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Global effects of soil and climate on leaf photosynthetic traits and rates

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ABSTRACT

Aim The influence of soil properties on photosynthetic traits in higher plants is poorly quantified in comparison with that of climate. We address this situation by quantifying the unique and joint contributions to global leaf-trait variation from soils and climate.

Location Terrestrial ecosystems world-wide.

Methods Using a trait dataset comprising 1509 species from 288 sites, with climate and soil data derived from global datasets, we quantified the effects of 20 soil and 26 climate variables on light-saturated photosynthetic rate (A_{area}), stomatal conductance (g_s), leaf nitrogen and phosphorus (N_{area} and P_{area}) and specific leaf area (*SLA*) using mixed regression models and multivariate analyses.

Results Soil variables were stronger predictors of leaf traits than climatic variables, except for *SLA*. On average, N_{area}, P_{area} and A_{area} increased and *SLA* decreased with increasing soil pH and with increasing site aridity. g_s declined and P_{area} increased with soil available P (P_{avail}). N_{area} was unrelated to total soil N. Joint effects of soil and climate dominated over their unique effects on N_{area} and P_{area}, while unique effects of soils dominated for A_{area} and g_s. Path analysis indicated that variation in A_{area} reflected the combined independent influences of N_{area} and g_s, the former promoted by high pH and aridity and the latter by low P_{avail}.

Main conclusions Three environmental variables were key for explaining variation in leaf traits: soil pH and P_{avail}, and the climatic moisture index (the ratio of precipitation to potential evapotranspiration). Although the reliability of global soil datasets lags behind that of climate datasets, our results nonetheless provide compelling evidence that both can be jointly used in broad-scale analyses, and that effects uniquely attributable to soil properties are important determinants of leaf photosynthetic traits and rates. A significant future challenge is to better disentangle the covarying physiological, ecological and evolutionary mechanisms that underpin trait–environment relationships.

Keywords

Least-cost theory of photosynthesis, nitrogen, phosphorus, photosynthesis, plant functional traits, soil fertility, soil pH, stomatal conductance.

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INTRODUCTION

Natural selection promotes coordination in plants between the acquisition of soil-derived resources (water and nutrients), capture of solar radiation and the uptake and fixation of CO_2 from the atmosphere. The relative availability of key resources to plants varies by orders of magnitude over biogeographical gradients (e.g. Vitousek, 2004; Huston, 2012). Identifying how this variation shapes the ecological strategies and key strategy traits of plants is one of the central questions for ecology and biogeography (Westoby & Wright, 2006).

Photosynthesis can be construed as an economic process (Givnish, 1986). A trade-off between the substitutable costs of maintaining the capacities for carboxylation (V_{cmax}) and transpiration was theoretically predicted and then confirmed by experimental observation along an Australian aridity gradient with annual precipitation ranging from *c.* 400 to 1100 mm (Prentice *et al.*, 2014). From dry to wet habitats, plants maintain comparable photosynthetic rates by increasing their water use with high stomatal conductance (g_s) while reducing investment in photosynthetic proteins resulting in low leaf N and V_{cmax} (Wright *et al.*, 2003). Analogously, along a gradient from nutrient-poor to nutrient-rich habitats, plants were shown to rely increasingly on high leaf N while reducing water use by operating at lower g_s (Wright *et al.*, 2001). However, along the gradient studied by Wright *et al.* (2001), covariation of soil texture, cation exchange capacity, organic matter content and total N and P concentrations precluded a more differentiated analysis of soil effects.

Moreover, the impact of soil on photosynthetic traits has rarely been studied at a global scale (Ordoñez *et al.*, 2009; Ordonez & Olff, 2013). Investigation of this relationship is challenging because climate is both a major control of photosynthetic traits (e.g. Reich & Oleksyn, 2004) and an important driver of soil development. According to Albrecht's conceptual model (Huston, 2012), soil total exchangeable bases, soil pH, soil total P and N content and plant productivity should all decline along a gradient from intermediate to high rainfall and from young high-latitude soils to older, low-latitude well-weathered soils (Walker & Syers, 1976). Soil fertility, sometimes defined by exchangeable base cations or soil pH (Quesada *et al.*, 2010), might thus be expected to be inversely related to water availability, and this trade-off might be reflected in both increasing stomatal conductance and decreasing carboxylation capacity towards warm and wet climates.

