

The global spectrum of plant form and function

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Earth is home to a remarkable diversity of plant forms and life histories, yet comparatively few essential trait combinations have proved evolutionarily viable in today's terrestrial biosphere. By analysing worldwide variation in six major traits critical to growth, survival and reproduction within the largest sample of vascular plant species ever compiled, we found that occupancy of six-dimensional trait space is strongly concentrated, indicating coordination and trade-offs. Three-quarters of trait variation is captured in a two-dimensional global spectrum of plant form and function. One major dimension within this plane reflects the size of whole plants and their parts; the other represents the leaf economics spectrum, which balances leaf construction costs against growth potential. The global plant trait spectrum provides a backdrop for elucidating constraints on evolution, for functionally qualifying species and ecosystems, and for improving models that predict future vegetation based on continuous variation in plant form and function.

Vascular plants are the main entry point for energy and matter into the Earth's terrestrial ecosystems. Their Darwinian struggle for growth, survival and reproduction in very different arenas has resulted in an extremely wide variety of form and function, both across and within habitats. Yet it has long been thought^{1–8} that there is a pattern to be found in this remarkable evolutionary radiation—that some trait constellations are viable and successful whereas others are not.

Empirical support for a strongly limited set of viable trait combinations has accumulated for traits associated with single plant organs, such as leaves^{7,9–12}, stems^{13,14} and seeds^{15–17}. Evidence across plant organs has been rarer, restricted geographically or taxonomically, and often contradictory^{18–29}. How tightly whole-plant form and function are restricted at the global scale remains unresolved.

Here we present the first global quantitative picture of essential functional diversity of extant vascular plants. We quantify the volume, shape and boundaries of this functional space via joint consideration of six traits that together capture the essence of plant form and function: adult plant height, stem specific density, leaf size expressed as

leaf area, leaf mass per area, leaf nitrogen content per unit mass, and diaspore mass. Our dataset, based on a recently updated communal plant trait database³⁰, covers 46,085 vascular plant species from 423 families and to our knowledge spans the widest range of growth-forms and geographical locations to date in published trait analyses, including some of the most extreme plant trait values ever measured in the field (Table 1, Extended Data Fig. 1). On this basis we reveal that the trait space actually occupied is strongly restricted as compared to four alternative null hypotheses. We demonstrate that plant species largely occupy a plane in the six-dimensional trait space. Two key trait dimensions within this plane are the size of whole plants and organs on the one hand, and the construction costs for photosynthetic leaf area, on the other. We subsequently show which sections of the plane are occupied, and how densely, by different growth-forms and major taxonomic groups. The design opportunities and limits indicated by today's global spectrum of plant form and function provide a foundation to achieve a better understanding of the evolutionary trajectory of vascular plants and help frame and test hypotheses as to where and

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Table 1 | Range of variation in functional traits, geographic distribution and climatic conditions

	Abbreviation	Range	No. of species
Adult plant height (m)	H	0.001* to 90†	24,720
Stem specific density (mg mm ⁻³)	SSD	0.06‡ to 1.39§	11,356
Leaf area (mm ²)	LA	0.79* to 2.79 × 10 ⁶	12,173
Leaf mass per area (g m ⁻²)	LMA	4.9¶ to 1,507#	10,490
N content per unit leaf mass (mg g ⁻¹)	N _{mass}	2.48★ to 68.98**	8,695
Diaspore mass (mg)	SM	5.15 × 10 ⁻⁶ †† to 2.05 × 10 ⁷ ‡‡	24,779
Diaspore mass (mg) excluding pteridophytes	SM	3.0 × 10 ⁻⁴ §§ to 2.05 × 10 ⁷ ‡‡	24,449
Latitude (degrees)		55 S to 83.17 N	
Altitude (m)		-59 to 5,249	
Mean annual temperature (°C)		-27.22 to 29.97	
Mean annual sum of precipitation (mm yr ⁻¹)		<5 to 7,693	

Latitude and altitude are based on species occurrences in the Global Biodiversity Information Facility database (<http://www.gbif.org>). Mean annual temperature and annual sum of precipitation refer to CRU0.5 degree climatology. **Wolffia arrhiza* and *Azolla microphylla*; †*Sequoia sempervirens* and *Eucalyptus regnans*; ‡*Utricularia vulgaris*; §*Caesalpinia sclerocarpa*; ||*Victoria amazonica*; ¶*Myriophyllum aquaticum*; #*Agave americana*; ★*Hakea erecta*; ***Dipcadi glaucum*; ††*Blechnaceae*; ‡‡*Lodoicea maldivica*; §§*Laelia undulata* and *Alectra vogelii*.

how ecological filtering and evolution might further shape the Earth's plant trait space.

The trait space occupied by plants worldwide

Certain traits can be thought of as indexing positions of species along key dimensions of plant ecological strategy directly relevant to growth, survival and reproduction^{19,20,22,31–33}. We chose six traits whose fundamental importance for ecological strategy has been established unequivocally and for which data have recently become available for an unprecedented number of species worldwide³⁰. Among the six key traits (see Methods for details and references) adult plant height (H) corresponds with the ability to pre-empt light resources and disperse diaspores. Stem specific density (SSD) reflects a trade-off between growth potential and mortality risk from biomechanical or hydraulic failure. Leaf area (LA, size of an individual leaf) has important consequences for leaf energy and water balance. Leaf mass per area (LMA) and leaf nitrogen content per unit mass (N_{mass}) express different aspects of leaf strategy for resource capture and conservation: LMA reflects a trade-off between carbon gain and longevity, while N_{mass} reflects a trade-off between the benefits of photosynthetic potential and the costs of acquiring nitrogen and suffering herbivory. Diaspore mass (the mass of an individual dispersed seed or spore; SM) reflects a trade-off between seedling survival versus colonization ability in space and time. Ranges of trait variation span from 2 (SSD, N_{mass}) to 13 orders of magnitude (SM) (Table 1).

We investigated which portion of the six-dimensional trait space is occupied by vascular plants that now live on Earth. There are two primary reasons why plants might occupy a subset of the potential trait space: (1) values of independent traits are distributed along each axis in a clumped, non-uniform manner; and (2) there are inherent correlations between the values of different traits. We therefore built four null models varying the trait distributions and their correlation structure. We computed the volume of the six-dimensional convex hull³⁴, i.e. the smallest convex volume in hyperspace that contains the (log₁₀- and z-transformed) observed values of H, SSD, LA, LMA, N_{mass} and SM (for a visualization see <https://sdray.shinyapps.io/globalspectr/>; Supplementary Application 1), and compared it against hypervolumes from four null hypotheses (hv_{nm1} to hv_{nm4}; shown diagrammatically in Fig. 1 and described in detail in Methods). Hypervolumes hv_{nm1} to hv_{nm3} assume that the traits vary independently, resulting in a functional space spanning along six orthogonal axes. Null model 1 assumes that any combination of trait values can arise and escape natural selection with equal probability (for example ref. 35), thus extreme and central values are equally likely, each trait having a uniform distribution, and hv_{nm1} approximating a hypercube. Null model 2 assumes that extreme trait values are selected against during evolution and each trait has a log-normal distribution, with hv_{nm2}

approximating a hypersphere. Null model 3 imposes no assumptions about trait distributions but instead allows each trait to be distributed as observed and assumes traits are independent of one other. Null model 4 assumes that extreme values are selected against (i.e., log-normally distributed) and maintains the observed correlation structure among traits. Relative to null models 1 to 3, null model 4 collapses the multidimensional trait-space occupied by plants (hv_{nm4}) into an elongated hyperellipsoid.

