boundaries are approximate.

Figure 4: Examples of trait frequency distributions for four ecologically relevant traits (Westoby 1998, Wright et al. 2004). Upper panels: (a) seed mass and (b) plant height for all data and three major plant growth forms (white: all database entries;

light grey: herbs/grasses; dark grey: trees; black: shrubs). Rug-plots provide data ranges hidden by overlapping histograms. Lower panels: (c) Specific leaf area (*SLA*) and (d) leaf nitrogen content per dry mass (N_m, white: all database entries excluding outliers (including experimental conditions), light grey: database entries from natural environment (excluding experimental conditions); medium grey: growth form trees, dark grey: PFT needle-leaved evergreen, black: *Pinus sylvestris*).

Figure 5: Fraction of variance explained by PFT or species for 10 relevant and well-covered traits. R^2: fraction of explained variance. Traits: Seed mass: seed dry mass, Plant height: maximum plant height, *LL*: leaf longevity; *SLA*: specific leaf area; N_m: leaf nitrogen concentration per dry mass; P_m: leaf phosphorus concentration per dry mass; N_a: leaf nitrogen content per area, $Amax_a$: maximum photosynthesis rate per leaf area, $Amax_m$: maximum photosynthesis rate per leaf dry mass, $Amax_N$: maximum photosynthesis rate per leaf nitrogen content.

Figure 6: Worldwide range in *SLA* along a latitudinal gradient for the main plant functional types. Grey: all data; black: data for the PFT under scrutiny.

Figure 7: Frequency distributions of specific leaf area (*SLA*, mm^2/mg) values (grey histograms) compiled in the TRY database and parameter values for SLA (red dashes) published in the context of the following global vegetation models: Frankfurt Biosphere Model (Ludeke et al. 1994, Kohlmaier et al. 1997), SCM (Friend and Cox 1995), HRBM (Kaduk and Heimann 1996), IBIS (Foley et al. 1996, Kucharik et al. 2000), Hybrid (Friend et al. 1997), BIOME-BGC (White et al. 2000), ED (Moorcroft et al. 2001), LPJ-GUESS (Smith et al. 2001), LPJ-DGVM (Sitch et al. 2003), LSM (Bonan et al. 2003), SEIB–DGVM (Sato et al. 2007). n: number of SLA data in the TRY database per PFT.

Figure 8: Frequency distributions of leaf nitrogen content per dry mass for major plant functional types as compiled in the TRY database compared to frequency distributions of the respective state-variable calculated within the O-CN vegetation model (Zaehle and Friend 2010). n: number of entries in the TRY database (left) and number of grid-elements in O-CN with given PFT (right).

Supplementary material:

S1: Detection of outliers

We consider individual trait values as outliers if they are not contained within an “accepted range” of values, defined as:

$$AcceptedRange = \overline{\ln(x_i)} \pm a * \left(\overline{SD(\ln(x_j))} + b * SD_{SD(\ln(x_j))}\right)$$

i= individual grouping element (respective species, genus, family, PFT)
j= grouping level (e.g. species, genus, family, PFT, or all data)
a, b: factors scaling the sensitivity of outlier detection
x: value of respective trait

The accepted range of values is defined by the mean value of the given group (e.g. a specific species) +/- the mean standard deviation of this grouping level. The mean standard deviation is modified to account for its uncertainty (see Figure S1). The distance of the trait entry under scrutiny from the group mean is calculated in terms of standard deviations. This information is added to the trait information. If the trait entry is out of range for one grouping level, it is marked as an outlier. The accepted range can be formulated with respect to different scaling of the data (e.g. on the original scale or logarithmic scale). Here the approach is formulated on a logarithmic scale, as according to the Jarque-Bera test (Bera and Jarque 1980) most traits were normally distributed on a logarithmic scale; Table 3.

This outlier detection, based on the average standard deviation and its uncertainty, allows a robust detection of outliers also for individual groups with few data entries, e.g. species with only two data entries: both entries could be identified as outliers. In the context of the analyses in this manuscript the scaling factors a and b were set to 2 and 1, respectively. This represents an average range of 2 SD plus the uncertainty of SD. Accordingly about 5% of the data has been identified as outliers and excluded from analyses. In the context of this manuscript we used this rather conservative approach, as individual double- and cross-checking of data for measurement and data errors is not possible for all the traits in the database.

Applying the outlier detection on the aggregation levels of species, genus, family, PFT and for all data, most outliers are detected on the species level in the centre of the distribution (e.g. Figure 1 S1 for *SLA*), only comparatively few entries on the high and low end of the distribution are identified as outliers.

Figure 1 S1: 'Funnel graph' indicating the dependence of standard deviation on sampling size.

Figure 2 S1: Outliers identified in case of *SLA* (2404 outliers out of 48140 entries, after exclusion of duplicates)

S2: Reasoning and consequences of normal distribution on logarithmic scale

Our results show that plant traits are typically normally distributed on a logarithmic scale (Table 3). This is most probably due to the fact that they often have a lower bound at zero but no upper bound relevant for the data distribution. Being log-normal distributed has several implications for data analysis and the presentation of results. (1) The standard deviation expressed on a logarithmic scale allows a direct comparison of variation between different traits independent of units and mean values (e.g. table 4 and 5). Providing mean value +/- standard deviation on a logarithmic scale corresponds to a multiplicative relation on the original scale, which corrects for the value of the mean, but also produces an asymmetric distribution, with a small range below and large range above the mean value: e.g. a standard deviation of 0.05 on log-10 scale corresponds to -10.9% and +12.2% on the original scale, while a standard deviation of 1.0 on log-10 scale corresponds to -90% (/10) and +900% (*10) on the original scale. (2) It implies that on the original scale relationships are to be expected being multiplicative rather than additive (Kerkhoff and Enquist 2009). The increase of a trait value by 100% corresponds to a reduction by 50% and not to a reduction by 100%, e.g. a doubling of seed mass from 4mg to 8mg corresponds to a reduction from 4mg to 2mg and not to a reduction from 4mg to 0mg. (3) Log- or log-log scaled plots are not sophisticated techniques to hide huge variations, but the appropriate presentation of the observed distributions (Wright et al. 2004). On the original scale bivariate plots show a heteroscedastic distribution e.g. (Kattge et al. 2009). (4) In the context of sensitivity analysis of model parameters and data-assimilation the trait related parameters and state-variables have to be assumed normally distributed on a logarithmic scale as well (Knorr and Kattge 2005) (e.g. Fig 7 and 8).

S3: Ranges of plant traits as a function of trait dimensionality

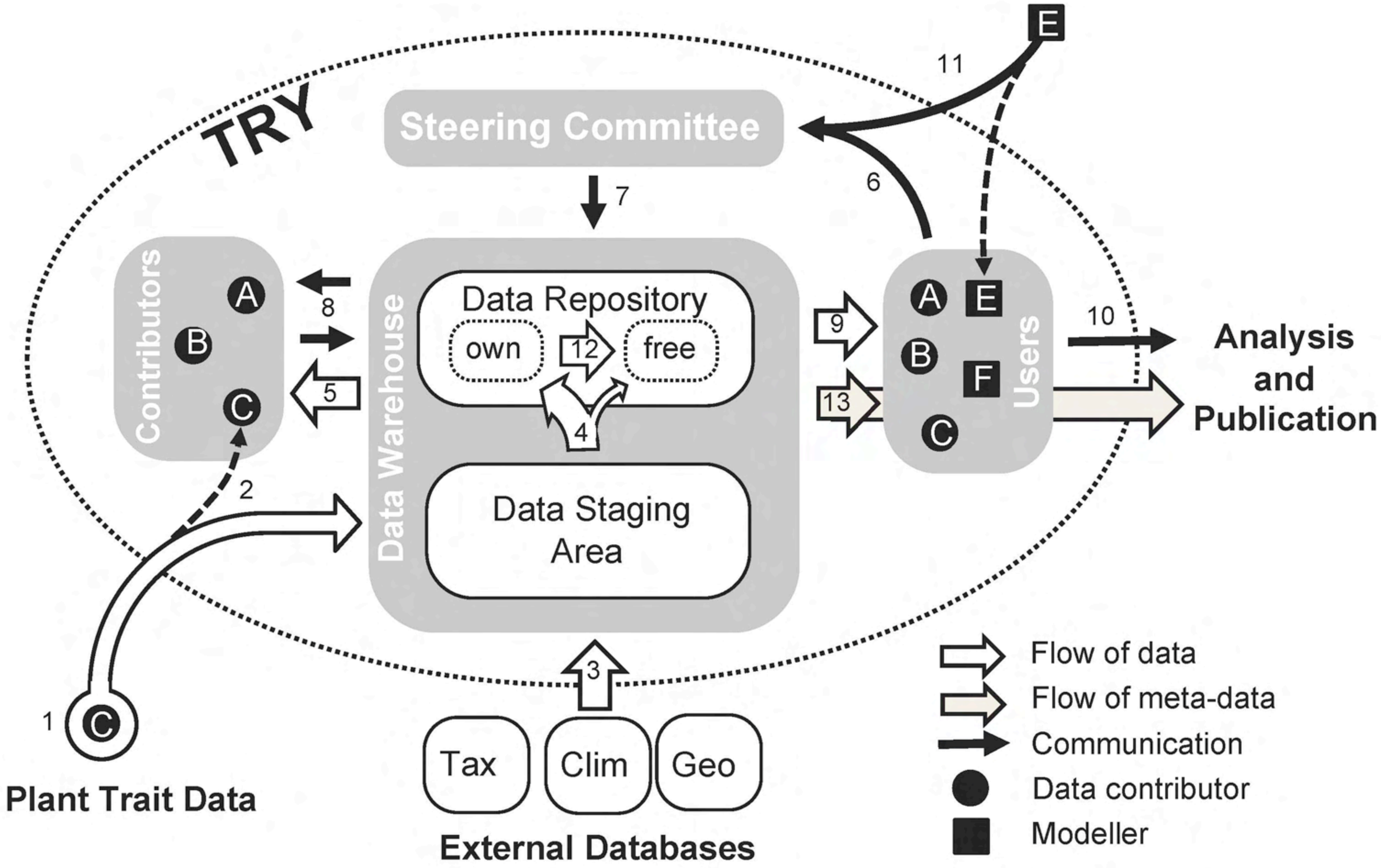
S3: Ranges of plant traits, presented as standard deviation on log-scale, for 50 different traits with respect to dimension. Dimension 1: e.g. length; 2: e.g. area; 3: e.g. volume, mass (variable due to potential changes in three dimensions); all traits that are calculated as fractional values (e.g. mg/g, or g/m2) are attributed a dimension of zero.