However, this one-dimensional view of covariation between soils and climate is likely to be an oversimplification. Soil fertility can also be defined in several other ways. Conceptual models of long-term ecosystem development have tended to focus on the negative covariation between time trajectories of the availability of P and N in soils, with the highest productivity at intermediate N : P ratios (Vitousek, 2004). In such schemes N is assumed to be more limiting in young soils, often at higher latitudes, since it accumulates mainly via atmospheric fixation of N_2 and becomes available to plants mainly via decomposition of organic matter. However, in old and deep soils, mostly at lower latitudes, P is provided mainly by the parent rock chemistry and its weathering rates becomes a limiting factor for plant growth (Reich & Oleksyn, 2004; Peltzer *et al.*, 2010). In this scheme the relative cost associated with the maintenance of carboxylation should increase at the extremities of time trajectories for soil development, either limited by soil and leaf N or by soil and leaf P (Niinemets *et al.*, 1999; Reich *et al.*, 2009; Maire *et al.*, 2012). Finally, biogeochemical models of ecosystems have tended to adopt a narrow definition of fertility, focused on the ability of soils to release plant-available forms of nutrients from litter and soil organic matter (SOM), the decomposition of which is supposed to be mainly a function of the initial SOM and temperature (Hakkenberg *et al.*, 2008), as well as which microorganisms are present (Fontaine *et al.*, 2011). The implications of this scheme for photosynthetic costs are less clear. Globally, these differing concepts of soil fertility continue to exist side-by-side in the literature but, to date, none of the broad concepts has been embedded in a global, predictive framework for plant traits. Indeed, shifting and ambiguous definitions of 'fertility' may have hindered the development of such a framework. With sufficient data, however, it should be possible to tease apart the effects of the various edaphic drivers on photosynthetic traits and to separate influences of edaphic and climatic determinants of photosynthesis.

Recently, a global soil dataset with consistency, reliability and resolution approaching those available for climate has become available with SoilGrids (ISRIC, 2013), which is complementary to the ongoing update of the conventional Harmonised World Soil Database (FAO *et al.*, 2012). These soil data can be linked with global datasets containing climate variables and plant traits, making it possible for the first time to quantify the unique contribution of soil variables to leaf traits across the range of global ecosystem types. We performed such an analysis, with the following questions.

1. How do leaf photosynthetic traits vary with different facets of soil fertility?

2. What are the most individually important soil and climate variables in terms of explaining variation in these leaf traits?

3. What proportions of leaf trait variation can be accounted for by joint effects of soils and climate, as opposed to the unique effects of soils and of climate? As climate and soil covary, the soil–climate joint effect may dominate the unique effects of climate and soil separately (Reich & Oleksyn, 2004). As different soils are encountered in a given climatic envelope, a significant unique effect of soils may be expected.

4. Variation among species in photosynthetic rates depends both on variation in leaf N and in g_s. Are these two independent trait dimensions promoted by independent climate and soil dimensions?

5. Finally, what is the minimum set of environmental and trait variables needed to represent interrelationships between photosynthetic rates and associated traits?

To answer each question, a step-by-step statistical approach was followed (described below), with the ultimate aim of disentangling soil and climate effects on leaf traits and photosynthetic rates.