We found that the observed hypervolume (hv_{obs}) is much smaller than hypervolumes expected under the first three null models (hv_{nm1} to hv_{nm3}) (Fig. 1). While closer in size to hv_{nm4}, it is still 20% smaller. It also shows greater aggregation of species ('lumpiness') in multivariate

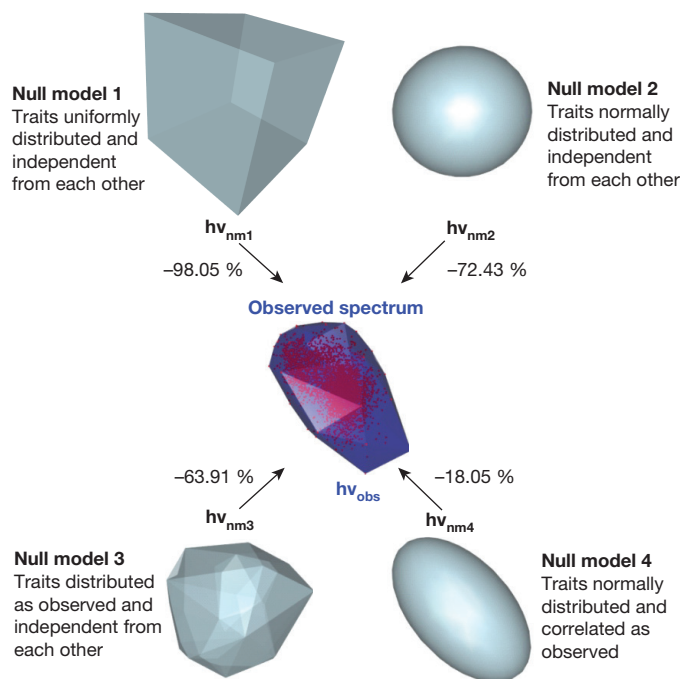


Figure 1 | The volume in trait space occupied by vascular plant species is strongly constrained compared to theoretical null models. The five diagrams are pictorial representations based on three out of the six trait dimensions forming the hypervolumes under scrutiny. The hypervolumes are constructed on the basis of log₁₀- and z-transformed observed values of H, SSD, LA, LMA, N_{mass} and SM (observed hypervolume = hv_{obs}), or on the bases of four different null models of multivariate variation of those traits (hv_{nm1} to hv_{nm4}) (see Methods). Numbers adjacent to arrows indicate percentage reductions in size of hv_{obs} compared to the null-model hypervolumes (all significant at $P < 0.001$).

space than expected under each of the null models (Supplementary Table 1). Thus the restriction of the observed hypervolume mainly reflects correlations among the six traits, and also—to a smaller degree—a greater concentration than expected under multivariate normality. In sum, the trait hypervolume occupied by living vascular plants is strongly constrained, converging towards a relatively small set of successful trait combinations.

Main trends of variation

Within the observed worldwide plant trait space we identified the main independent dimensions of variation. Seventy-four percent of the variation in the six-dimensional space was accounted for by the plane defined by the first two principal components (PC), the only PC found to contain significant, non-redundant information (Fig. 2, Extended Data Table 1 and Extended Data Fig. 2; all PC displayed at <https://sdray.shinyapps.io/globalspectrPC/>; Supplementary Application 2). Within this plane two notable dimensions of trait variation stand out. One dimension runs from short species tending to have small diaspores to tall species tending to have large diaspores (lower left to upper right in Fig. 2a, 'H-SM', more strongly associated with PC1 than PC2). The other (upper left to lower right in Fig 2a, 'LMA- N_{mass} ', more strongly associated with PC2 than PC1) runs from species with

cheaply constructed, 'acquisitive' leaves (low-LMA, nitrogen-rich) to species with 'conservative' leaves (high-LMA, nitrogen-poor) that are expected to have longer leaf lifespan and higher survival in the face of abiotic and biotic hazards^{7,10,36}. Stem specific density (SSD) and leaf area (LA) also load heavily on the plane and are correlated with both the H-SM and the LMA- N_{mass} dimensions (Fig 2a, Extended Data Table 1). Although SSD and SM increase with plant height, at any given H there is considerable independent variation in both (Extended Data Fig. 3a, f), and at any given LMA and N_{mass} there is considerable independent variation in LA (Extended Data Figs 3b, c). These general patterns are robust (Extended Data Table 1) with respect to species selection (for example, considering angiosperms rather than all species), to re-running analyses on a 45,507-species 'gap-filled' trait matrix rather than the 2,214-species six-trait matrix, and to exclusion of individual traits (for example, using only one rather than both leaf economic traits). The outer reaches of the main plane of variation represent extreme combinations of plant size and leaf structure and function (see circled numbers in Fig. 2a, and Extended Data Table 2 for illustrative species), with a wide gradient of intermediate trait combinations between them, together expressing the rich variety of ways in which plants balance the challenges of growth, survival and reproduction.

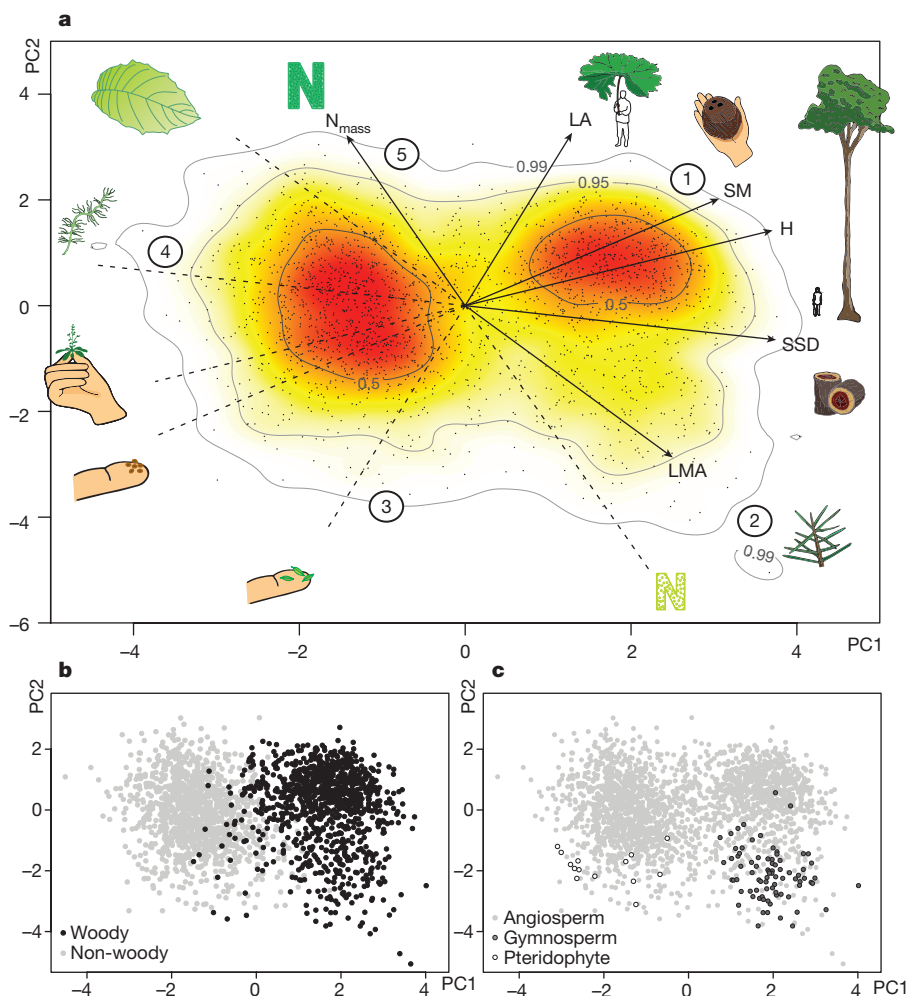


Figure 2 | The global spectrum of plant form and function. **a**, Projection of global vascular plant species (dots) on the plane defined by principal component axes (PC) 1 and 2 (details in Extended Data Table 1 and Extended Data Fig. 2). Solid arrows indicate direction and weighing of vectors representing the six traits considered; icons illustrate low and high extremes of each trait vector. Circled numbers indicate approximate position of extreme poles of whole-plant specialization, illustrated by typical species (Extended Data Table 2). The colour gradient indicates

regions of highest (red) to lowest (white) occurrence probability of species in the trait space defined by PC1 and PC2, with contour lines indicating 0.5, 0.95 and 0.99 quantiles (see Methods, kernel density estimation). Red regions falling within the limits of the 0.50 occurrence probability correspond to the functional hotspots referred to in main text. **b**, **c**, location of different growth-forms (**b**) and major taxa (**c**) in the global spectrum.