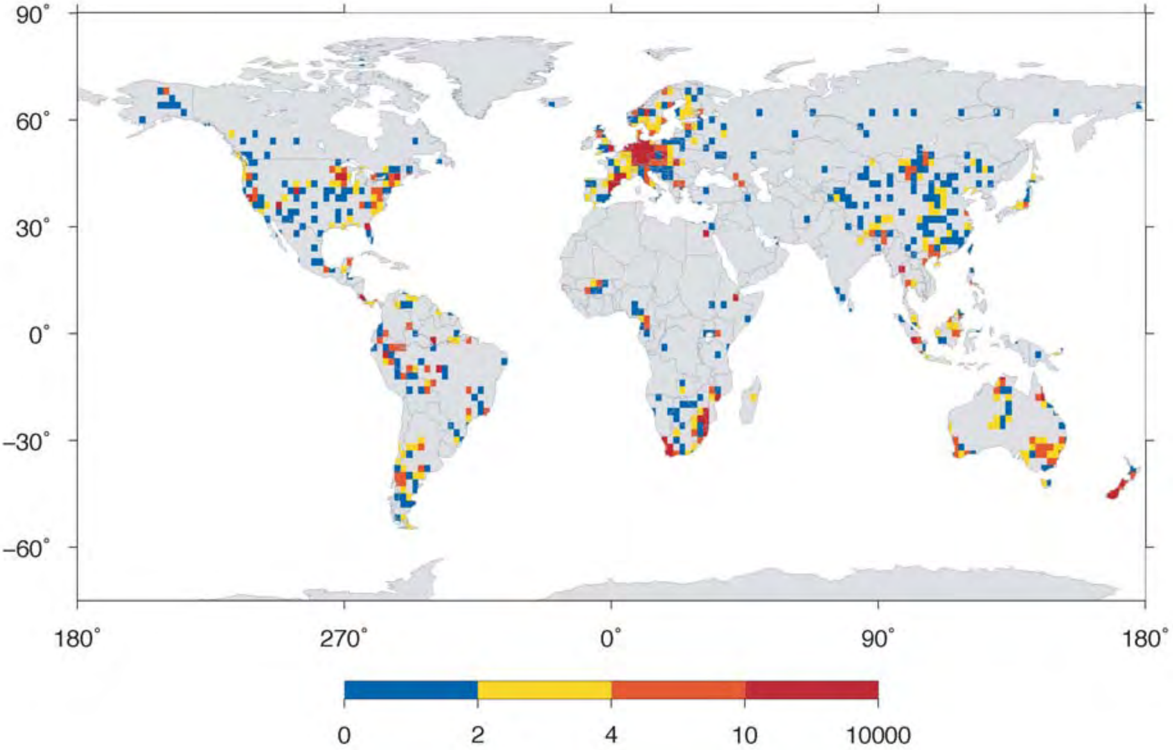
S4: Reduction of number of species with complete data coverage with increasing number of traits

S4: Reduction of number of species with complete data coverage with increasing number of traits. n: number of species with full coverage; n_{max}: number of species in case of trait with highest coverage; f_{joint}: average fraction of species overlap of different traits; ntraits: number of traits of interest in the multivariate analysis. First experiences show that in TRY f_{joint} is in a range of about 0.5 to 0.7, depending on the selected traits.

S5: Latitudinal range of SLA

S5: Worldwide range in *SLA* along a latitudinal gradient for the main plant functional types. Density distributions presented as box and whisker plots. The height of boxes indicates the number of respective data entries.


TRY
Steering Committee
7
6
11
E
Contributors
A
B
C
8
5
Data Warehouse
Data Repository
own
12
free
4
Data Staging Area
9
13
Users
A
E
B
F
C
10
Analysis and Publication
2
1
C
Plant Trait Data
3
Tax
Clim
Geo
External Databases
Flow of data
Flow of meta-data
Communication
Data contributor
Modeller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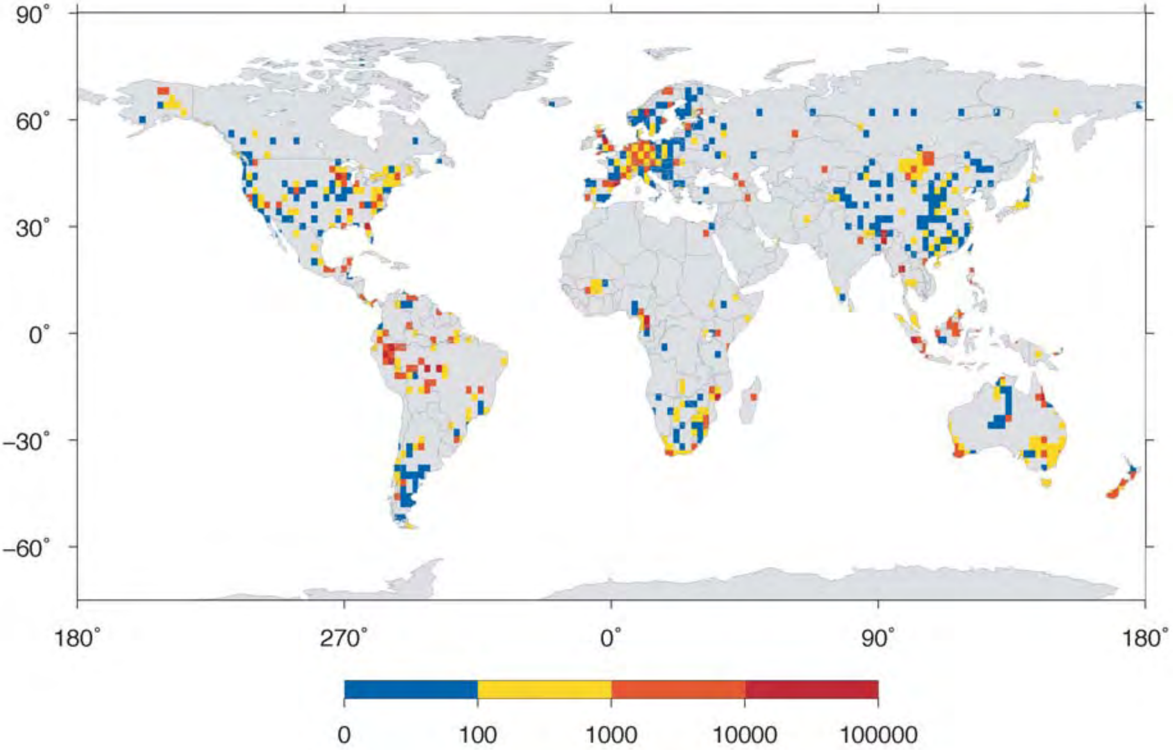
4
10
10000


90°
60°
30°
0°
−30°
−60°
180°
270°
0°
90°
180°
0
100
1000
10000
100000


a
b
c
d
Arctic Alpine
Cold Temperate
Warm Temperate
Tropical
Tu
BF
TeG
TeDF
TeRF
De
Sa
TrDF
TrRF
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mean annual precipitation (mm)
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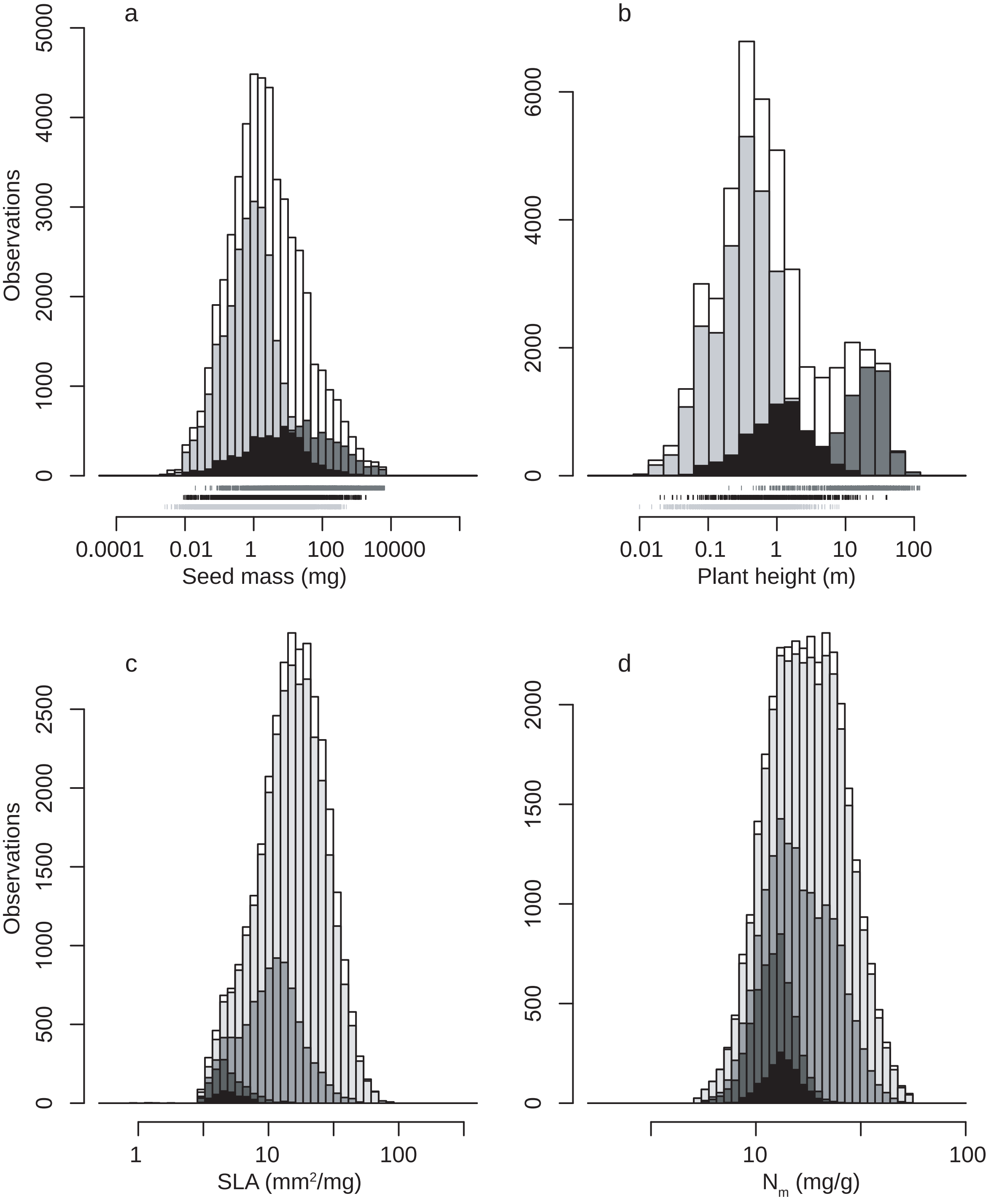
-10
0
10
20
30
0
2000
4000
6000
8000