MATERIAL AND METHODS

Trait data

The 'Glopnet' dataset (Wright *et al.*, 2004) provided the starting point for the present analyses. Data on field-measured photosynthetic capacity (A_{area}, μmol m^{-2} s^{-1}), stomatal conductance to water vapour (g_s, mmol m^{-2} s^{-1}), N and P per unit leaf area (N_{area} and P_{area}, g m^{-2}, respectively) and specific leaf area (*SLA*, cm^2 g^{-1}) were supplemented by other sets of georeferenced observations of these traits (Appendix S1 in Supporting Information). The final database (Appendices S2 & S3, doi:10.5061/dryad.j42m7) consisted of 2400 species × site combinations including 288 sampled sites and 1509 species from 165 families. Three hundred and twenty-five species occurred at more than one site. The dataset contained a variety of growth forms (661 trees, 399 shrubs, 313 herbs, 88 grasses, 32 ferns and 16 vine species), phenologies (316 deciduous, 14 semi-deciduous and 735 evergreen species) and physiologies (i.e. C_3 and C_4 species, N_2-fixing and non-fixing species). A_{area} varied 190-fold across the dataset (from 0.34 to 65.05 μmol m^{-2} s^{-1}; $n = 2337$), g_s varied *c.* 110-fold (from 21 to 2272 mmol m^{-2} s^{-1}; $n = 1035$), N_{area} and P_{area} varied by *c.* 40-fold (from 0.26 to 9.47 g N m^{-2}; $n = 1643$) and 50-fold (from 0.017 to 0.923 g P m^{-2}; $n = 512$), respectively, and *SLA* varied *c.* 50-fold (from 12.8 to 608 cm^{-2} g^{-1}; $n = 1965$). By comparison, the 2004 Glopnet dataset had A_{area} data for 825 species × site combinations and g_s data for 500.

Environmental data

Climatic drivers

Photosynthetically active quantum flux density, temperature, rainfall and aridity are key climatic determinants of plant processes. Twenty-six climate variables representing these aspects of climate were considered (Table S3-1 in Appendix S3). When available, mean annual temperature and precipitation data were taken from the source publications for the leaf data. Otherwise, climate data were extracted from a global, three-dimensionally interpolated 10′ × 10′ data set for 1961–90 (Climatic Research Unit, CRU CL2.0; New *et al.*, 2002). We obtained monthly and annual means of temperature, rainfall, fractional sunshine duration and relative humidity. We also considered maximum and minimum values, seasonal variability and growing-season mean values (defined alternatively based on a 0 °C and a 5 °C basis) of temperature, precipitation and sunshine duration. Next, several bioclimatic variables were calculated following Wang *et al.* (2014): annual global radiation, total annual incident radiation during the growing season and annual equilibrium evapotranspiration (a function of net radiation and temperature). Aridity was (inversely) described by the moisture index (*MI*; the ratio between precipitation and potential evapotranspiration, *PET*), with *PET* calculated in two ways: PET_F (using the Penman–Monteith formulation; FAO, 2004) and PET_Q (using equilibrium evapotranspiration to represent potential evapotranspiration; Wang *et al.*, 2014), yielding MI_F and MI_Q, respectively (see Table S3-1 in Appendix S3 for a full list of descriptions).

Edaphic drivers

Soil variables that express long-term pedogenetic characteristics, to which plants adapt over generations, can be contrasted with those reflecting more rapid within-season changes (Peltzer *et al.*, 2010). We considered only the former type, choosing to avoid fast-changing variables like N mineralization rate. Key edaphic determinants of plant processes include the texture and structure of soils, ion exchange capacity and macronutrient content of the top soil layer (see Table S3-1 in Appendix S3 for a full list). Soil data were extracted using the 'raster' package in R 3.0.1 (R Core Team, 2013) from three spatially interpolated global datasets. SoilGrids (0–22.5 cm layer, ISRIC, 2013) – an automated system that produces soil datasets derived from digital soil mapping (Hengl *et al.*, 2014) – and the Harmonized World Soil Database (0–30 cm layer, FAO *et al.*, 2012) are interpolated at 30″ × 30″ resolution and provide the majority of soil variables (organic matter content, pH, cation exchange capacity, texture and structure of soils). Soil N content and C : N ratio, aluminium saturation and the available water holding capacity of the 0–20 cm layer were extracted from the 5′ × 5′ ISRIC-WISE dataset (Batjes, 2012). If several soil types occurred within a grid cell, soil property estimates correspond to the area-weighted profile mean.