Major taxa, growth-forms, and functional hotspots

Different plant groups distribute unevenly in the global spectrum of form and function. Both herbaceous and woody growth-forms show considerable variation along the two main dimensions (Fig. 2b). The two groups are offset along the H–SM dimension (Fig. 2b), with woody species, on average, being taller and having larger seeds and leaves; woody species also tend to have higher SSD and LMA than herbaceous species (Extended Data Fig. 3a–e). Also, although taller species have larger seeds in both herbaceous and woody species-groups, the relationship is only very weak in herbaceous species (Extended Data Figs 3f and 4). In sum, the distinction in traits between herbaceous and woody growth-forms goes beyond the obvious difference in height and stem structure that has been recognized since antiquity³⁷. At the same time, there exist commonalities in trait coordination and trade-offs across both herbaceous and woody plants, shown here at a global scale for the first time. For example, herbaceous and woody plants overlap widely along the LMA– N_{mass} dimension (Fig. 2b), particularly in regard to N_{mass} (Extended Data Fig. 3c), and LMA and N_{mass} are largely independent from LA in both groups (Extended Data Fig. 3b, c). Further, while neither SSD nor LMA increases with plant stature within either group (Extended Data Figs 3a, e and 4), LA increases with H in both (Extended Data Fig. 3d). These multivariate trends are summarised by the clear distinction of herbaceous and woody species-groups along PC1, and their broad overlap along PC2 (Extended Data Fig. 2a).

There are also strong differences in trait-space occupancy by major taxa. For gymnosperms, high costs of seed packaging and abortion are thought to set a lower bound on seed size^{38,39}. Accordingly in Fig. 2c gymnosperms are confined to the right hand side (see also Extended Data Fig. 2b, and, for examples, Extended Data Table 2). The emergence of angiosperms allowed a considerable extension into smaller seed size⁴⁰ that is manifest in extant species. This also opened up lifestyles involving colonization of open ground, shorter lifespans and herbaceous growth-form (towards the left of Fig. 2a). The second major angiosperm innovation whose footprint is evident in the trait space concerns xylem vessels. Angiosperm vessels are longer and larger-diameter conduits than gymnosperm and pteridophyte tracheids, permitting much higher hydraulic conductivities. This, together with a greater density of leaf veins, has allowed angiosperms to deliver a faster transpiration stream while requiring less volume within the leaf⁴¹. These anatomical innovations have made it possible for angiosperms to extend the range of leaf stomatal conductances and photosynthetic capacities to higher values (requiring coordinated higher N_{mass}) and the range of LMA to lower values compared to gymnosperms and pteridophytes (Fig. 2c). Higher hydraulic conductivity presumably also enabled the evolution of very large leaves in angiosperms, and a far wider variety in leaf morphology too. Nevertheless, while angiosperm innovations have expanded trait space considerably towards higher leaf N_{mass} and LA and (compared with gymnosperms) lower diaspore mass, angiosperms also converged on the same zones of trait space as gymnosperms and pteridophytes, as seen in the lower right and lower left of the global trait plane (Fig. 2c).

There are two clear functional hotspots—areas of particularly dense species occupation—in trait space (Fig. 2a). The bimodality resides in H and in SSD, rather than in LMA, N_{mass} or LA (Extended Data Fig. 4). The first hotspot almost entirely corresponds to herbaceous plants and lies at the core of the distribution of both graminoid (grass-like) and non-graminoid herbs, having small, acquisitive leaves and small seeds. The second hotspot lies within the trait space occupied by woody plants, positioned towards the upper right corner of Fig. 2a. It consists mostly of tree species of moderate to great height with large leaves and large seeds; plants other than angiosperms are almost completely absent from it. Many phylogenetically distant families and orders of angiosperms are represented within each hotspot (Supplementary Table 2), indicating that these prevalent ecological trait constellations represent successful solutions acquired repeatedly through the evolutionary history of vascular plants.

Discussion

Our findings show that the trait space currently occupied by vascular plants is quite restricted compared to the range of possibilities that would exist if traits varied independently. Importantly, this finding arises from the combined analysis of six traits describing different plant organs, and from a wider spread of taxa and life histories than has previously been possible. It yields the most comprehensive picture to date of how the remarkable functional diversity of vascular plants seen on Earth today has been able to evolve within very general constraints. This worldwide functional six-trait space is wide, diverse and lumpy, with its fringes occupied by species (indicated with circled numbers in Fig. 2a) ranging from the short model plant thale cress (*Arabidopsis thaliana*) to the 60-m tall Brazil Nut tree (*Bertholletia excelsa*), from flimsy watermilfoil (*Myriophyllum spicatum*) to tough monkey puzzle tree (*Araucaria araucana*), from the tender but toxic devil's snare (*Datura stramonium*) to the hardy needlewood (*Hakea leucophaea*), from the minute leaves and seeds of heather (*Calluna vulgaris*) to the large leaves and seeds of lotus (*Nelumbo nucifera*) (description and additional illustrative species in Extended Data Table 2). Yet, this variation of the six key traits is largely concentrated into a plane.

Stem density, leaf size and diaspore size represent trade-offs within distinct aspects of plant biology³², and in previous studies of trends across different plant organs, these traits have shown considerable variation that is independent from whole-plant size and leaf carbon economy. However, those analyses were based on far more restricted datasets than considered here, in terms of growth-forms, habitats, or both, considering for example tropical woody species^{21–23,26}, temperate semiarid pine forests²⁴, or countrywide herbaceous floras²⁷. At the global scale of our study, these three traits do not constitute major independent dimensions; rather, substantial variation in them is captured by the plane that summarizes global variation in vascular plant design (Fig. 2). Our results are correlative and cannot prove rigorously why such a large share of the potential trait volume is not occupied. Still, from first principles many more combinations of traits than those observed seem feasible as far as biomechanics and evolutionary genetics are concerned. We suggest the concentration into two dimensions and the lumpiness within that plane reflect the major trait constellations that are competent and competitive across the ecological situations available on Earth today.

The patterns described here pertain to fundamental aspects of form and function critical to growth, survival and reproduction of the vast majority of vascular plants on Earth. Importantly, plants converge and diverge in many more ways than explored here, through variation in a vast array of traits beyond the scope of our analysis, related to the fine-tuning of different taxa to specific abiotic and biotic conditions in their habitat (for example refs 42–44). Such variation fits within the more general patterns shown here.

More broadly, our findings are directly relevant to a number of long-running and emerging broad-scale scientific initiatives. First, our findings provide the widest empirical context so far for examining theories that have focused on plant ecological strategies—on different aspects of the Darwinian struggle for existence. For example, the H–SM dimension could be seen as reflecting the *r* (colonization) versus *K* (exploitation) continuum^{4,45}. The LMA– N_{mass} dimension reflects the *A* (adversity-selection) continuum^{4,46}, acquisitive-conservative continuum^{5,7,19,20} or leaf economic spectrum¹⁰. The positions signalled by numbers 3, 4, and 5 in Fig. 2a (and described in Extended Data Table 2) could arguably roughly correspond to the stress-tolerant, ruderal, and competitor strategies of Grime^{3,11,19}. Interestingly, the functional hotspots lie at intermediate positions on the plane rather than at any of these extreme positions (that is, *r* versus *K*, acquisitive versus conservative resource economy, *C*, *S* or *R*-strategy).

Second, the global spectrum we describe has potential to improve emerging large-scale vegetation and ecosystem models (for example see refs 47–49) because we clearly show (Fig. 2a and Extended

Data Fig. 4) that only a limited set of combinations are observed from six plant traits most fundamental to survival, growth and reproduction.

More generally, our findings—as encapsulated in the plane of Fig. 2—establish a backdrop against which many other facets of plant biology can be placed into a broader context. Plant lineages, evolutionary trajectories, and historical and contemporary plant communities and biomes can be mapped onto this global trait spectrum. Trait variation in any given physical setting can be compared to the worldwide background. Model species such as *Arabidopsis thaliana* (located at one extreme of the spectrum) can be positioned against this backdrop, helping to judge how typical or otherwise their physiology and natural history might be. The global spectrum of plant form and function is thus, in a sense, a galactic plane within which we can position any plant—from star anise to sunflower—based on its traits.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

Received 16 September; accepted 26 November 2015.

Published online 23 December 2015.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We are grateful to the many researchers who contributed to this study by making their data available, helping to check information, and/or providing comments at various stages. The study was supported by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY database is hosted at the Max Planck Institute for Biogeochemistry (Jena, Germany) and supported by DIVERSITAS/Future Earth, the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, and BACI (grant ID 640176). The study has also been partially supported by the following institutions and grants to S.D.: Universidad Nacional de Córdoba and CONICET, FONCYT (PICT 554) and SECYT (Argentina), The Leverhulme Trust, UK, and Inter-American Institute for Global Change Research (IAI) SGP-CRA2015 (supported by US National Science Foundation grant GEO-1138881).