a
Observations
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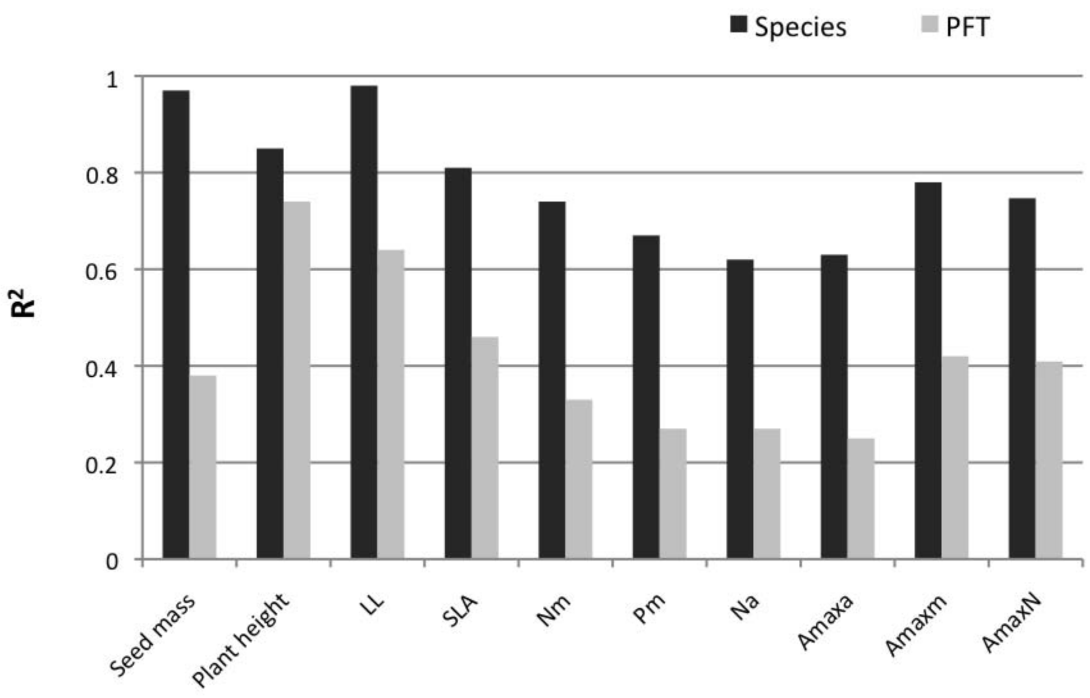
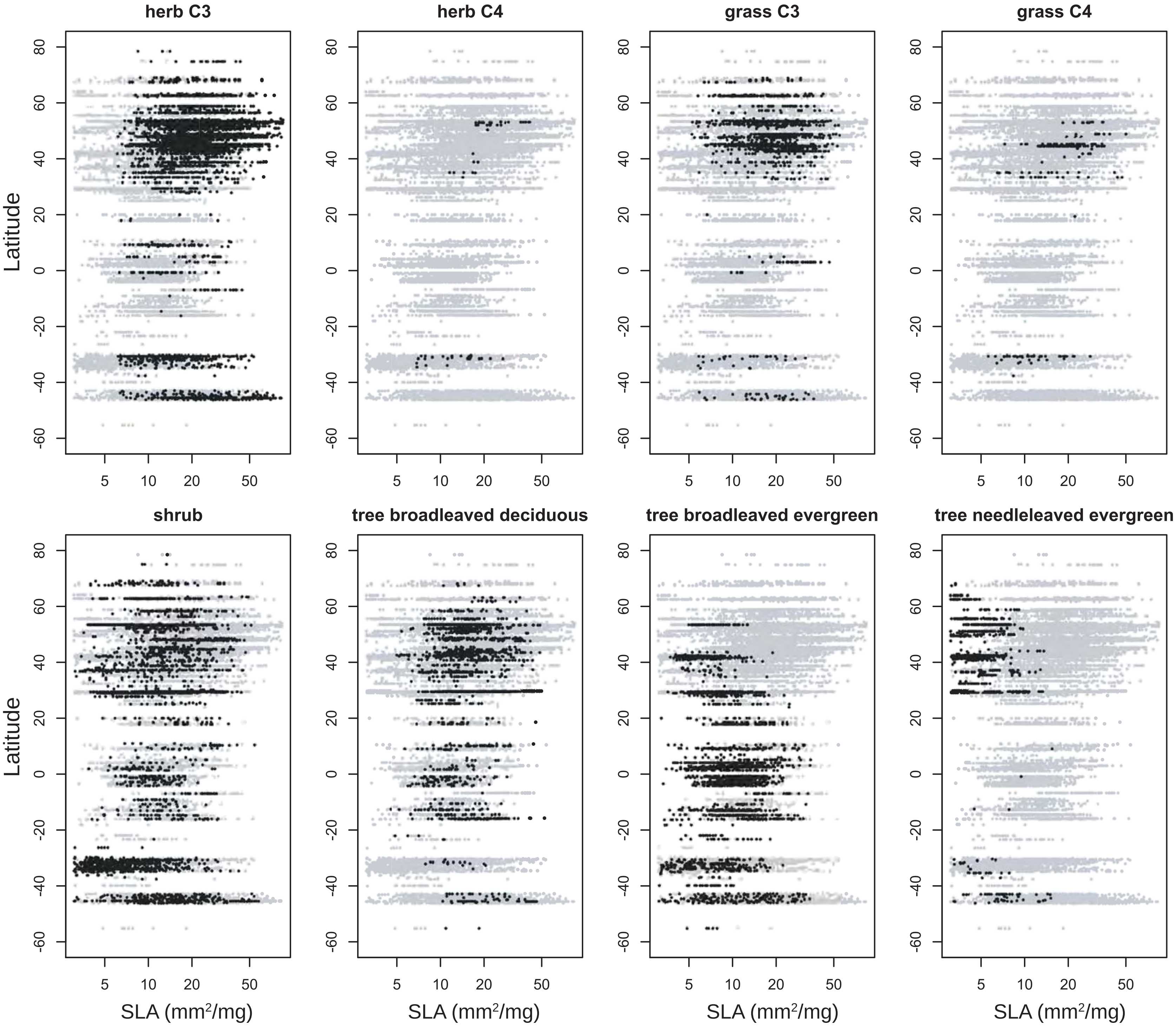
1000
2000
3000
4000
5000
0.0001
0.01
1
100
10000
Seed mass (mg)
b
0
2000
4000
6000
0.01
0.1
1
10
100
Plant height (m)
c
Observations
0
500
1000
1500
2000
2500
1
10
100
SLA (mm²/mg)
d
0
500
1000
1500
2000
10
100
N_m (mg/g)


■ Species
■ PFT
R²
1
0.8
0.6
0.4
0.2
0
Seed mass
Plant height
LL
SLA
Nm
Pm
Na
Amaxa
Amaxm
AmaxN


herb C3
herb C4
grass C3
grass C4
shrub
tree broadleaved deciduous
tree broadleaved evergreen
tree needleleaved evergreen
Latitude
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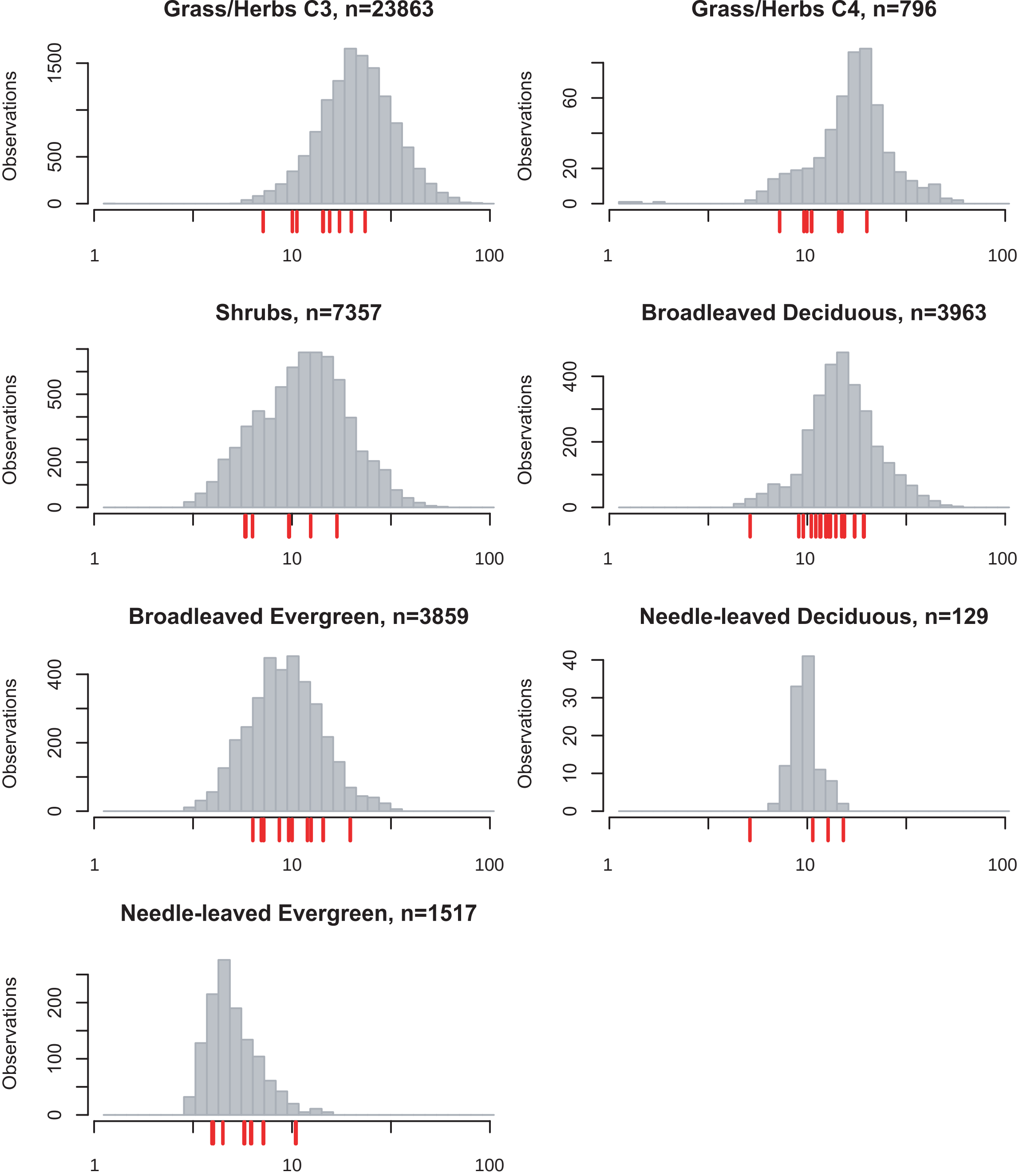
60
40
20
0
-20
-40
-60
5
10
20
50
SLA (mm^2/mg)