We also constructed a dataset for soil available P concentration (P_{avail}) based on information from several sources (see Appendix S4 for details). In brief, we first assembled geolocated soil profiles from several soil phosphorus datasets (e.g. Batjes, 2011a; Shangguan *et al.*, 2013; Tóth *et al.*, 2013). When the distance from the nearest profile was less than 100 km we recorded the nearest soil profiles for each site in the plant trait dataset. Otherwise, we did a literature survey to search for data from closer locations. The values for P_{avail} were harmonized to a single chemical extraction method (Bray & Kurtz, 1945) based on published conversion factors. The broad-scale reliability of the harmonized P_{avail} data was confirmed using categorical information: the global distribution of soil P retention potential (Batjes, 2011b) and the weathering stage associated with the soil orders of plant trait sites (Appendix S4).

Climate conditions varied widely among the 288 study sites: mean annual temperature ranged from –21.4 to 27.3 °C, annual precipitation from 23 to 5406 mm and mean annual *MI* from 0.09 to 6.54, covering most of the temperature–rainfall space in which higher plants are found. Soil conditions also varied widely: total exchangeable bases (*TBA*) ranged from 75 to 1801 cmol kg^{-1}, soil pH from 3.5 to 8.4, total soil N (N_{tot}) from 0.3 to 16.7 g kg^{-1}, P_{avail} from 0.2 to 960 mg P_2O_5 kg^{-1} and clay fraction from 2 to 42% (Fig. S3-2 in Appendix S3).

Data analysis

Data selection and transformation

Being right-skewed, all plant traits were log-transformed. Environmental variables were subjected to the Yeo–Johnson transformation ('car' package; R core team, 2013); this provides a powerful way of reducing skewness and can be applied to variables that include negative values (see details in Table S6-1 in Appendix S6).

Five methodological steps were defined, each one dedicated to one of the five questions presented in the introduction. The details, benefits and limitations of each step are described in Table S6-2 in Appendix S6.

Step 1. Defining key dimensions of soil fertility and quantifying their relationships with leaf traits

A general theoretical approach based on existing conceptual models of soil and ecosystem development over geological timescales (Vitousek, 2004; Peltzer *et al*., 2010; Huston, 2012) was used to predict relationships between soil pH and each of several main facets of soil fertility, i.e. *TBA*, organic C content (C_{org}), N_{tot}, P_{avail} and available water holding capacity (*AWHC*). We compared the observed relationships with the predicted ones, first fitting quadratic regressions (to accommodate nonlinearity) and then linear models whenever the square term of the quadratic model was non-significant (see Appendix S8 for more details). A systematic analysis of the impact of each soil and climate variable on each trait was realized (Figs 2 & S8 in Appendix S8). In mixed models, the fixed-effect term was the soil or climate variable allocated to each site; site and species were considered as random intercepts (making standard assumptions of normality, independence and homoscedasticity). The site and species effects were included to reflect the hierarchical structure (multiple species at multiple sites) and the unbalanced and nested structure (different number of samples/species between sites) in the sampling design. Models were fitted using the R package 'lme4' and adjusted r^2 values (r_a^2) were calculated following Moles *et al.* (2009).

Step 2. Selecting the most important climatic and soil variables for explaining leaf trait variation

Next, for each trait we used a stepwise multiple mixed regression model to select up to four explanatory variables from among the various available climate and soil variables (Table S3-1 in Appendix S3), by minimizing the Akaike information criterion (Legendre & Legendre, 2012). Site and species effects were treated as random factors. The R packages 'lme4' and 'MuMIn' were used.