Author Contributions Order in list of authors reflects overall participation in this article. S.D., J.K. and S.L. designed the study. S.D., J.K., J.H.C.C., I.J.W., S.L., M.K., C.W., E.G., I.C.P., M.W., H.P., P.B.R., A.T.M., J.D., A.N.G., A.E.Z., J.C., S.J.W., S.N.S., H.J., C.B., B.C., S.P., B. S. and D.K. contributed substantial amounts of data. S.D., J.K., G.B., A.G. and V.F. constructed the database. S.D., J.K., J.H.C.C., I.J.W., S.L., S.Dr., B.R., M.K., C.W., E.G., F.C., J.S.J., N.R., M.D.M. and L.D.G. carried out analyses. S.D., J.K., J.H.C.C., I.J.W., S.L., M.K., C.W., I.C.P., M.W. and P.B.R. wrote the article with contributions from S.Dr., B.R., E.G., H.P., A.T.M., J.D., A.N.G., A.E.Z., J.C., S.J.W., S.N.S., H.J., C.B., B.C., S.P., B.S., D.K., F.C., M.D.M. and L.D.G.

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METHODS

Plant trait definitions and ecological meaning. Adult plant height (typical height of the upper boundary of the main photosynthetic tissues at maturity; hereafter *H*) is the most common measure of whole plant size and indicates ability to pre-empt resources, including the ability of taller plants to display their leaves above those of others and therefore outcompete them; it also relates to whole plant fecundity and facilitation of seed dispersal^{32,50–53}. Taller plants intercept more light but, trading off against that, construction and maintenance costs and risk of breakage increase with height^{22,54}. Large stature has been repeatedly selected for in different lineages during the evolution of land plants, although achieved very differently in different clades⁵⁵.

Stem specific density (dry mass per unit of fresh stem volume; SSD) is a second key index of construction costs and structural strength. Although SSD is more commonly measured on trees, here we used data for both herbaceous and woody species. At least among woody species, stem specific density is positively linked with plant mechanical strength, hydraulic safety and resistance to biotic agents^{13,14,56}. In high-precipitation systems wood density underpins a successional continuum running from low-SSD, fast-growing, light-demanding species to high-SSD, slow-growing, shade-tolerant species. More broadly SSD characterizes a trade-off between fast growth with high mortality rates versus slow growth with high survival^{25,57}.

Leaf area (one-sided surface area of an individual lamina; LA) is the most common measure of leaf size. It is relevant for light interception and has important consequences for leaf energy and water balance^{58–60}. LA affects leaf temperature via boundary layer effects. The larger the lamina, the lower the heat exchange, the diffusion of carbon dioxide and water vapour per unit leaf area between a leaf and the surrounding air. LA is known to be constrained by climatic and microclimatic conditions and also by the allometric consequences of plant size, anatomy and architecture^{61–63}.

Leaf dry mass per unit of lamina surface area (leaf mass per area; LMA) and leaf nitrogen content per unit of lamina dry mass (N_{mass}) reflect different aspects of leaf-level carbon-gain strategies, in particular the ‘leaf economic spectrum’ running from ‘conservative’ species with physically robust, high-LMA leaves with high construction costs per unit leaf area and long expected leaf lifespan (and thus duration of photosynthetic income) to ‘acquisitive’ species with tender, low-cost low-LMA leaves, and short leaf lifespan^{5,9,10,18–20,32,64,65}. LMA relates the area of light interception to leaf biomass, being an expression of how much carbon is invested per unit of light-intercepting area, and thus reflecting a trade-off between construction cost and longevity of lamina. N_{mass} is directly related to photosynthesis and respiration, as the majority of leaf nitrogen is found in metabolically active proteins. N_{mass} reflects a trade-off between, on the one hand, two different costs that increase with higher N_{mass} (to acquire N, and potentially suffer more herbivory) and, on the other hand, the greater photosynthetic potential that higher N_{mass} allows.

Diaspore mass (mass of an individual seed or spore plus any additional structures that assist dispersal and do not easily detach; SM) indexes species along a dimension describing the trade-off between seedling competitiveness and survival on the one hand, and dispersal and colonization ability on the other^{16,66–68}. As a broad generalization small seeds can be produced in larger numbers with the same reproductive effort and, at a given plant height, be dispersed further away from the parent plant and form persistent seed banks, whereas large seeds facilitate survival through the early stages of recruitment, and higher establishment in the face of environmental hazards (for example deep shade, drought, herbivory)^{32,69–72}.

Dataset description. We compiled a global dataset containing 46,085 species and 601,973 cells, of which 92,212 correspond to quantitative species-level trait information, based on > 800,000 trait measurements for the six traits of interest on > 500,000 plant individuals. The vast majority of data were compiled from pre-existing smaller datasets contributed to the TRY Plant Trait Database³⁰ (<https://www.try-db.org>, accessed May 2015). The dataset was supplemented by published data not included in TRY and a small number of original unpublished data by W. J. Bond, J.H.C.C., S.Di., L. Enrico, M. T. Fernandez-Piedade, L.D.G., D.K., M.K., N. Salinas, E.-D. Schulze, K. Thompson, and R. Urrutia. The final dataset (BLOB) was derived from 175 studies^{10,11,13,20,21,23–25,56,57,64,65,73–235}.

In this global analysis, each species, identified subspecies or local variety is represented by a single value for each trait. This value is the geometric mean of all the observations of a trait present in the TRY Plant Trait Database and additional databases incorporated to the present dataset. The number of observations per trait and species range from a single one (in the case of rare, geographically restricted species) to hundreds (in the case of common species with wide geographical distribution). In this way, the analysis incorporates the high intraspecific variation that is sometimes observed in widespread species^{30,185,236–238}. In addition and fully acknowledging their existence, intraspecific variations are assumed to

be comparatively small in the context of the vast range of variation contained in this worldwide dataset³⁰.

Species names were standardized and attributed to families according to The Plant List (<http://www.theplantlist.org/>; accessed 2015). Attribution of families to higher-rank groups was made according to APG III (2009) (<http://www.mobot.org/MOBOT/research/APweb/>). Information about primary growth-form (woodiness, woody, semi-woody, non-woody) and secondary growth-form (herbaceous non-graminoid, herbaceous graminoid, herbaceous non-graminoid/shrub, shrub, shrub/tree, tree, climber, succulent, other) was added based on a look-up table of categorical plant-traits³⁰ (<https://www.try-db.org/TryWeb/Data.php#3>) and additional information from various sources; >86% species were allocated to categories according to primary growth-form, and >80% according to secondary growth-form.

Species distribution data were derived from the Global Biodiversity Information System (GBIF; <http://www.gbif.org>) and combined with 0.5 × 0.5 degree gridded long term climate information derived from CRU (<http://www.cru.uea.ac.uk/data>). **Trait measurement.** In the case of published datasets, trait measurement methods are in the original publications listed in Dataset description. In the case of unpublished records, they were measured following the protocols specified in the context of the LEDA project (<https://www.leda-traitbase.org>) or in ref. 239 (<http://www.nucleodiversus.org/index.php?mod=page&id=79>). All data were unit-standardized and subjected to error detection and quality control (see below).

Treatment of pteridophyte spore mass. The trait values for diaspore mass of pteridophytes were estimated based on literature data for spore radius (*r*). We made crude assumptions that spores would be broadly spherical, with volume = $(4/3)\pi r^3$, and that their density would be 0.5 mg mm⁻³. Although these assumptions were clearly imprecise, we are confident they result in spore masses within the right order of magnitude (and several orders of magnitude smaller than seed mass of spermatophytes). Most data were from ref. 240, data for *Sadleria pallida* were from ref. 241, for *Pteridium aquilinum* from ref. 242, and for *Diphysastrum* spp. from ref. 243.