Grass/Herbs C3, n=23863
Observations
0
500
1500
1
10
100
Grass/Herbs C4, n=796
Observations
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20
60
1
10
100
Shrubs, n=7357
Observations
0
200
500
1
10
100
Broadleaved Deciduous, n=3963
Observations
0
200
400
1
10
100
Broadleaved Evergreen, n=3859
Observations
0
200
400
1
10
100
Needle-leaved Deciduous, n=129
Observations
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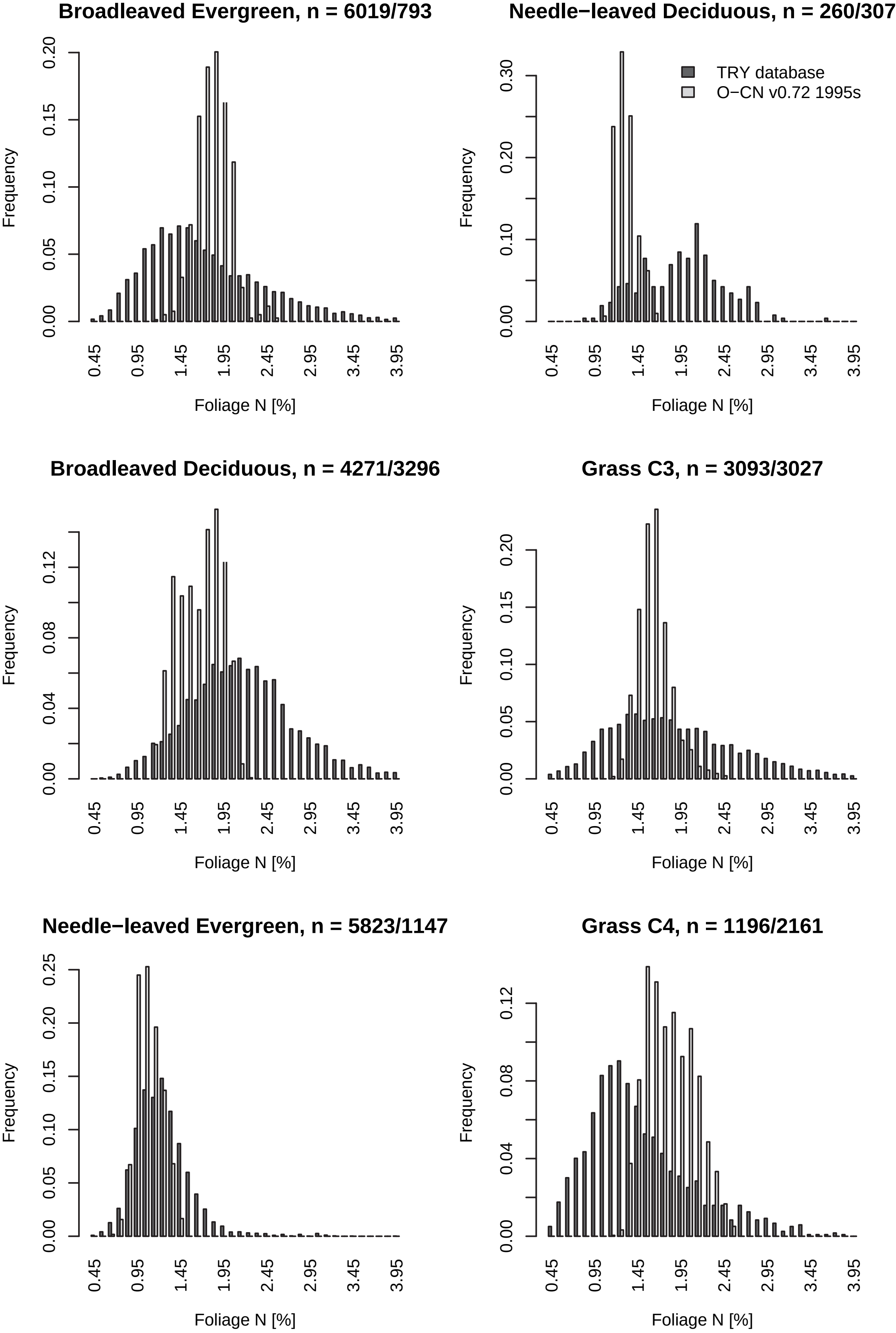
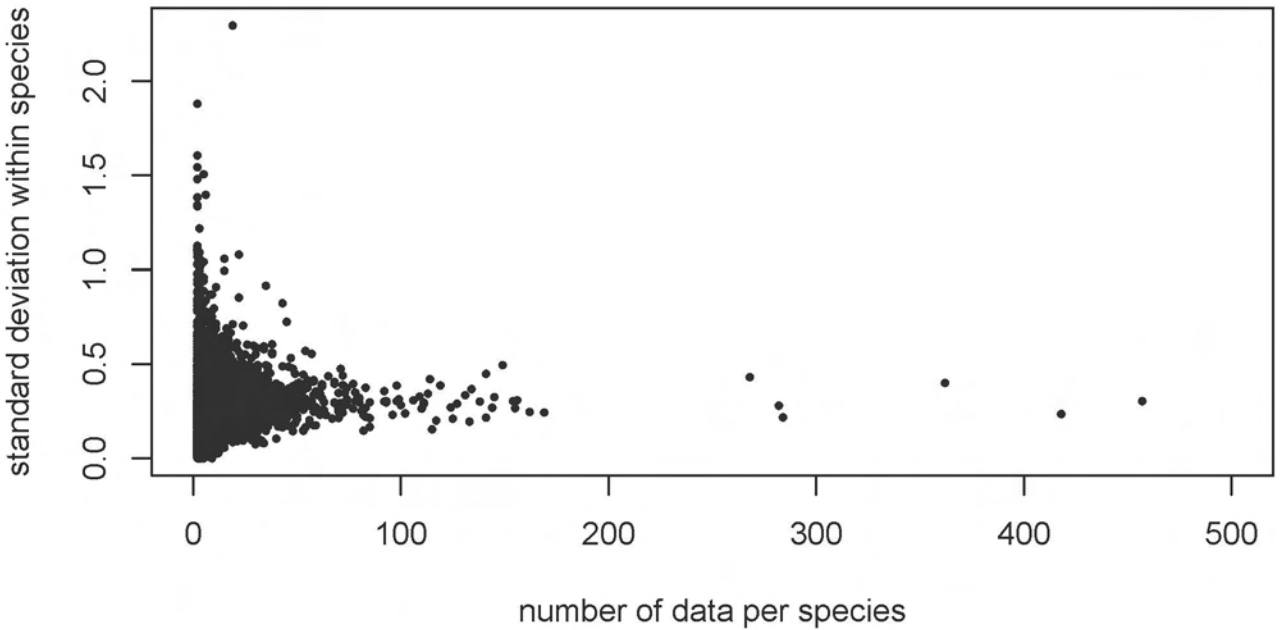
10
20
30
40
1
10
100
Needle-leaved Evergreen, n=1517
Observations
0
100
200
1
10
100


Broadleaved Evergreen, n = 6019/793
Needle−leaved Deciduous, n = 260/307
TRY database
O−CN v0.72 1995s
Broadleaved Deciduous, n = 4271/3296
Grass C3, n = 3093/3027
Needle−leaved Evergreen, n = 5823/1147
Grass C4, n = 1196/2161
Frequency
Foliage N [%]
0.45
0.95
1.45
1.95
2.45
2.95
3.45
3.95
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.04
0.08
0.12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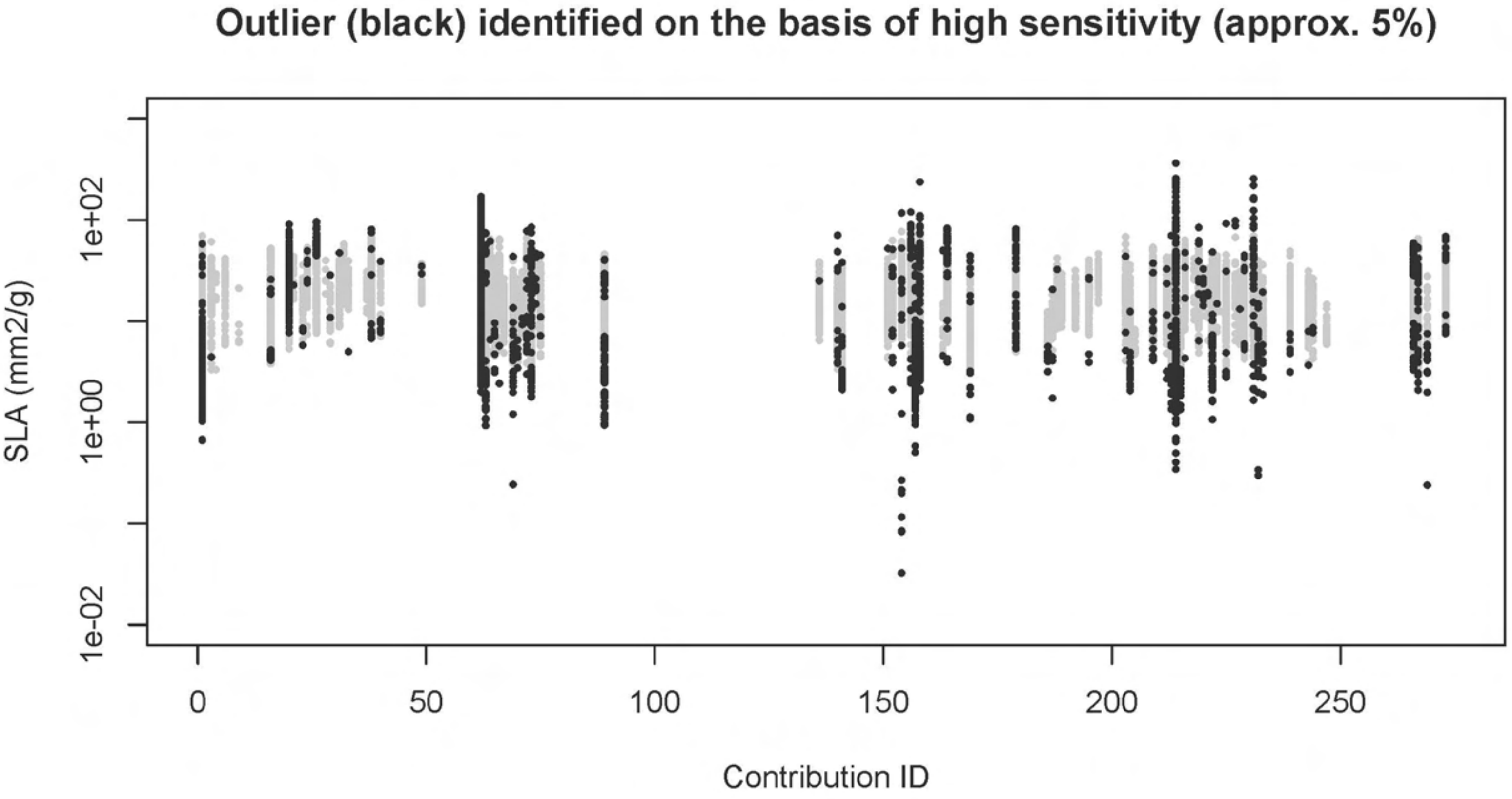
1.0
1.5
2.0
0
100
200
300
400
500
number of data per species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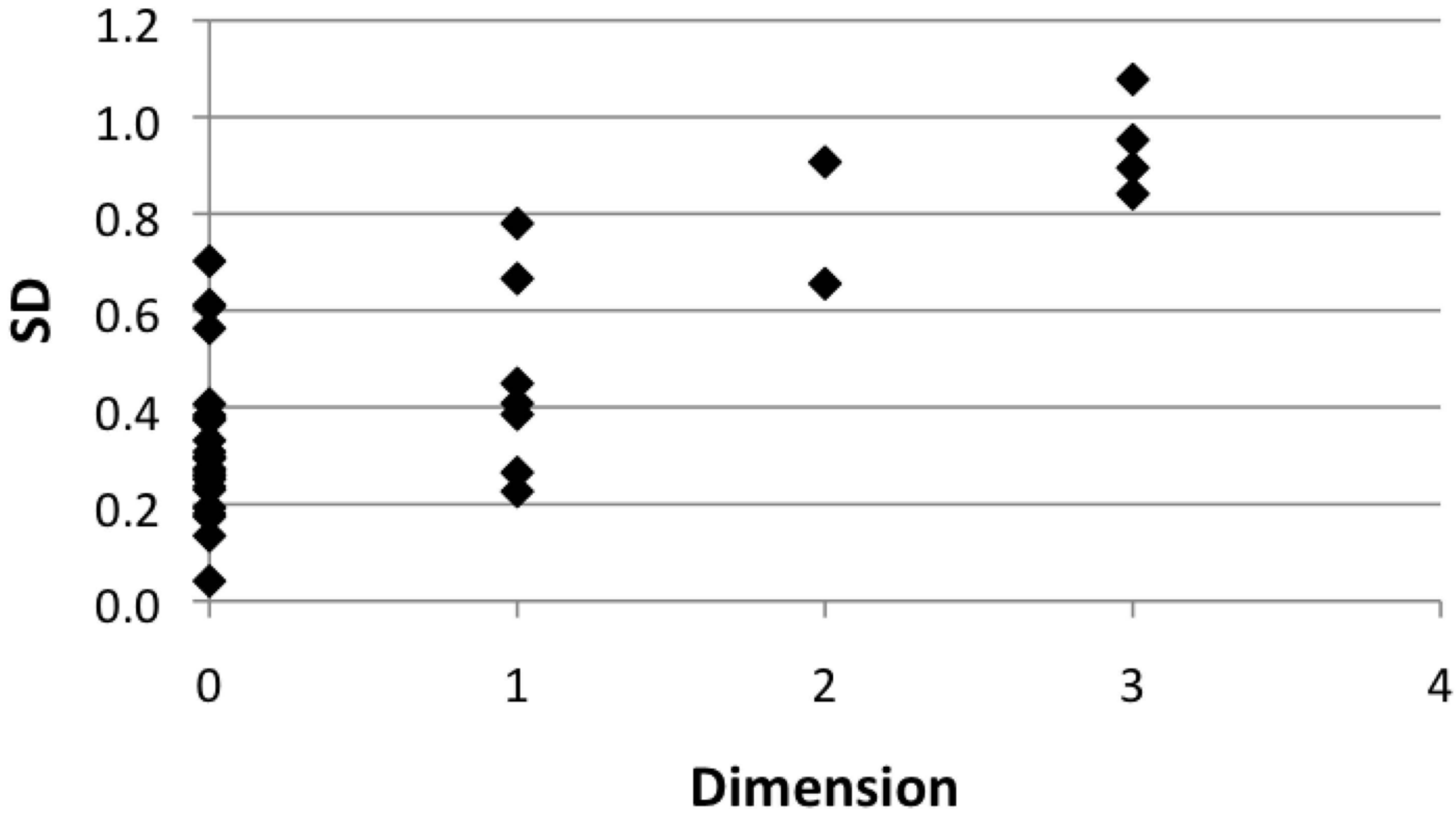
1e+00
1e-02
0
50
100
150
200
250
Contribution ID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0.2
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SD
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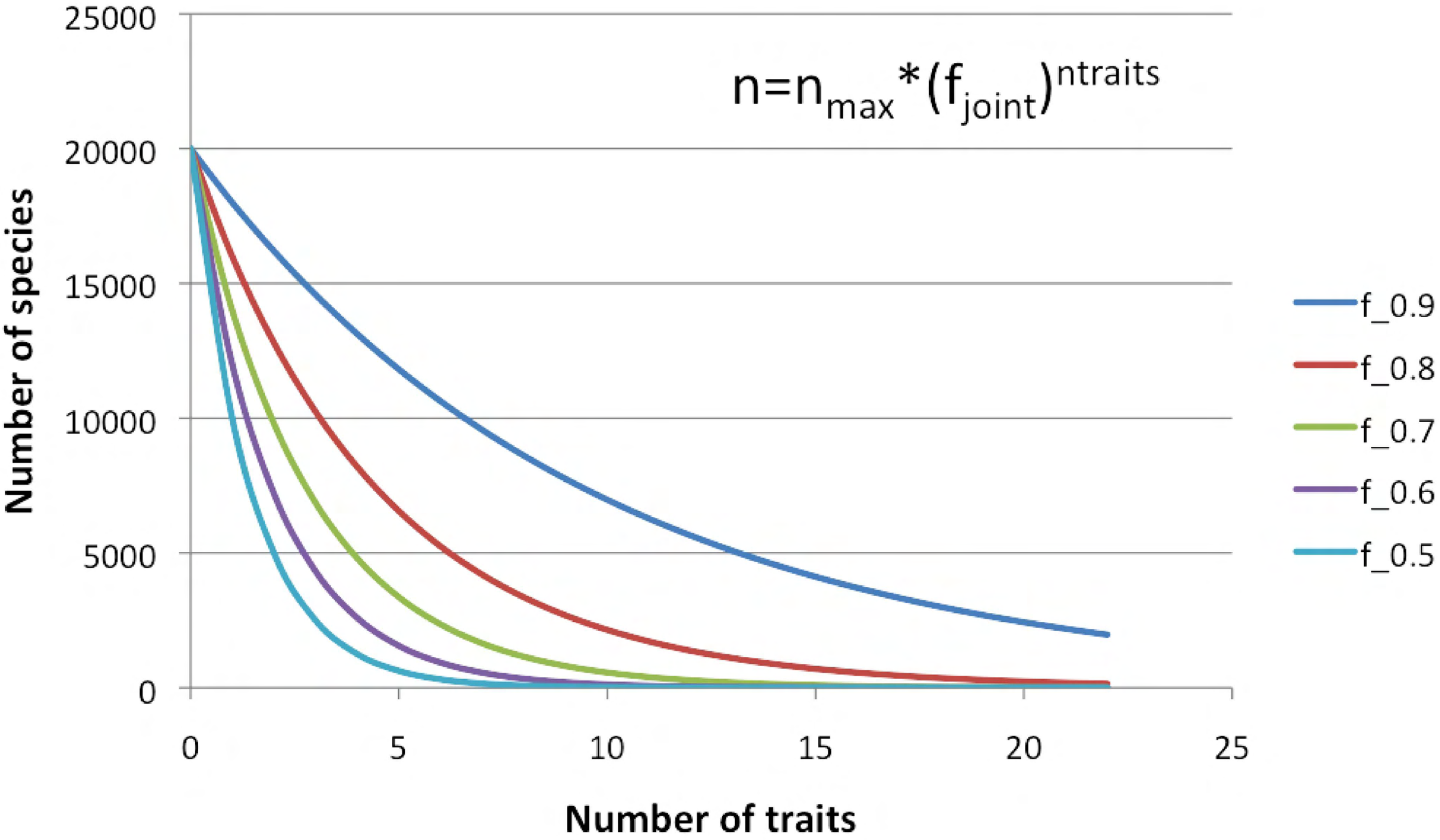
Dimension