Step 3. Quantifying unique and joint effects of soils and climate for explaining variation in each leaf trait

In this step we used variation partitioning and Venn diagrams (Legendre & Legendre, 2012) to partition the total variation explained in each leaf trait into components explained uniquely by the matrix of soil variables, uniquely by the matrix of climate variables or (jointly) explained by the combined soil and climate matrices. For these analyses we used the soil and climate variables identified as part of Step 2 (see Table 1 for the selected soil and climate variables) and multiple mixed regression models. The unique effect of soil (or climate) was calculated as the r_a^2 difference between the full model and the climate (or soil) model. The joint effect of soil and climate was calculated as the difference between the summed r_a^2 of soil and climate models and the r_a^2 of the full model.

Step 4. Quantifying the explanatory power of soils and climate for the matrix of leaf traits

Photosynthetic rates can be understood as the outcome of coordinated investments in water transport capacity, needed to support a high rate of g_s, versus Rubisco carboxylation capacity, indexed by Rubisco activity (V_{cmax}) – potentially related to both N_{area} (e.g. Wright *et al*., 2003) and P_{area} (e.g. Niinemets *et al*., 1999). To test whether and how soil and climate variables can distinctively promote these different drivers of leaf photosynthesis it is important to consider the relationships among leaf traits in the same analysis (Steps 4 and 5). First, we used redundancy analysis (the '*vegan*' package; R Core Team, 2013) to quantify how much of the variation in the matrix of leaf traits could be explained by the matrices of the most important soil and climate variables selected at Steps 2 and 3. For leaf traits we used A_{area}, g_s, N_{area} and *SLA* (giving a dataset of 647 species from 99 sites). P_{area}, with its considerably smaller sample size, was left out of this analysis.

Step 5. Disentangling direct and indirect effects of leaf traits, soil and climate on photosynthetic capacity

We used path analysis (the '*lavaan*' package; R Core Team, 2013) to explore how variation among species in A_{area} can best be understood as driven by both direct and indirect effects of g_s, N_{area}, *SLA* and the key environmental drivers identified in previous steps, selecting the model that was the least different from the observations (P-value > 0). Note that Steps 4 and 5 are complementary (Table S6-1 in Appendix 6), with Step 4 testing the relationships between matrices without *a priori* constraints, while Step 5 allowed us to evaluate possible *causal* effects of soil independent of climate on leaf traits (Legendre & Legendre, 2012).

RESULTS

Step 1a. Two dimensions of soil 'fertility'

Figure 1(a)–(e) summarizes expected relationships between soil pH and each of several dimensions of soil fertility. From high to low soil pH (right to left), i.e. conceivably from young soils where the parent rock supplies cations and phosphorus to older and more highly weathered soils, remote from the parent material but enriched in SOM, Fig. 1 indicates the following.

1. A decrease of total exchangeable bases, but an increase in Al and Fe content (Fig. 1a).

2. An increase in total C and N and *AWHC*, due to the accumulation of SOM (Fig. 1b–d). In addition, soil available nitro-

Table 1 Multiple mixed regression relationships between area-based leaf functional traits (A_{area}, leaf photosynthetic rate; g_s, stomatal conductance; N_{area}, leaf nitrogen content; P_{area}, leaf phosphorus content; and *SLA*, specific leaf area) and soil and climate subsets of environmental variables.

Trait	Factors	n	r^2	AIC	F, factor 1	F, factor 2	F, factor 3	F, factor 4
Climate model								
A_{area}	$MI_Q + TMP_{range} + SUN_{max}$	2337	0.098***	−886	↓20.8***	↓5.6*	↑3.5(*)	–
g_s	$TMP_{max} + TMP0_{nb} + PPT_{season}$	1035	0.102***	−38	↑8.7**	↓5.4*	↑7.9**	–
N_{area}	$MI_Q + TMP_{range}$	1643	0.178***	−1726	↓53.9***	↓5.5*	–	–
P_{area}	$MI_Q + RH$	512	0.312***	−353	↓27.9***	↑16.3***	–	–
SLA	$SUN_{max} + TMP_{max} + TMP0_{nb}$	1965	0.146***	−1474	↓41.1***	↑13.6***	↓30.8***	–
Soil model								
A_{area}	$pH + N_{tot} + CECS$	2337	0.195***	−928	↑90.0***	↑19.1***	↓25.6***	–
g_s	$pH + N_{tot} + CECS + P_{avail}$	1035	0.241***	−128	↑28.0***	↑24.8***	↓19.3***	↓67.0***
N_{area}	$pH + N_{tot} + SALT$	1643	0.193***	−1736	↑38.0***	↓5.5*	↑9.2**	–
P_{area}	$pH + P_{avail} + SALT + SAND$	512	0.440***	−361	↑8.8**	↑19.5***	↑6.7*	↓7.2**
SLA	$pH + N_{tot} + SILT + BULK$	1965	0.159***	−1461	↓15.4***	↑3.2(*)	↑14.4***	↓5.0*