Treatment of stem specific density in herbaceous species. Data on stem specific density (SSD) are available for a very large number of woody species, but only for very few herbaceous species. To incorporate this fundamental trait in our analysis, we complemented SSD of herbaceous species using an estimation based on leaf dry matter content (LDMC), a much more widely available trait, and its close correlation to stem dry matter content (StDMC, the ratio of stem dry mass to stem water-saturated fresh mass). StDMC is a good proxy of SSD in herbaceous plants with a ratio of approximately 1:1 (ref. 100), despite substantial differences in stem anatomy among botanical families²⁴⁴, including those between non-monocotyledons and monocotyledons (where sheaths were measured). We used a data set of 422 herbaceous species collected in the field across Europe and Israel, and belonging to 31 botanical families¹⁴⁴ to parameterize linear relationships of StDMC to LDMC. The slopes of the relationship were significantly higher for monocotyledons than for other angiosperms ($F = 12.3$; $P < 0.001$); within non-monocotyledons, the slope for Leguminosae was higher than that for species from other families. We thus used three different equations to predict SSD for 1963 herbaceous species for which LDMC values were available in TRY: one for monocotyledons ($\text{SSD} = 0.888 \times \text{LDMC} + 2.69$), one for Leguminosae ($\text{SSD} = 0.692 \times \text{LDMC} + 47.65$), and a third one for other non-monocotyledons ($\text{SSD} = 0.524 \times \text{LDMC} + 95.87$).

Error detection and data quality control. The curation of the dataset faced a double challenge: (1) detecting erroneous entries (due to errors in sampling, measurement, unit conversion, etc.); and (2) ensuring that extreme values that correspond to truly extreme values of traits in nature are not mistakenly identified as outliers and therefore excluded from the dataset. To deal with these challenges, we took the following approach: Trait records measured on juvenile plants and on plants grown under non-natural environmental conditions were excluded from the dataset. Duplicate trait records (same species, similar trait values, no information on different measurement locations or dates) and obvious errors (for example LMA < 0) were excluded from the dataset. We then identified potential outliers following the approach described in ref. 30. Trait records with a distance of >4 standard deviations from the mean of species, genus, family or higher-rank taxonomic group were excluded from the dataset unless their retention could be justified from external sources. Trait records with a distance of >3 standard deviations from the mean of species, genus, family or phylogenetic group were identified, checked by domain experts for plausibility and retained or excluded accordingly. The remaining dataset was used to calculate species mean trait values. Finally, the ten most extreme species mean values of each trait (smallest and largest) were again checked for reliability against external sources.

Construction of observed and simulated six-trait convex hull hypervolumes. In order to explore the constraints underlying the trait space occupied by species in our dataset, we used the convex hull approach of ref. 34, which has been applied

successfully to a wide range of datasets, including disjoint ones²⁴⁵. The application of a recently developed—and therefore less widely tested—method proposed for “holey” datasets²⁴⁵ yielded similar results.

We computed a six-dimensional convex hull volume (i.e. a six-dimensional measure of the minimum convex volume of trait space occupied by species in our dataset, hereafter Hv_{obs}) on the basis of the observed values of H , SSD , LA , LMA , N_{mass} and SM , and compared it to four null model volumes (h_{vnm1-4}) constructed under four different sets of assumptions. In all four cases the null hypothesis was $H_0: Hv_{obs} = h_{vnm}$ and the alternative hypothesis was $H_1: Hv_{obs} < h_{vnm}$ (‘the volume of the convex hull defined by the observed species is smaller than the volume occupied by species if their traits were generated under the null hypothesis’). Observed data were \log_{10} -transformed and standardized to zero mean and unit variance (z -transformation). Percentages in Fig. 1 indicate the reduction in size of the observed hypervolume compared to the average of 999 hypervolumes generated from the assumptions of each null model (Monte-Carlo permutations²⁴⁶). To control for outliers, computation of volumes were performed on the observed and simulated convex hulls containing 95% of species located closest to the centroid. A visualization of the observed dataset and the four null models in three-dimensional trait spaces is available at <https://sdray.shinyapps.io/globalspectr/> (Supplementary Application 1). The R script used for hypervolume computation is provided at ftp://pbil.univ-lyon1.fr/pub/datasets/drays/Diaz_Nature/.

Null model 1. Species traits vary independently and each of them comes from a uniform distribution. This null model assumes that each of the six traits represents an independent axis of specialization (i.e. the traits define a six-dimensional manifold) and that the occurrence of extreme and central values is equally probable. This uniform independent trait distribution represents a “Darwinian Demon”³⁵ scenario, where any combination of trait values can arise from mutation and escape from the natural selection process with equal probability. Simulated data are generated by randomly and independently sampling from independent uniform distributions whose range limits are constrained to the 0.025 and 0.975 quantiles of the observed trait values. The shape of the hypervolume under this null model (h_{vnm1}) is a hypercube.

Null model 2. Species traits vary independently and each of them comes from a normal distribution. This null model assumes that all six traits evolve independently, as in null model 1. However, extreme trait values are selected against during evolution. Simulated data were obtained by randomly and independently selecting from univariate normal distributions with standard deviation determined by the transformed observed data. The corresponding hypervolume (h_{vnm2}) is a hypersphere.

Null model 3. Species traits vary independently but—unlike in the previous models—there is no assumption about the distribution of trait variation; each trait varies according to the observed univariate distributions. Simulated data were obtained by permuting the values for each trait independently and therefore destroying the covariance amongst traits. Under this null hypothesis (h_{vnm3}) the hypervolume can take many potential shapes, emerging from the possible combinations of independently sampled plant trait observations.

Null model 4. Species traits are normally distributed and follow the estimated correlation structure of the observed dataset. This null model assumes that there are less than six independent axes of specialization and that extreme values are selected against. Simulated data were obtained by generating multivariate normal variables with standard deviations of the transformed observed data using the correlation structure of the observed dataset. The corresponding hypervolume (h_{vnm4}) is a hyperellipsoid. Deviations of observed data from null model 4 can be explained by deviations of the transformed observed univariate distributions from normal distributions, either showing lower tails than those expected in a normal distribution or by the non-observation of some combinations of extreme trait values, leading to truncated distributions, or by bimodal distributions.

Test for concentration of species within the observed convex hull. For each trait, values were partitioned in 10 bins so that the multivariate space was divided in 10^6 cells. The number of species per cell was computed and cumulative frequency curves were built for observed data and null models. For each null model, we simulated 999 datasets and computed the 0.025–0.975 interquartile range and the median. We then determined N_{10} and N_{50} , the minimum number of cells needed to cover 10% or 50% of species.

Principal component analysis (PCA). We performed PCAs on different versions of the observed dataset and a gap-filled version using the statistical software package InfoStat²⁴⁷ and the R-function ‘princomp’. Again all analyses were carried out on the correlation matrix of \log_{10} -transformed variables (traits), which is equivalent to using standardized data (z -transformation), which is considered appropriate for data with different measurement scales²⁴⁸. The number of significant PCA axes to be retained in order to minimize both redundancy and loss of information was determined using the procedure proposed by ref. 249, which allows one to test the significance of dimensionality in PCA. A visualization of the space occupied by

vascular plants in the space defined by all six PCA axes (three at a time) is available at <https://sdray.shinyapps.io/globalspectrPC/> (Supplementary Application 2).

Differences in the position of different major taxa and growth forms along PC1 and PC2 were tested using analysis of variance (Extended Data Fig. 2). Because of the large number of data, we used an alpha level of 0.01 to reject the null hypothesis. ANOVA was carried out using a linear mixed model to take into account the lack of homoscedasticity due to different group sizes. We used AIC and BIC criteria to select the best model considering heterogeneous variances. When the ANOVA null hypothesis was rejected, means were compared using Fisher's least significant difference ($P = 0.01$). Data were analysed using the lme function of the nlme²⁵⁰ and lme4²⁵¹ R-packages²⁵² interfaced by InfoStat Statistical Software version 2015 (ref. 247).