n=n_max*(f_joint)^ntraits
Number of species
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20000
15000
10000
5000
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Number of traits
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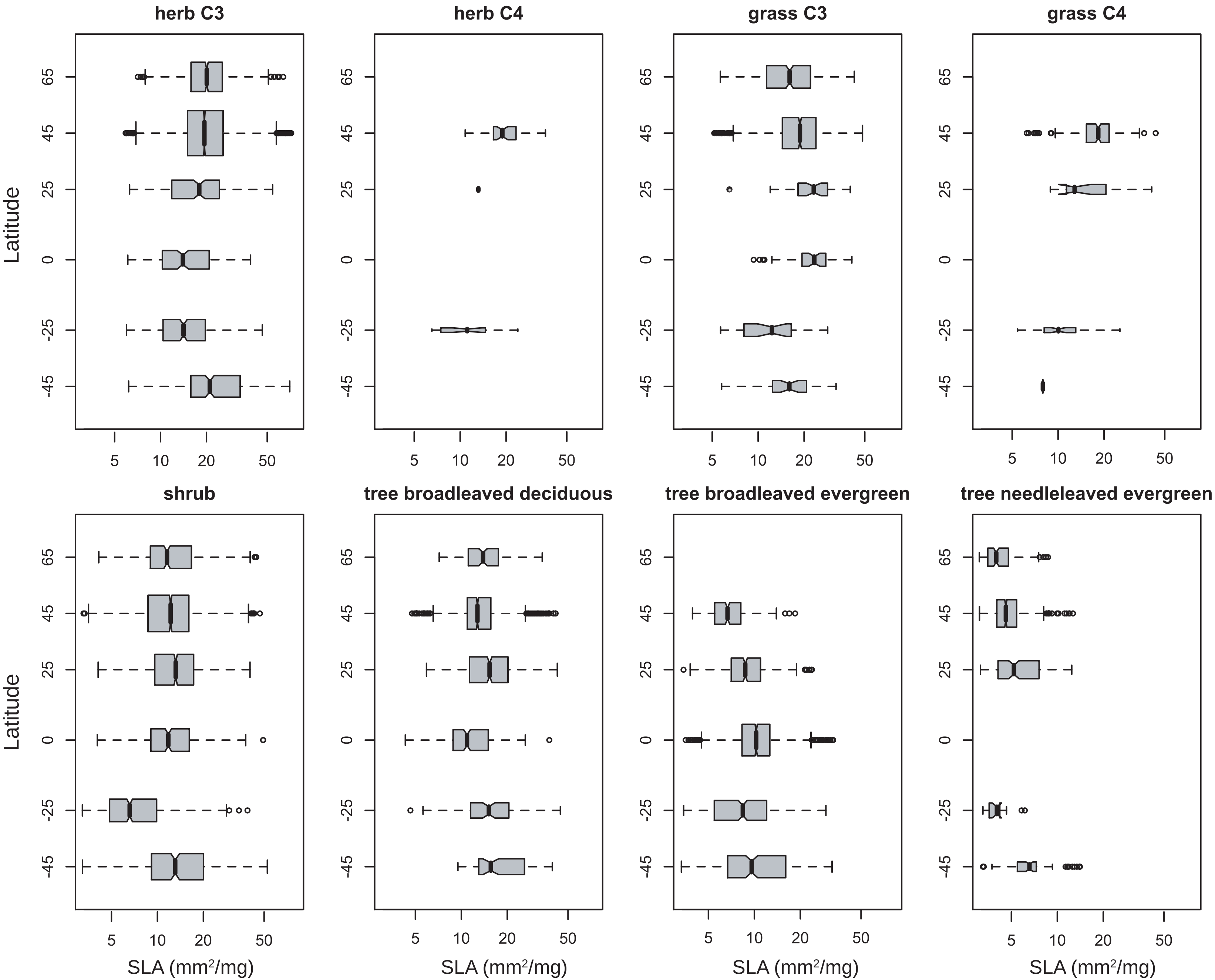
10
15
20
25
f_0.9
f_0.8
f_0.7
f_0.6
f_0.5


herb C3
herb C4
grass C3
grass C4
shrub
tree broadleaved deciduous
tree broadleaved evergreen
tree needleleaved evergreen
Latitude
65
45
25
0
-25
-45
5
10
20
50
SLA (mm^2/mg)