(*)$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Following a stepwise procedure criterion selecting the most important variables among 26 climate or 20 soil variables (see Materials and Methods and Table S3-1 in Appendix S3 for details) based on an Aikaike information criterion (AIC), linear mixed regression models were used to measure the impact of environmental variables on each trait. Site and species were treated as random factors (intercepts). The adjusted r^2 and AIC are provided for each regression model (see Materials and Methods for details of r^2 calculation). F- and P-values for Type III error models are specified for each fixed soil factor. Factors 1 to 4 correspond to the rank of each fixed factor that was selected in the regression model. Leaf trait variables were log-transformed and environmental variables were power-transformed as described in Materials and Methods. Arrows indicate the sign of the coefficient estimate. See Tables S8-4 & 8-5 in Appendix S8 for equation details.

MI_Q, moisture index representing the ratio between annual precipitation and equilibrium evapotranspiration; TMP_{range}, mean diurnal temperature range; SUN_{max}, maximum monthly fractional sunshine duration; TMP_{max}, maximal monthly temperature; $TMP0_{nb}$, number of days with daily temperature above 0 °C; PPT_{season}, seasonality of precipitation; *RH*, relative humidity; pH, soil pH; N_{tot}, soil total nitrogen content; *CECS*, cation exchange capacity, P_{avail}, available soil phosphate content; *SALT*, soil salinity; *SAND*, soil sand content; *SILT*, soil silt content; *BULK*, soil bulk density.

gen (N_{avail}) is expected to follow N_{tot} up to a maximal value at intermediate pH, where optimal conditions for microbial nitrogenase activity are reached. Thereafter, N_{avail} decreases steeply with increasing pH (Walker & Syers, 1976).

3. A decrease in P_{tot} (Lambers *et al.*, 2008; Fig. 1e) with increasing distance (and time) to the parent rock, where P is sourced. However, P_{avail} may show a humped distribution as P can co-precipitate with Ca at high pH and with Fe and Al at low pH.

Our data substantially matched these predictions (Fig. 1f–i). As soil pH increased, so did *TBA*, soil base saturation and, to a lesser extent, soil carbonate content, while Al saturation decreased (correlations given in Table S7-3 in Appendix S7). Quadratic relationships accounted for the relationships between pH and C_{org} and between pH and N_{tot} (Fig. 1g,h). *AWHC* and the climatic MI decreased linearly with pH (Fig. 1i). Contrary to expectation, however, no relationship was found between pH and P_{avail} (Fig. 1j). High P_{avail} was encountered at high-pH sites that were characterized by a low carbonate content, but also at low pH sites characterized by low Al saturation.

These relationships suggested the existence of two principal dimensions of soil fertility. Soil pH indexes a first dimension along which exchangeable bases, N_{avail}, C_{org}, N_{org} and *AWHC* covary, and the availability of micronutrients and N trade off with the availability of water. A second, largely independent, dimension is indexed by P_{avail}, which covaries negatively with Al saturation, soil depth and clay content, and positively with gravel content (Table S7-3 in Appendix S7).