Test for robustness and representativeness of multivariate analysis results. In order to test if results shown in Fig. 2 and Extended Data Table 1 were robust with respect to the selection of traits and species and representative for vascular plants, we conducted a number of analyses: exclusion of gymnosperms and pteridophytes (‘angiosperms only’), exclusion of individual traits, and comparison to a gap-filled dataset representing about 15% of extant vascular plant species worldwide. The trait exclusion tests excluded the following individual traits, one at a time: LMA , N_{mass} and SSD , because analyses indicated that LMA and N_{mass} , although providing information on different aspects of leaf function (see Methods), are both part of the leaf economic spectrum^{7,10}, and SSD and plant height both reflect plant size when woody and herbaceous plants are considered together. To test if the results of the multivariate analysis presented in Fig. 2 were representative of vascular plants, we constructed a gap-filled dataset based on those species that entered the global dataset via the TRY Plant Trait Database. We extracted 328,057 individual plant-level trait observations, which provide a substantial number of additional data not used in the main analysis. We applied the data selection process as described above (section: Error detection and data quality control). The resulting dataset contained 78% missing entries (gaps), which were filled by Bayesian hierarchical probabilistic matrix factorization (BHPMF)^{253–255}. The gap-filled dataset was then used to calculate species mean trait values, resulting in a gap-filled dataset for 45,507 species. To quantitatively compare the results of the PCA presented in Fig. 2 and Extended Data Table 1 with those of the angiosperms-only and the gap-filled datasets, we applied a Procrustes test²⁵⁶ using the ‘procrustes’ and ‘protest’ functions in R package ‘vegan’²⁵⁷. Function protest tests the non-randomness between two configurations. Significant results (for example significance < 0.05) indicate that the shapes of two datasets are non-random to each other, but similar.