Name of the Database	Contact Person(s)	Reference(s)
Databases public, maintained on the Internet		
1 *Seed Information Database (SID)	J. Dickie, K. Liu	Royal Botanic Gardens Kew Seed Information Database (SID), 2008
2 *Ecological Flora of the British Isles	A. Fitter, H. Ford	Fitter & Peat (1994)
3 VegClass CBM Global Database	A. Gillison	Gillison & Carpenter (1997)
4 *PLANTSdata	W. Green	Green (2009)
5 *The LEDA Traitbase	M. Kleyer	Kleyer et al. (2008)
6 *BiolFlor Database	I. Kühn, S. Klotz	Klotz et al. (2002), Kühn et al. (2004)
7 *BROT plant trait database	J. Pausas, S. Paula	Paula & Pausas (2009), Paula et al. (2009)
Databases public, fixed		
8 Tropical Respiration Database	J. Chambers	Chambers et al. (2004, 2009)
9 *ArtDeco Database	W. Cornwell, H. Cornelissen	Cornwell et al. (2008)
10 The Americas N&P database	B. Enquist, A. Kerkhoff	Kerkhoff et al. (2006)
11 ECOCRAFT	B. Medlyn	Medlyn et al. (1999 a,b, 2001)
12 *Tree Tolerance Database	Ü. Niinemets	Niinemets & Valladares (2006)
13 *Leaf Biomechanics Database	Y. Onoda	Onoda et al. (2011)
14 *BIOPOP: Functional Traits for Nature Conservation	P. Poschlod	Poschlod et al. (2003)
15 *BIOME-BGC Parameterization Database	M. White, P. Thornton	White et al. (2000)
16 *GLOPNET - Global Plant Trait Network Database	I. J. Wright, P. B. Reich	Wright et al. (2004, 2006)
17 *Global Wood Density Database	A. Zanne, J. Chave	Chave et al. (2009), Zanne et al. (2009)
Databases not-public, fixed in the majority of cases		
18 Plant Traits in Pollution Gradients Database	M. Anand	Unpublished Data
19 Plant Physiology Database	O. Atkin	Atkin et al. (1997, 1999), Loveys et al. (2003), Campbell et al. (2007)
20 European Mountain Meadows Plant Traits Database	M. Bahn	Bahn et al. (1999), Wohlfahrt et al. (1999)
21 Photosynthesis Traits Database	D. Baldocchi	Wilson et al. (2000), Xu et al. (2003)
22 Photosynthesis and Leaf Characteristics Database	B. Blonder, B. Enquist	Unpublished Data
23 Wetland Dunes Plant Traits Database	P. van Bodegom	Bakker et al. (2005, 2006), van Bodegom et al. (2005, 2008)
24 Ukraine Wetlands Plant Traits Database	P. van Bodegom	Unpublished Data
25 Plants Categorical Traits Database	P. van Bodegom	Unpublished Data
26 South African Woody Plants Trait Database (ZLTP)	W. Bond, M. Waldram	Unpublished Data
27 *Australian Fire Ecology Database	R. Bradstock	Unpublished Data
28 Cedar Creek Plant Physiology Database	D. E. Bunker, S. Naeem	Unpublished Data
29 Floridian Leaf Traits Database	J. Cavender-Bares	Cavender-Bares, Keen & Miles (2006)
30 Tundra Plant Traits Databases	S. Chapin	Unpublished Data
31 *Global Woody N&P Database	G. Esser, M. Clüsener-Godt	M. Clüsener-Godt (1989)
32 Abisko & Sheffield Database	H. Cornelissen	Cornelissen (1996), Cornelissen, Diez & Hunt (1996), Cornelissen et al. (1997, 1999, 2001, 2003, 2004), Castro-Diez et al. (1998, 2000), Quested et al. (2003)
33 Jasper Ridge Californian Woody Plants Database	W. Cornwell, D. Ackerly	Cornwell et al. (2006), Preston et al. (2006), Ackerly & Cornwell (2007), Cornwell & Ackerly (2009)
34 Roots Of the World (ROW) Database	J. Craine	Craine et al. (2005)
35 Global 15N Database	J. Craine	Craine et al. (2009)
36 CORDOBASE	S. Diaz	Diaz et al. (2004)
37 *Sheffield-Iran-Spain Database	S. Diaz	Diaz et al. (2004)
38 Chinese Leaf Traits Database	J. Fang	Han et al. (2005), He et al. (2006, 2008)
39 Costa Rica Rainforest Trees Database	B. Finegan, B. Salgado	Unpublished Data
40 Plant Categorical Traits Database	O. Flores	Unpublished Data
41 Subarctic Plant Species Trait Database	G. Freschet, H. Cornelissen	Freschet et al. (2010 a,b)
42 Climbing Plants Trait Database	R. Gallagher	Gallagher et al. (2011)
43 The VISTA Plant Trait Database	E. Garnier, S. Lavorel	Garnier et al. (2007), Pakeman et al. (2008, 2009), Fortunel et al. (2009)
44 VirtualForests Trait Database	A. Gutiérrez	Gutiérrez (2010)
45 Dispersal Traits Database	S. Higgins	Unpublished Data
46 Herbaceous Traits from the Öland Island Database	T. Hickler	Hickler (1999)
47 Global Wood Anatomy Database	S. Jansen, F. Lens	Unpublished Data
48 Gobal Leaf Element Composition Database	S. Jansen	Watanabe et al. (2007)
49 *Leaf Physiology Database	J. Kattge, C. Wirth	Kattge et al. (2009)
50 KEW African Plant Traits Database	D. Kirkup	Kirkup et al. (2005)
51 Photosynthesis Traits Database	K. Kramer	Unpublished Data
52 Traits of Bornean Trees Database	H. Kurokawa	Kurokawa & Nakashizuka (2008)
53 Ponderosa Pine Forest Database	D. Laughlin	Laughlin et al. (2010)
54 New South Wales Plant Traits Database	M. Leishman	Unpublished Data
55 The RAINFOR Plant Trait Database	J. Lloyd, N. Fyllas	Baker et al. (2009), Fyllas et al. (2009), Patiño et al. (2009)
56 French Grassland Trait Database	F. Louault, J. -F. Soussana	Louault et al (2005)
57 The DIRECT Plant Trait Database	P. Manning	Unpublished Data
58 Leaf Chemical Defense Database	T. Massad	Unpublished Data
59 Panama Leaf Traits Database	J. Messier	Messier et al. (2010)
60 *Global Seed Mass Database	A. Moles	Moles et al. (2004, 2005a,b)
61 *Global Plant Height Database	A. Moles	Moles et al. (2004)
62 Global Leaf Robustness and Physiology Database	Ü. Niinemets	Niinemets (1999, 2001)
63 The Netherlands Plant Traits Database	J. Ordonez, P. van Bodegom	Ordonez et al. (2010 a,b)
64 The Netherlands Plant Height Database	W. Ozinga	Unpublished Data
65 Hawaiian Leaf Traits Database	J. Penuelas, Ü. Niinemets	Peñuelas et al. (2010 a,b)
66 Catalonian Mediterranean Forest Trait Database	J. Penuelas, R. Ogaya	Ogaya & Peñuelas (2003, 2006, 2007, 2008), Sardans et al. (2008)
67 Catalonian Mediterranean Shrubland Trait Database	J. Penuelas, M. Estiarte	Peñuelas et al. (2007), Prieto et al. (2009)
68 ECOQUA South American Plant Traits Database	V. Pillar, S. Muller	Pillar et al. (2003), Overbeck (2005), Blanco et al. (2007), Duarte et al. (2007), Muller et al. (2007), Overbeck & Pfadenhauer (2007)
69 *The Tansley Review LMA Database	H. Poorter	Poorter et al. (2009)
70 Categorical Plant Traits Database	H. Poorter	Unpublished Data
71 Tropical Rainforest Traits Database	L. Poorter	Poorter & Bongers (2006), Poorter (2009)
72 *Frost Hardiness Database	A. Rammig	Unpublished Data
73 Reich-Oleksyn Global Leaf N, P Database	P. B. Reich, J. Oleksyn	Reich, Oleksyn, Wright (2009)
74 Global A, N, P, SLA Database	P. B. Reich	Reich, Oleksyn, Wright (2009)
75 Cedar Creek Savanna SLA, C, N Database	P. B. Reich	Willis et al. (2009)
76 Global Respiration Database	P. B. Reich	Reich et al. (2008)
77 Leaf and Whole-Plant Traits Database: Hydraulic and Gas Exchange Physiology, Anatomy, Venation Structure, Nutrient Composition, Growth and Biomass Allocation	L. Sack	Sack et al. (2003, 2005, 2006), Sack (2004), Nakahashi et al. (2005), Sack & Frole (2006), Cavender-Bares et al. (2007), Choat et al. (2007), Cornwell et al. (2007), Martin et al. (2007), Coomes et al. (2008), Hoof et al. (2008), Quero et al. (2008), Scoffoni et al. (2008), Dunbar-Co et al. (2009), Hao et al. (2010), Waite & Sack (2010), Markesteijn et al. (2011)
78 Tropical Traits from West Java Database	S. Shiodera	Shiodera et al. (2008)
79 Leaf And Whole Plant Traits Database	B. Shipley	Shipley (1989, 1995, 2002), Shipley & Parent (1991), McKenna & Shipley (1999), Meziane & Shipley (1999a,b, 2001), Pyyankov et al. (1999), Shipley & Lechowitz (2000), Shipley & Vu (2002), Vile D. (2005), Kazakou et al. (2006), Vile et al. (2006)

Group of traits	Traits per group	Data sets	Species	Entries	Geo-referenced	Location	Soil
1 Plant growth form*	**7**	**62**	**39715**	**130527**	**45683**	**48355**	**19630**
2 Plant life form*	1	9	7870	64949	55476	58575	53008
3 Plant resprouting capacity*	4	7	3248	5219	410	319	2462
4 Plant height	15	63	18071	105422	43351	50154	34325
5 Plant longevity	4	23	8198	18844	3709	2336	5109
6 Plant age of reproductive maturity	3	3	1506	2024	0	24	0
7 Plant architectural relationships	72	43	10227	356188	340540	340390	332608
8 Plant crown size	4	8	276	4180	1450	846	33
9 Plant surface roughness	1	1	31	31	0	0	0
10 Plant tolerance to stress	40	14	8275	62362	877	1286	33799
11 Plant phenology	10	16	7630	26765	2900	8816	6868
12 Leaf type*	**1**	**15**	**33519**	**49668**	**6261**	**4490**	**2511**
13 Leaf compoundness*	1	15	34523	50502	13495	13558	230
14 Leaf photosynthetic pathway*	**1**	**29**	**31641**	**40807**	**6305**	**4442**	**5495**
15 Leaf phenology type*	**1**	**35**	**15512**	**65536**	**36579**	**37888**	**24900**
16 Leaf size	17	67	16877	205165	158066	138105	74424
17 Leaf longevity	4	18	1080	1953	1705	1515	551
18 Leaf angle	2	6	4693	41882	41848	41805	39820
19 Leaf number per unit shoot length	1	4	4135	10751	1340	2007	1265
20 Leaf anatomy	41	10	1076	26649	24014	23950	0
21 Leaf cell size	14	6	310	1196	339	462	0
22 Leaf mechanical resistance	7	17	4206	11645	5608	6295	227
23 Leaf absorbance	1	4	137	363	0	0	61
24 Specific leaf area (SLA)	13	89	8751	87064	63730	53830	18149
25 Leaf dry matter content	5	35	3098	33777	26125	19767	6919
26 Leaf carbon content	3	32	3028	18887	15295	11938	7857
27 Leaf nitrogen content	4	62	7122	58064	43417	41844	25857
28 Leaf phosphorus content	2	35	4870	26065	19022	21095	7390
29 Tissue carbon content (other plant organs)	19	18	659	4273	2726	2040	1093
30 Tissue nitrogen content (other plant organs)	55	40	4848	32438	24598	22317	21904
31 Tissue phosphorus content (other plant organs)	16	18	3763	17058	10115	12519	2445
32 Tissue chemical composition (apart from C,N,P)	136	28	5031	84743	26272	74076	25152
33 Photosynthesis	49	34	2049	19793	9446	9980	11127
34 Stomatal conductance	76	23	918	11811	4386	6409	4729
35 Respiration	105	18	633	14898	6423	12519	3621
36 Litter decomposability	2	8	972	2172	2013	1568	968
37 Pollination mode*	1	10	4211	16571	780	853	299
38 Dispersal mode*	6	19	9728	43502	5410	6357	341
39 Seed germination stimulation*	6	7	3407	7074	112	206	4437
40 Seed size	17	30	26839	158881	13225	6780	3755
41 Seed longevity	3	5	1862	11466	3	97	3
42 Seed morphology	5	9	2326	3811	567	1253	0
43 Stem bark thickness	1	3	52	183	183	183	0
44 Wood porosity*	1	1	5221	7059	0	0	0
45 Woodiness*	**1**	**23**	**44385**	**74891**	**24957**	**26237**	**19609**
46 Wood anatomy	77	13	8506	252072	126	24	965
47 Wood density	10	34	11907	43871	19422	31522	3121