Step 1b. Relationships between individual leaf traits and soil variables

We quantified bivariate relationships between the five photosynthetic traits and five soil variables (P_{avail} and four variables from fertility dimension 1: soil pH, C_{org}, N_{tot} and *AWHC*). A_{area}, N_{area} and P_{area} all increased linearly with soil pH ($r^2 = 0.12$–0.17; Fig. 2), while *SLA* decreased ($r^2 = 0.06$). Note that the corresponding mass-basis traits also increased with soil pH, but with notably lower r^2 than on an area basis (all $r^2 < 0.03$, $P < 0.002$; not shown).

As expected from their negative covariation with soil pH along fertility dimension 1 (Fig. 1), C_{org}, N_{tot} and *AWHC* affected *SLA*, N_{area}, P_{area} and A_{area} in the directions opposite to the pH-related effects (Fig. 2). The pH–leaf trait relationships all remained significant after accounting for covariation with mean annual temperature and precipitation (dashed lines in Fig. 2). However, this was not the case for relationships involving C_{org}, N_{tot} and *AWHC*.

Stomatal conductance, g_s, showed little patterning along fertility dimension 1, the strongest relationship being a very weak dependence on soil N ($r^2 = 0.02$; Fig. 2l). By contrast, both g_s (negative) and P_{area} (positive) showed strong patterning along fertility dimension 2 (i.e. varying with P_{avail}). These relationships were little changed by concurrently accounting for climate (dashed fitted lines, Fig. 2v,x). Unexpectedly, P_{avail} was the strongest single environmental predictor of g_s (the strongest