Kernel density estimation. To estimate the occurrence probability of given combinations of trait values in a two-dimensional space defined by PC axes 1 and 2 (Fig. 2), and bivariate trait combinations (Extended Data Fig. 4), we used two-dimensional kernel density estimation²⁵⁸. Because results depend on the choice of the bandwidth used for the smoothing kernel, we used unconstrained bandwidth selectors²⁵⁹. To visualize the occurrence probability of a given trait combination in the PCA space as well as for all possible bivariate trait combinations, we constructed contour plots from two-dimensional kernel density distributions. The colour gradient and contour lines in Fig. 2 and Extended Data Fig. 4 correspond to the 0.5, 0.95 and 0.99 quantiles of the respective probability distribution, thus highlighting the regions of highest and lowest trait occurrence probability. For kernel density estimation we used the ‘kde’ function and for optimal bandwidth selection carried out for each trait combination separately, we used the SAMSE pilot bandwidth selector²⁶⁰, both implemented in the R-package ‘ks’²⁵⁹. The R script used is provided at ftp://pbil.univ-lyon1.fr/pub/datasets/drays/Diaz_Nature/. **Code availability.** The R scripts used to generate the hypervolumes (Fig. 2) and kernel density analyses associated to Fig. 2 and Extended Data Fig. 4 are available at ftp://pbil.univ-lyon1.fr/pub/datasets/drays/Diaz_Nature/.

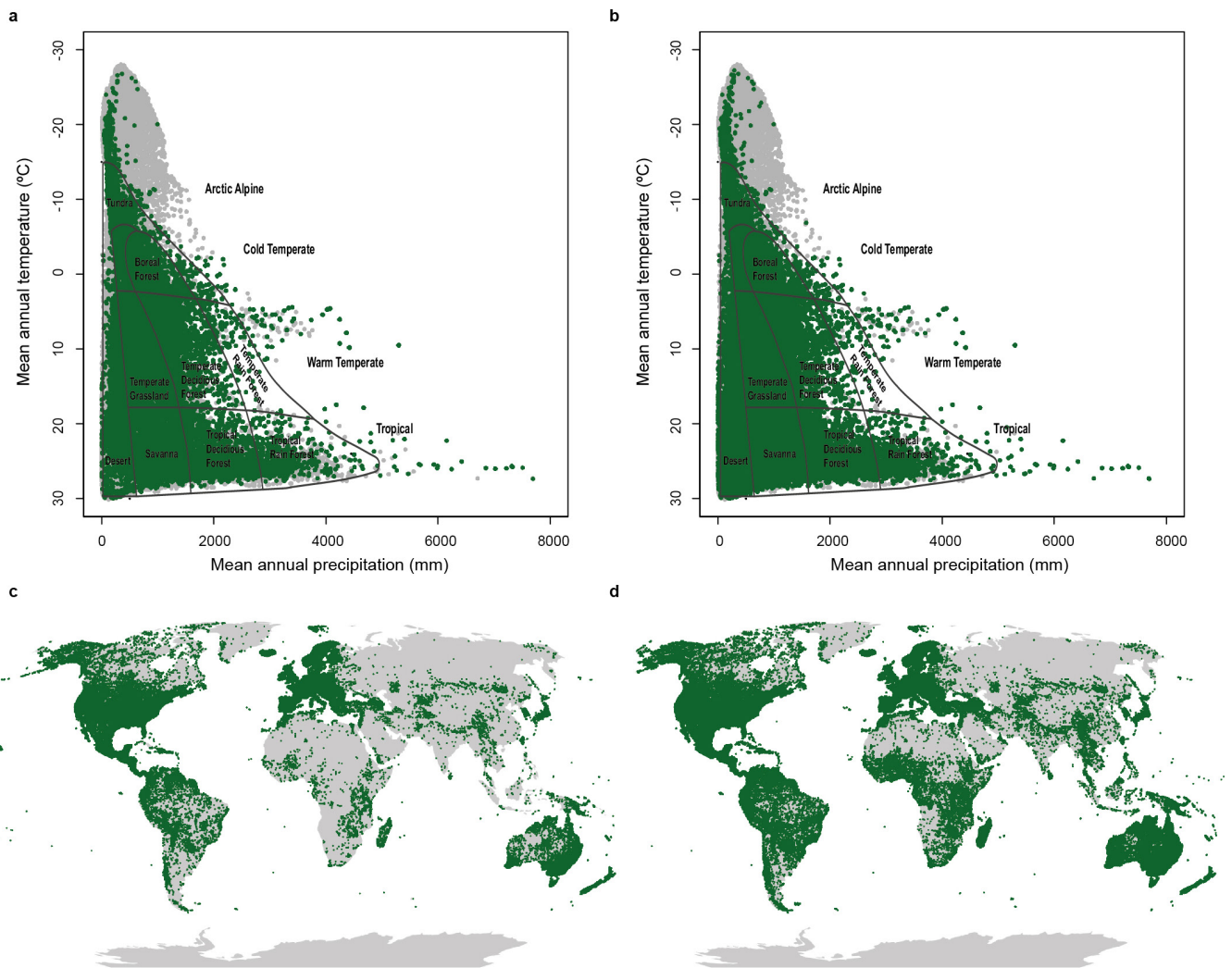
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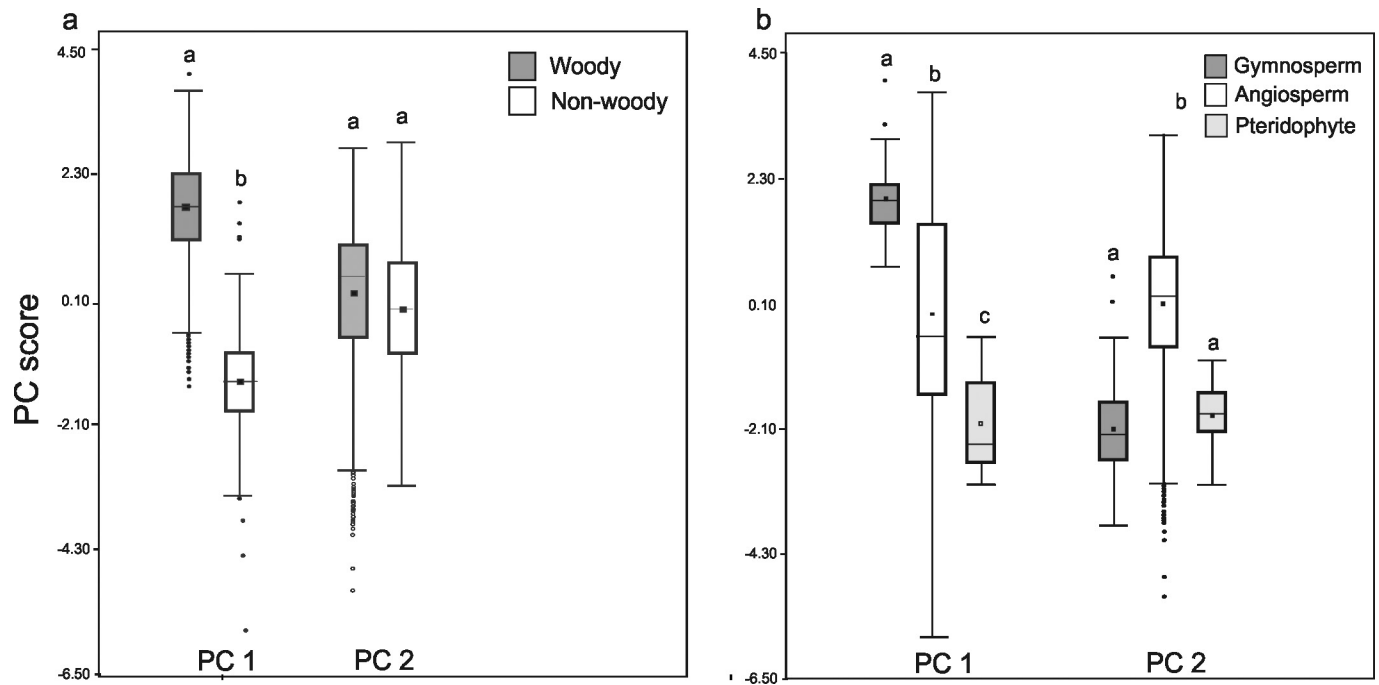
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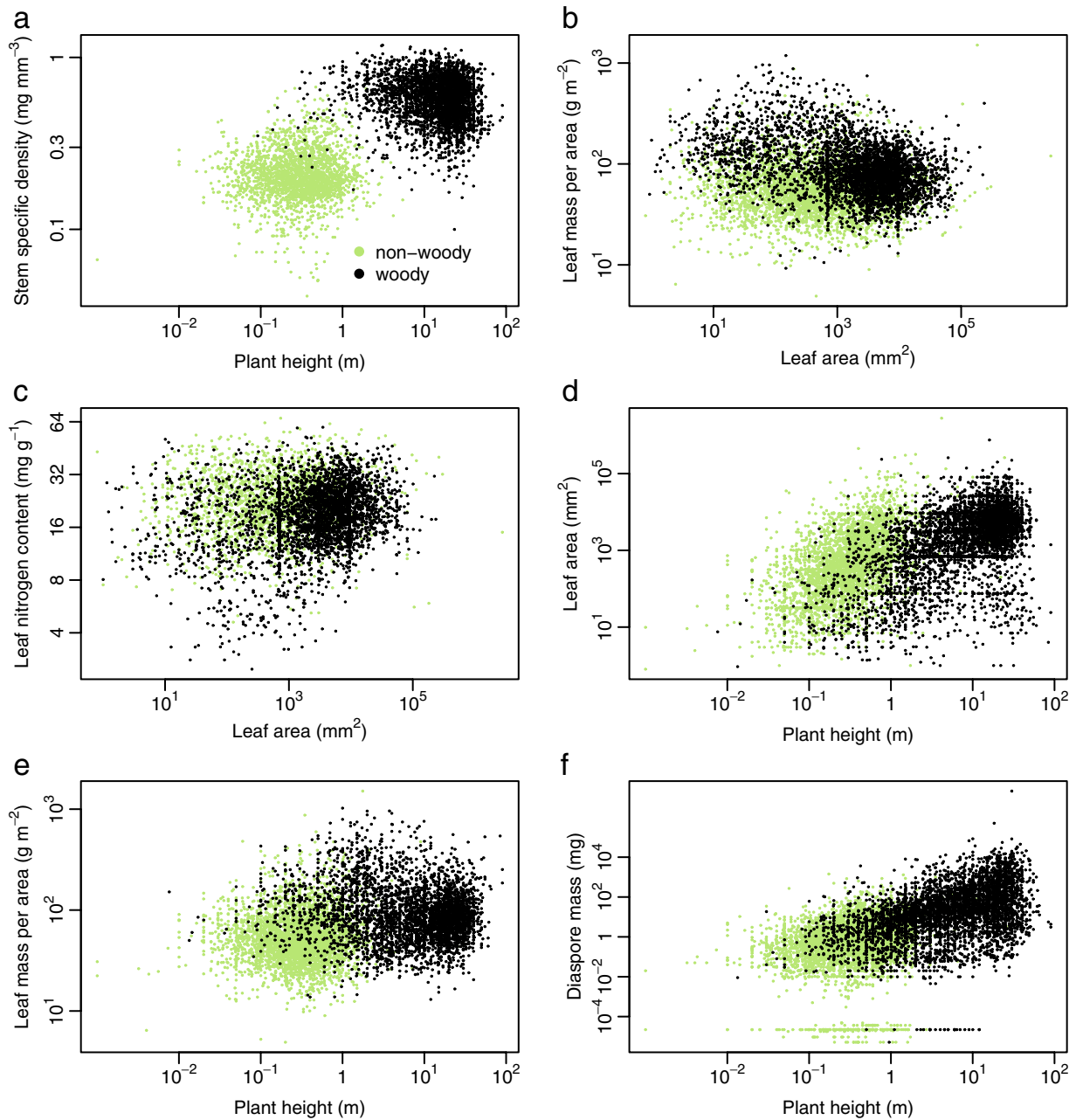
Extended Data Figure 1 | Climatic and geographical coverage of the dataset. **a–d**, Green points, occurrence according to GBIF (<http://www.gbif.org>) of species with information on all six traits (**a, c**) and at least one trait (**b, d**). Upper panels (**a, b**) show distribution in major climatic regions of the world; grey, MAP and MAT as in CRU0.5 degree climatology²⁶¹,