Trait	Number of entries	Original scale				Logarithmic scale				Change of normality
		Skew-ness	Kurto-sis	JB test	p-value	Skew-ness	Kurto-sis	JB test	p-value	
Seed dry mass	**53744**	**123.02**	**19457.16**	**8.E+11**	**<2.20E-16**	**0.53**	**0.42**	**2915**	**<2.20E-16**	**8.E+11**
Leaf dry mass	26220	161.48	26118.88	7.E+11	<2.20E-16	-0.45	0.90	1748	<2.20E-16	7.E+11
Leaf area	76883	65.47	6990.13	2.E+11	<2.20E-16	-0.54	0.02	3798	<2.20E-16	2.E+11
Conduit (vessel and tracheid) density	5454	68.93	4968.04	6.E+09	<2.20E-16	-0.03	-0.43	43	<2.20E-16	6.E+09
Leaf Fe content per dry mass	3128	31.84	1084.72	2.E+08	<2.20E-16	1.51	8.78	11229	<2.20E-16	2.E+08
Releasing height	19668	13.86	292.85	7.E+07	<2.20E-16	0.70	2.33	6068	<2.20E-16	7.E+07
Leaf Mn content per dry mass	3273	12.04	222.70	6842757	<2.20E-16	-0.02	-0.51	35	2.41E-08	6842722
Seed length	9336	7.41	89.35	3191250	<2.20E-16	0.31	0.47	239	<2.20E-16	3191011
Whole leaf nitrogen content	1006	12.84	248.60	2618135	<2.20E-16	-0.53	0.08	48	4.06E-11	2618087
Leaf Na content per dry mass	3180	9.55	126.32	2162452	<2.20E-16	0.19	0.79	100	<2.20E-16	2162352
Specific leaf area (SLA)	**48142**	**2.85**	**27.49**	**1581085**	**<2.20E-16**	**-0.54**	**1.06**	**4555**	**<2.20E-16**	**1576530**
Leaf phosphorus content per dry mass (P_m)	**17920**	**3.58**	**42.89**	**1412132**	**<2.20E-16**	**-0.38**	**0.98**	**1155**	**<2.20E-16**	**1410977**
Leaf phosphorus content per area	5290	5.33	71.12	1139938	<2.20E-16	-0.04	0.75	125	<2.20E-16	1139813
Leaf Zn content per dry mass	3278	8.04	84.86	1018873	<2.20E-16	1.35	2.55	1880	<2.20E-16	1016993
Maximum plant longevity	2006	7.31	97.69	815546	<2.20E-16	-0.91	1.40	442	<2.20E-16	815104
Leaf lifespan (longevity)	**1654**	**7.26**	**91.59**	**592617**	**<2.20E-16**	**0.31**	**-0.35**	**34**	**4.30E-08**	**592583**
Whole leaf phosphorus content	444	10.23	141.53	378307	<2.20E-16	-0.27	-0.34	7	0.02529	378299
Leaf K content per dry mass	4144	4.09	33.47	204954	<2.20E-16	0.09	0.33	24	6.64E-06	204930
Leaf Al content per dry mass	3448	5.14	35.08	191974	<2.20E-16	1.13	1.01	876	<2.20E-16	191098
Leaf nitrogen/phosphorus (N/P) ratio	11612	3.03	17.65	168595	<2.20E-16	0.25	0.41	199	<2.20E-16	168396
Seed terminal velocity	1178	3.91	50.26	126989	<2.20E-16	-0.45	-0.77	69	9.99E-16	126920
Leaf mechanical resistance: tear resistance	758	6.53	59.82	118402	<2.20E-16	0.86	1.11	132	<2.20E-16	118270
Leaf thickness	2934	4.24	29.88	117951	<2.20E-16	0.77	0.71	351	<2.20E-16	117600
Maximum Plant height	**28248**	**2.35**	**6.99**	**83464**	**<2.20E-16**	**0.11**	**-0.89**	**983**	**<2.20E-16**	**82481**
Leaf respiration per dry mass	2234	4.28	24.65	63393	<2.20E-16	0.29	0.62	66	4.77E-15	63327
Wood phosphorus content per dry mass	1056	4.93	35.87	60888	<2.20E-16	0.71	0.31	94	<2.20E-16	60794
Leaf nitrogen content per area (N_a)	**13528**	**1.73**	**8.25**	**45047**	**<2.20E-16**	**-0.27**	**0.34**	**224**	**<2.20E-16**	**44823**
Leaf Mg content per dry mass	3485	2.55	15.68	39460	<2.20E-16	-0.14	0.13	14	0.001098	39446
Conduit (vessel and tracheid) area	3050	3.31	15.89	37636	<2.20E-16	-0.24	-0.09	31	2.15E-07	37605
Leaf S content per dry mass	1092	4.60	24.78	31788	<2.20E-16	1.45	4.21	1189	<2.20E-16	30600
Leaf Ca content per dry mass	3755	2.11	10.09	18721	<2.20E-16	-0.83	1.19	656	<2.20E-16	18065
Leaf nitrogen content per dry mass (N_m)	**35862**	**1.21**	**2.33**	**16905**	**<2.20E-16**	**-0.22**	**-0.38**	**407**	**<2.20E-16**	**16498**
Vessel diameter	3209	2.61	9.61	15977	<2.20E-16	0.27	-0.35	54	1.83E-12	15923
Conduit lumen area per sapwood area	2280	2.41	9.75	11243	<2.20E-16	-0.37	0.97	140	<2.20E-16	11102
Canopy height observed	40510	1.25	1.04	12416	<2.20E-16	-0.15	-1.22	2654	<2.20E-16	9762
Leaf dry matter content (LDMC)	17339	1.10	2.68	8693	<2.20E-16	-0.46	0.85	1141	<2.20E-16	7551
Leaf respiration per dry mass at 25 C	1448	2.70	9.24	6907	<2.20E-16	0.49	0.63	82	<2.20E-16	6825
Stomatal conductance per leaf area	1093	2.39	10.69	6250	<2.20E-16	-0.73	1.27	171	<2.20E-16	6079
Photosynthesis per leaf dry mass ($Amax_m$)	**2549**	**2.09**	**6.01**	**5699**	**<2.20E-16**	**-0.36**	**0.13**	**58**	**2.85E-13**	**5642**
Leaf Si content per dry mass	1057	2.35	9.82	5219	<2.20E-16	-0.54	0.84	82	<2.20E-16	5137
Vessel element length	3048	1.63	5.12	4668	<2.20E-16	-0.28	0.35	55	9.89E-13	4613
Wood nitrogen content per dry mass	1259	2.22	8.24	4591	<2.20E-16	0.33	0.15	24	5.93E-06	4567
Photosynthesis per leaf area ($Amax_a$)	**3062**	**1.49**	**3.20**	**2436**	**<2.20E-16**	**-0.63**	**1.32**	**422**	**<2.20E-16**	**2014**
Leaf K content per area	240	3.12	12.28	1898	<2.20E-16	0.37	0.55	9	0.01393	1890
Leaf carbon/nitrogen (C/N) ratio	2615	0.95	1.99	824	<2.20E-16	-0.12	-0.18	10	0.008102	815
Wood density	26414	0.44	-0.15	887	<2.20E-16	-0.17	-0.40	298	<2.20E-16	589
Leaf density	1463	1.01	2.59	655	<2.20E-16	-0.56	0.79	115	<2.20E-16	540
Root nitrogen content per dry mass	1263	1.33	1.35	466	<2.20E-16	-0.05	-0.54	16	0.0003217	450
Leaf respiration per area	1303	1.22	2.00	542	<2.20E-16	-0.79	1.80	312	<2.20E-16	230

Trait	Number of entries	Unit	Mean value	SD$_{lg}$	2.5% Quantile	Median	97.5% Quantile
Seed dry mass	**49837**	**mg**	**2.38**	**1.08**	**0.02**	**1.95**	**526**
Canopy height observed	37516	m	1.62	0.92	0.04	1.5	30
Whole leaf phosphorus content	426	mg	0.0685	0.83	0.0018	0.08	1.96
Leaf area	71929	mm^2	1404.0	0.81	25	2025	36400
Maximum plant height	**26625**	**m**	**1.84**	**0.78**	**0.1**	**1.25**	**40**
Leaf dry mass	24663	mg	38.9	0.78	0.96	43.5	1063.9
Whole leaf nitrogen content	961	mg	1.31	0.77	0.03	1.69	27.6
Conduit (vessel and tracheid) area	2974	mm^2	0.00349	0.63	0.00024	0.0032	0.04
Leaf Mn content per dry mass	3159	mg/g	0.189	0.58	0.01	0.19	2.13
Maximum plant longevity	1854	year	155.8	0.55	6.22	175	1200
Leaf Al content per dry mass	3203	mg/g	0.128	0.55	0.02	0.1	4.49
Leaf Na content per dry mass	3086	mg/g	0.200	0.55	0.01	0.2	3.24
Conduit (vessel and tracheid) density	5301	mm^{-2}	37.6	0.54	4	38	380
Seed terminal velocity	1108	m/s	1.08	0.42	0.17	1.4	4.69
Releasing height	18472	m	0.347	0.42	0.05	0.35	2
Leaf lifespan (longevity)	**1540**	**month**	**9.40**	**0.41**	**2**	**8.5**	**60**
Leaf tannins content per dry mass*	394	%	2.01	0.41	0.19	2.35	8.04
Wood phosphorus content per dry mass	1016	mg/g	0.0769	0.37	0.02	0.05	0.56
Leaf respiration per dry mass	2005	µmol/g/s	0.0097	0.36	0.0025	0.0097	0.04
Seed length	8770	mm	1.80	0.34	0.4	1.8	9
Photosynthesis per leaf dry mass (Amax$_m$)	**2384**	**µmol/g/s**	**0.115**	**0.34**	**0.02**	**0.12**	**0.49**
Leaf mechanical resistance: tear resistance	722	N/mm	0.814	0.34	0.19	0.76	5.11
Leaf Ca content per dry mass	3594	mg/g	9.05	0.34	1.57	9.83	34.7
Vessel diameter	3102	µm	51.4	0.32	15	50	220
Stomatal conductance per leaf area	1032	mmol/m/s	241.0	0.31	52.4	243.7	895.7
Root nitrogen content per dry mass	1158	mg/g	9.67	0.31	2.6	9.3	36.1
Leaf Si content per dry mass	1027	mg/g	0.163	0.29	0.04	0.17	0.53
Leaf Zn content per dry mass	3080	mg/g	0.0226	0.28	0.0065	0.02	0.1
Leaf respiration per dry mass at 25 C	1305	µmol/g/s	0.0092	0.28	0.0035	0.0082	0.03
Leaf K content per dry mass	3993	mg/g	8.44	0.27	2.56	8.3	28.2
Photosynthesis per leaf N content (Amax$_N$)	**3074**	**µmol/g/s**	**10.8**	**0.27**	**1.59**	**6.32**	**19.2**
Leaf phenolics content per dry mass*	454	%	12.1	0.26	2.43	11.9	25.1
Specific leaf area (SLA)	**45733**	**mm^2/mg**	**16.6**	**0.26**	**4.5**	**17.4**	**47.7**
Leaf K content per area	231	g/m^2	0.760	0.26	0.24	0.72	2.60
Leaf Mg content per dry mass	3360	mg/g	2.61	0.25	0.83	2.64	8.0
Leaf Fe content per dry mass	3040	mg/g	0.077	0.25	0.02	0.07	0.26
Photosynthesis per leaf area (Amax$_a$)	**2883**	**µmol/m^2/s**	**10.3**	**0.24**	**3.28**	**10.5**	**29**
Leaf respiration per area	1201	µmol/m^2/s	1.19	0.24	0.38	1.2	3.4
Leaf phosphorus content per dry mass (P$_m$)	**17057**	**mg/g**	**1.23**	**0.24**	**0.40**	**1.25**	**3.51**
Leaf thickness	2815	mm	0.211	0.24	0.08	0.19	0.7
Conduit lumen area per sapwood area	2210	mm^2/mm^2	0.137	0.23	0.04	0.14	0.37
Leaf phosphorus content per area	5083	g/m^2	0.104	0.23	0.03	0.1	0.28
Vessel element length	2964	µm	549.5	0.21	200	555	1350
Leaf nitrogen/phosphorus (N/P) ratio	11200	g/g	12.8	0.21	5.33	12.6	33.2
Leaf nitrogen content per area (N$_a$)	**12860**	**g/m^2**	**1.59**	**0.19**	**0.64**	**1.63**	**3.6**
Wood nitrogen content per dry mass	1210	mg/g	1.20	0.19	0.55	1.21	2.95
Leaf S content per dry mass	1023	mg/g	1.66	0.18	0.78	1.59	4.75
Leaf nitrogen content per dry mass (N$_m$)	**33880**	**mg/g**	**17.4**	**0.18**	**7.99**	**17.4**	**38.5**
Leaf dry matter content (LDMC)	16185	g/g	0.213	0.17	0.1	0.21	0.42
Leaf density	1372	g/cm^3	0.426	0.15	0.2	0.43	0.77

Leaf carbon/nitrogen (C/N) ratio	2498	g/g	23.4	0.14	12.39	23.5	42.2
Wood density	26391	mg/mm^3	0.597	0.12	0.33	0.6	0.95
Leaf carbon content per dry mass*	7856	mg/g	476.1	0.03	404.5	476.3	540.8

		Seed mass			*Plant height*			*LL*			*SLA*			N_m			P_m			N_a			$Amax_a$			*Ama*	
		n	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mean**	**SD**	**n**	**mea**
All data		49837	2.38	1.08	26624	1.84	0.78	1540	9.40	0.41	45733	16.60	0.26	33880	17.40	0.18	17056	1.23	0.24	12860	1.59	0.19	3145	10.11	0.25	2919	0.
PFT summary	**mean**		5.27	0.79		2.67	0.43		11.42	0.25		15.08	0.20		17.46	0.16		1.24	0.21		1.53	0.17		10.22	0.22		0.
	SD		0.90			0.69			0.40			0.18			0.10			0.14			0.11			0.16			0.
	n/PFT	2623			1401			91			2407			1783			898			677			208			198	
	sign. p	***			***			***			***			***			***			***			***			***	
Species summary	**mean**		2.12	0.13		3.06	0.18		9.09	0.03		18.84	0.09		18.37	0.08		1.22	0.11		1.48	0.10		10.13	0.14		0.
	SD		1.03			0.81			0.40			0.22			0.16			0.23			0.16			0.22			0.
	nsp	2707			882			363			2423			1250			649			519			168			120	
	n/sp	11			10			3			16			18			16			15			13			11	
	sign. p	***			***			***			***			***			***			***			***			***	
Plant Functional Types																											
Fern (218)		3	0.08	0.83	329	0.75	0.47	13	28.48	0.25	647	18.86	0.22	143	14.77	0.19	91	0.72	0.21	50	1.14	0.20	2	9.15	0.18	2	0.
Grass C3 (594)		3935	0.61	0.70	1242	0.44	0.31	81	3.85	0.22	5033	20.12	0.20	2669	17.84	0.16	1435	1.43	0.23	1075	1.14	0.17	341	13.25	0.21	232	0.
Grass C4 (248)		635	0.58	0.60	383	0.64	0.33	6	1.68	0.18	583	19.23	0.22	1128	14.14	0.15	150	1.36	0.23	232	0.93	0.16	97	19.78	0.20	70	0.
Herb C3 (3129)		15506	0.77	0.82	3404	0.38	0.38	215	3.49	0.25	18830	22.83	0.19	4893	23.31	0.16	1870	2.02	0.21	2798	1.29	0.18	1015	12.81	0.25	663	0.
Herb C4 (63)		183	0.49	0.53	36	0.25	0.55		1.00	0.00	212	20.20	0.25	87	18.78	0.24	47	1.86	0.25	127	1.31	0.14	102	21.87	0.22	33	0.
Climber non-woody (233)		751	15.25	0.57	268	1.05	0.48	17	8.99	0.35	949	23.40	0.20	295	25.34	0.17	143	1.38	0.26	154	1.33	0.19	29	10.04	0.24	30	0.
Climber woody (73)		102	15.16	0.43	76	3.74	0.51	7	16.68	0.35	443	14.73	0.19	157	21.34	0.14	101	1.62	0.23	42	1.32	0.20	13	11.21	0.21	3	0.
Shrub broadleaved deciduous (596)		1573	6.67	0.99	1221	3.59	0.49	167	4.68	0.19	3838	15.36	0.18	2223	21.50	0.14	1209	1.56	0.20	748	1.45	0.18	233	9.97	0.17	242	0.
Shrub broadleaved evergreen (116		1911	4.02	0.98	1694	1.61	0.55	284	15.88	0.26	3216	8.99	0.21	2623	13.73	0.18	1504	0.84	0.25	1033	1.90	0.19	390	8.96	0.23	345	0.
Shrub needleleaved (83)		256	2.55	1.28	121	3.53	0.58	17	36.66	0.25	303	7.43	0.15	223	10.11	0.15	123	0.74	0.26	89	1.83	0.17	19	8.03	0.24	19	0.
Tree broadleaved deciduous (699)		1606	33.80	1.09	1471	20.82	0.28	240	5.83	0.17	3963	15.40	0.17	4343	21.32	0.13	2225	1.44	0.20	1723	1.57	0.16	539	9.34	0.18	520	0.
Tree broadleaved evergreen (2136)		1487	27.64	1.07	1973	16.56	0.36	360	16.83	0.29	3859	9.46	0.19	5921	16.89	0.16	3177	0.86	0.20	2723	1.87	0.15	652	7.79	0.23	484	0.
Tree needleleaved deciduous (16)		64	6.88	0.57	88	32.98	0.20	12	6.08	0.01	129	10.09	0.09	248	19.37	0.10	155	1.83	0.15	37	1.80	0.13	11	6.90	0.20	12	0.
Tree needleleaved evergreen (134)		889	13.77	0.63	882	27.20	0.30	63	39.71	0.21	1517	5.00	0.13	5558	12.09	0.10	3622	1.23	0.16	984	2.62	0.14	196	9.45	0.24	121	0.
Plant Species (exemplary):																											
Carex bigelowii		23	0.47	0.304	6	0.23	0.137	2	3.62	0.003	14	12.19	0.124	41	20.32	0.107	16	1.94	0.186	7	1.65	0.059	3	15.16	0.107	3	0.
Dactylis glomerata		88	0.81	0.154	39	0.73	0.153	3	2.75	0.125	139	24.58	0.109	50	24.67	0.128	22	1.98	0.183	11	1.32	0.098	7	13.45	0.160	7	0.
Poa pratensis		57	0.26	0.139	22	0.50	0.140	1	3.01		169	23.96	0.131	63	17.36	0.172	11	2.28	0.178	6	1.19	0.184	8	13.75	0.200	6	0.
Trifolium pratense		61	1.53	0.117	45	0.39	0.277				141	22.85	0.084	34	38.65	0.086	14	2.07	0.123	7	1.65	0.090	5	16.94	0.061	4	0.
Prunus spinosa		22	165.01	0.244	14	2.92	0.216	3	5.60	0.024	86	14.54	0.091	16	28.05	0.114	13	2.15	0.099	11	1.87	0.081	3	11.17	0.048	3	0.
Acacia doratoxylon		3	15.40	0.000	7	6.09	0.268	3	19.80	0.003	3	4.57	0.000	7	20.37	0.012	6	0.83	0.003	3	4.38	0.001	2	14.51	0.002	2	0.
Phyllota phylicoides		6	2.83	0.026	6	0.67	0.345	2	22.43	0.001	6	7.44	0.059	5	12.94	0.025				2	1.49	0.002	2	8.35	0.003	2	0.
Pultenaea daphnoides		5	3.98	0.141	3	2.86	0.036	2	9.36	0.002	3	13.76	0.192	6	19.40	0.004	5	0.35	0.013	3	1.83	0.003	2	9.58	0.002	2	0.
Lepechinia calycina		4	12.35	0.186	2	2.79	0.174	2	4.39	0.003	5	11.23	0.075	5	18.38	0.139	3	1.20	0.000	3	1.48	0.153	2	12.56	0.001	2	0.
Leptospermum polygalifolium		4	0.18	0.056	3	4.00	0.000	2	7.38	0.003	2	10.93	0.002	6	13.35	0.014	5	0.49	0.048	3	1.20	0.001	3	8.56	0.002	2	0.
Banksia marginata		7	8.51	0.073	3	5.45	0.326	3	36.36	0.001	11	5.72	0.072	11	8.30	0.050	4	0.34	0.051	8	1.41	0.032	2	19.52	0.001	2	0.
Grevillea buxifolia		7	46.39	0.114	6	1.35	0.271	2	15.07	0.003	4	8.18	0.094	6	7.16	0.006	2	0.29	0.000	3	0.78	0.001	2	8.68	0.002	2	0.
Persoonia levis		3	206.27	0.068	6	3.60	0.130	2	45.59	0.002	6	5.68	0.068	6	5.87	0.004	2	0.30	0.000	3	1.08	0.001	2	8.16	0.002	2	0.
Dodonaea viscosa		28	6.89	0.189	26	2.63	0.320	6	9.29	0.054	18	6.61	0.107	19	19.23	0.058	16	1.20	0.099	9	2.61	0.071	6	11.64	0.051	1	0.
Pimelea linifolia		5	2.85	0.114	6	1.19	0.134	2	12.64	0.002	4	13.76	0.121	6	14.39	0.022	5	0.50	0.034	3	0.85	0.003	3	7.91	0.002	2	0.
Quercus ilex		7	2241.03	0.085	14	17.41	0.285	1	22.75		283	6.24	0.109	449	14.00	0.070	297	0.88	0.129	30	1.89	0.129	20	7.24	0.181	18	0.
Quercus robur		8	3219.44	0.155	33	26.48	0.233	2	6.01	0.001	103	14.07	0.090	227	23.35	0.097	190	1.78	0.151	48	1.67	0.153	3	7.40	0.001	2	0.
Fagus sylvatica		16	194.92	0.120	23	30.96	0.189	2	6.01	0.001	273	15.39	0.161	260	22.61	0.078	148	1.42	0.108	205	1.21	0.149	6	5.18	0.160	10	0.
Simarouba amara		5	221.99	0.243	3	34.28	0.020	2	11.63	0.040	6	8.40	0.183	5	20.08	0.109	4	0.73	0.094	3	2.30	0.132	1	13.84	0.000	1	0.
Synoum glandulosum		6	197.77	0.126	10	3.80	0.307	2	11.75	0.001	10	11.68	0.065	6	16.22	0.014	5	0.87	0.022	3	1.46	0.002	2	6.46	0.000	2	0.
Eucalyptus socialis		4	0.81	0.031	7	6.94	0.186	2	28.78	0.001	6	3.49	0.012	15	10.83	0.059	14	0.54	0.096	9	3.67	0.024	2	16.23	0.000	2	0.
Brachychiton populneus		6	108.17	0.217	8	7.76	0.221	3	13.21	0.001	8	8.70	0.070	11	16.99	0.045	10	0.91	0.040	6	2.13	0.046	4	8.49	0.070	4	0.
Larix decidua		9	6.42	0.099	20	37.65	0.184	5	6.01	0.001	90	9.73	0.063	89	19.81	0.072	76	1.79	0.156	12	2.10	0.112	5	5.42	0.161	5	0.
Picea abies		23	6.37	0.078	24	40.02	0.246	3	88.85	0.109	146	4.45	0.134	954	12.40	0.081	812	1.42	0.134	109	3.07	0.116	5	7.67	0.071	5	0.
Pinus sylvestris		29	7.32	0.133	31	25.38	0.244	5	27.71	0.016	430	4.92	0.103	1422	13.06	0.088	1245	1.30	0.117	359	2.80	0.121	6	10.97	0.031	6	0.
Pseudotsuga menziesii		25	11.36	0.054	29	61.79	0.184	2	64.68	0.001	10	6.30	0.153	105	12.29	0.079	82	1.69	0.138	5	1.58	0.135	35	9.12	0.158	4	0.