Biome classification according to ref. 262. Lower panels (**c, d**) show distribution in the global map (Robinson projection); grey, land surface. Maps based on the R package 'maps', accessed at The Comprehensive R Archive Network (<https://cran.r-project.org/web/packages/maps/index.html>).

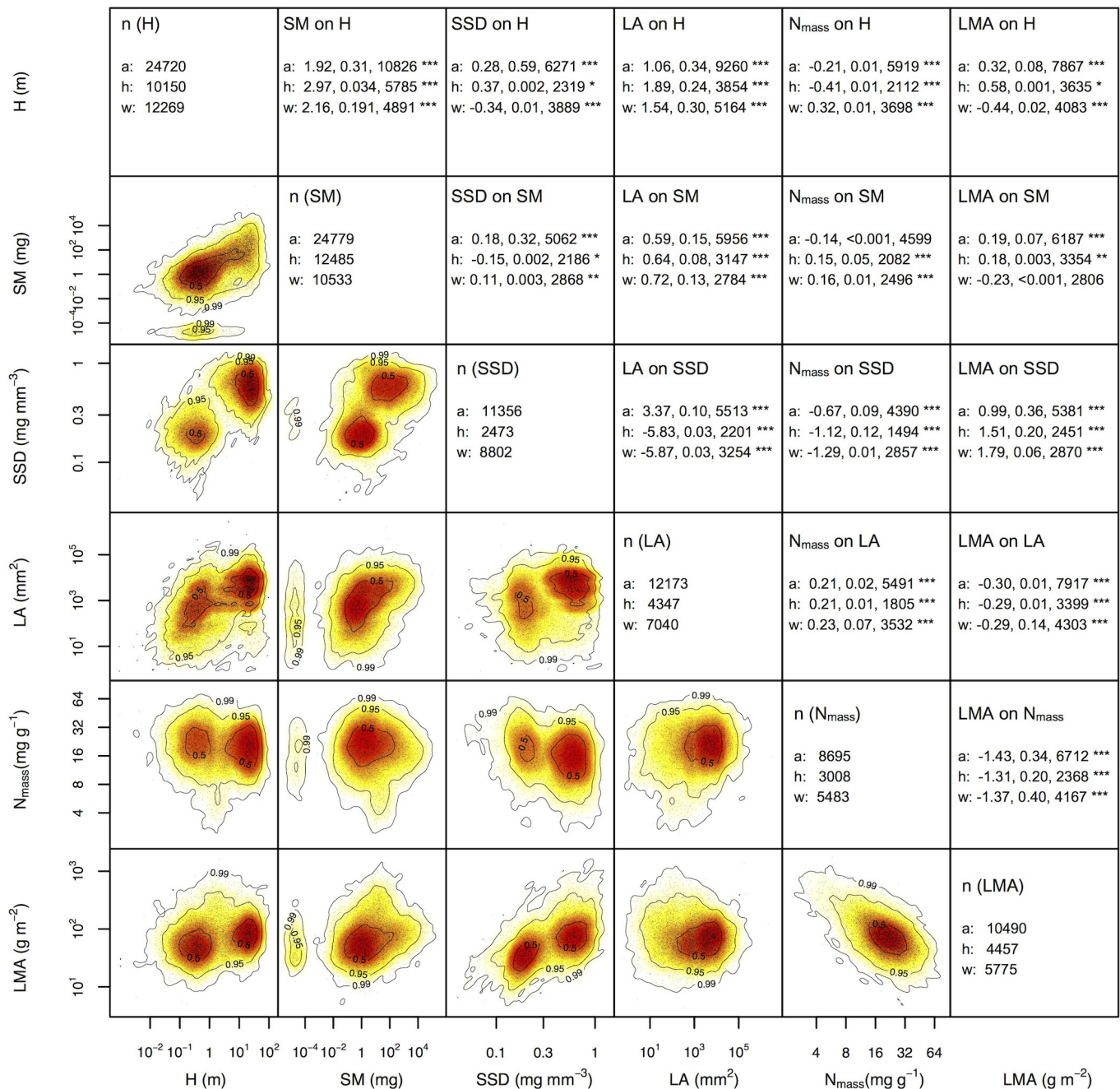


Extended Data Figure 2 | Tests of the distribution of growth-forms (a) and major taxa (b) in trait space. Woody and non-woody species differed significantly in their positions along PC1 but not along PC2. Angiosperms differed significantly from gymnosperms and pteridophytes in their positions along both axes; gymnosperms and pteridophytes differed in their position along PC1 but not along PC2 (see Methods for details

of PCA analysis and a posteriori tests). Whiskers denote ± 3 s.d. from mean; n woody = 1,001; n non-woody = 1,209; n angiosperms = 2,120; n gymnosperms = 80; n pteridophytes = 14). Horizontal bars and dots within boxes indicate mean and median, respectively. Means with the same letter are not significantly different (Fisher's least significant difference; $P > 0.01$).



Extended Data Figure 3 | Selected bivariate relationships underlying the global spectrum of plant form and function, showing herbaceous (green) and woody (black) species separately. See Extended Data Fig. 4 for standardized major axes statistics (slope, r^2 , sample size) of these and all other pairwise trait combinations.



Extended Data Figure 4 | Bivariate relationships between the six traits that underlie the global spectrum of plant form and function. The lower left portion of the matrix shows two-dimensional probability density distributions of bivariate trait relationships derived through kernel density estimation (see Methods). The colour gradient indicates regions of highest (red) to lowest (white) occurrence probability of trait combinations with contour lines indicating 0.5, 0.95 and 0.99 quantiles. The upper right portion contains standardized major axis (SMA)²⁶³ statistics (slope, r^2 , sample size n , and statistical significance, NS, $P > 0.05$; $*0.05 > P > 0.01$; $**0.01 > P > 0.001$; $***P < 0.001$) for the corresponding

relationships for all species (a), and for herbaceous (h) and woody species (w) separately. The diagonal displays the total sample sizes for each trait. For traits showing a strongly bimodal distribution, the all-species slope and correlation should be treated with caution. Pteridophytes show a discontinuous distribution in SM, but otherwise fall well within the general distribution of points; they represent less than 1% of the dataset, therefore including or excluding them does not significantly alter any of the relationships. SMAs were fitted using SMATR v.2 (<http://www.bio.mq.edu.au/ecology/SMATR/>).

Extended Data Table 1 | Principal component analyses (PCAs) of global plant trait data

	Main analysis		Angiosperms only		Excl. LMA		Excl. N _{mass}		Excl. SSD		Gap-filled	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Variation explained (%)	49	25	50	24	52	24	56	23	45	30	42	24
Eigenvalue	2.93	1.50	3.01	1.44	2.60	1.19	2.81	1.17	2.26	1.48	2.53	1.44
Significance of Procrustes test			0.0014								0.0014	
Variable loadings												
Leaf area (LA)	0.23	0.58	0.30	0.51	0.33	0.56	0.28	0.73	0.34	0.53	0.34	0.44
Leaf nitrogen per mass (N _{mass})	-0.25	0.57	-0.21	0.60	-0.17	0.76	-	-	-0.27	0.62	-0.21	0.65
Leaf mass per area (LMA)	0.40	-0.46	0.37	-0.49	-	-	0.36	-0.60	0.42	-0.52	0.36	-0.56
Plant height (H)	0.52	0.20	0.52	0.22	0.57	0.02	0.54	0.10	0.59	0.13	0.54	0.09
Diaspore mass (SM)	0.45	0.30	0.46	0.25	0.51	0.16	0.49	0.19	0.54	0.23	0.49	0.24
Stem specific density (SSD)	0.51	-0.09	0.50	-0.14	0.52	-0.30	0.51	-0.26	-	-	0.42	0.03

Eigenvalues and trait loadings of principal components (PC1 and PC2) in six different PCAs. Main analysis corresponds to the PCA performed on 2,214 species for which values of all six traits were available, and which is reported in the main text and expressed graphically in Fig. 2. The rest of the columns correspond to PCAs carried out on angiosperms only (2,120 species), on all taxa but excluding LMA, N_{mass} or SSD one at a time (2,214 in all cases), and on a gap-filled dataset of 45,507 species with missing trait records imputed using BHPMF (See Methods). The results of all PCAs show strong similarity, indicating robustness of the pattern obtained in the main analysis. Only PC1 and PC2 were identified as significant (see Methods) and therefore are reported here. All PCAs were performed on the correlation matrix of log₁₀-transformed traits.

Extended Data Table 2 | Description and illustrative examples of species at different positions at the margin of the global spectrum of plant form and function

Brief description and examples	
①	Tall, very large-seeded trees with large leaves of intermediate LMA and N_{mass} . Examples include the Neotropical <i>Bertholettia excelsa</i> (Brazil nut), <i>Gustavia superba</i> , <i>Pentaclethra macroloba</i> , and <i>Omphalea</i> spp.
②	Relatively large-seeded shrubs and trees of various heights, with small, sclerophyllous, highly conservative (high LMA, low N_{mass}) leaves. Examples include, among gymnosperms, monkey puzzle tree (<i>Araucaria araucana</i>), giant sequoia (<i>Sequoiadendron giganteum</i>) and junipers (<i>Juniperus</i> spp.). Among angiosperms, it includes members of the Proteaceae (e.g. the Australian <i>Hakea</i> and the South African <i>Leucadendron</i> genera) and Myrtaceae families (<i>Melaleuca uncinata</i> and <i>Eucalyptus dumosa</i>).
③	Sclerophyllous, high-LMA, low- N_{mass} species, of small stature, leaves, and seeds, varying from shrubs (such as <i>Fumana thymifolia</i> , heathers <i>Calluna vulgaris</i> and <i>Erica tetralix</i> , and chamise <i>Adenostoma fasciculatum</i>), to small forbs or sub-shrubs (such as <i>Diapensia lapponica</i> , <i>Draba</i> spp. and <i>Sedum</i> spp.), to graminoids (e.g. <i>Muhlenbergia ramulosa</i> and <i>Aristida purpurea</i>).
④	Submerged and semi-submerged aquatics (such as bladderwort <i>Utricularia vulgaris</i> , watermilfoil <i>Myriophyllum spicatum</i> , <i>Zannichellia palustris</i> , and <i>Ranunculus aquatilis</i>) and ephemeral, small-seeded and small- and acquisitive-leaved (low LMA, high N_{mass}) species of very short stature, with very low investment in vegetative structures other than leaves (such as thale cress <i>Arabidopsis thaliana</i> , annual bluegrass <i>Poa annua</i> , and <i>Nama dichotoma</i>).
⑤	Large-leaved, high- N_{mass} herbaceous plants with little carbon investment in support tissue. These are illustrated by robust aquatic species such as larger pondweeds (<i>Potamogeton</i> spp.) and sacred lotus (<i>Nelumbo nucifera</i>), species with nitrogen-rich secondary compounds (presumably anti-herbivore defences; e.g. devil's snare <i>Datura stramonium</i> , henbane <i>Hyoscyamus niger</i>), and some common crop and agricultural weed species such as <i>Beta vulgaris</i> , <i>Phaseolus vulgaris</i> , <i>Cannabis sativa</i> , and <i>Arctium minus</i> . Also includes Boreal 'mega-herb' <i>Angelica archangelica</i> .

Circled numbers in the first column refer to extreme poles of whole-plant specialization, whose approximate positions in the plane defined by PC1 and PC2 are indicated within circles in Fig. 2a.