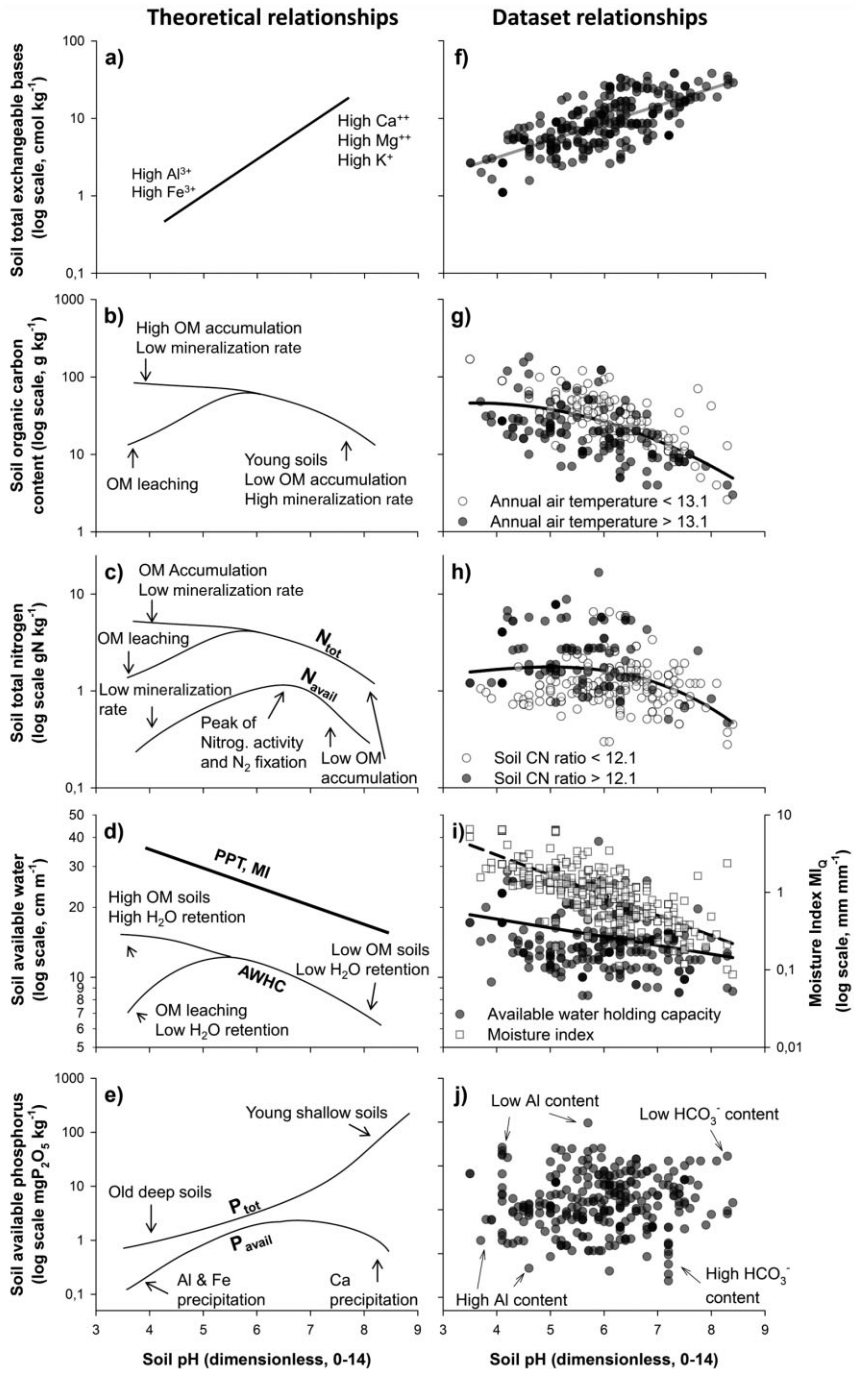

Figure 1 Theoretical (a–d) and observed (e–h) relationships between soil variables describing the availability of the main resources (cations, nitrogen, phosphorus and water) that plants use in photosynthesis. Soil pH_{water} is considered here as a proxy of the stage of soil evolution, and thus as a key variable expressing the dynamics of soil resources between the different sites used in this study. The various panels show dynamics of: (a, f) total soil exchangeable bases; (b, g) soil organic C content; (c, h) soil available nitrogen and total N content; (d, i) soil available water holding capacity, considering also precipitation (*PPT*) and moisture index (*MI*); and (e, j) soil available phosphorus and total P content (prediction for P_{tot} based on Lambers *et al.*, 2008). Regression models ($n = 288$ sites): (f) $\log(TBA) = -0.40 + 0.22 \cdot pH$, $r^2 = 0.50$; (g) $\log(C_{org}) = 1.09 - 0.04 \cdot pH^2 + 0.31 \cdot pH$, $r^2 = 0.33$; (h) $\log(N_{tot}) = -0.91 - 0.05 \cdot pH^2 + 0.47 \cdot pH$, $r^2 = 0.12$; (i) $\log(AWHC) = 1.40 - 0.38 \cdot pH$, $r^2 = 0.10$; $pH = 5.9 - 2.1 \cdot \log(MI_Q)$, $r^2 = 0.54$. All relationships were significant at the $P = 0.001$ level. *OM*, organic matter; *TBA*, total exchangeable bases; *AWHC*, available water holding capacity.

climate predictor being precipitation seasonality, $r^2 = 0.06$; Fig. S8-1 in Appendix S8). Indeed, the single strongest predictor for each leaf trait was a soil variable (pH for A_{area}, N_{area} and *SLA*; P_{avail} for g_s and P_{area}; full details in Fig. S8-1 in Appendix S8).

Step 2. Selection of the most important soil and climate variables

As in bivariate relationships (Figs S8-1 & S8-2 in Appendix S8) but using stepwise multiple regressions, soils did a better job than climate for explaining variation in each trait, and in the case of A_{area} and g_s soils explained more than twice as much variation as climate ($r^2 = 0.195$ and 0.241 vs. 0.098 and 0.102, respectively; Table 1). As judged by *F*-values, soil pH and P_{avail} were the two soil variables that had the greatest effect on leaf traits, while MI_Q was the most important climate variable (Table 1).

Step 3. Quantification of unique and joint effects of soil and climate on leaf traits

Using variation partitioning, 21–31% of variation was explained for each trait except P_{area} (54%) (Fig. 3). Overall, soils explained more variation in leaf traits than did climate, with this effect

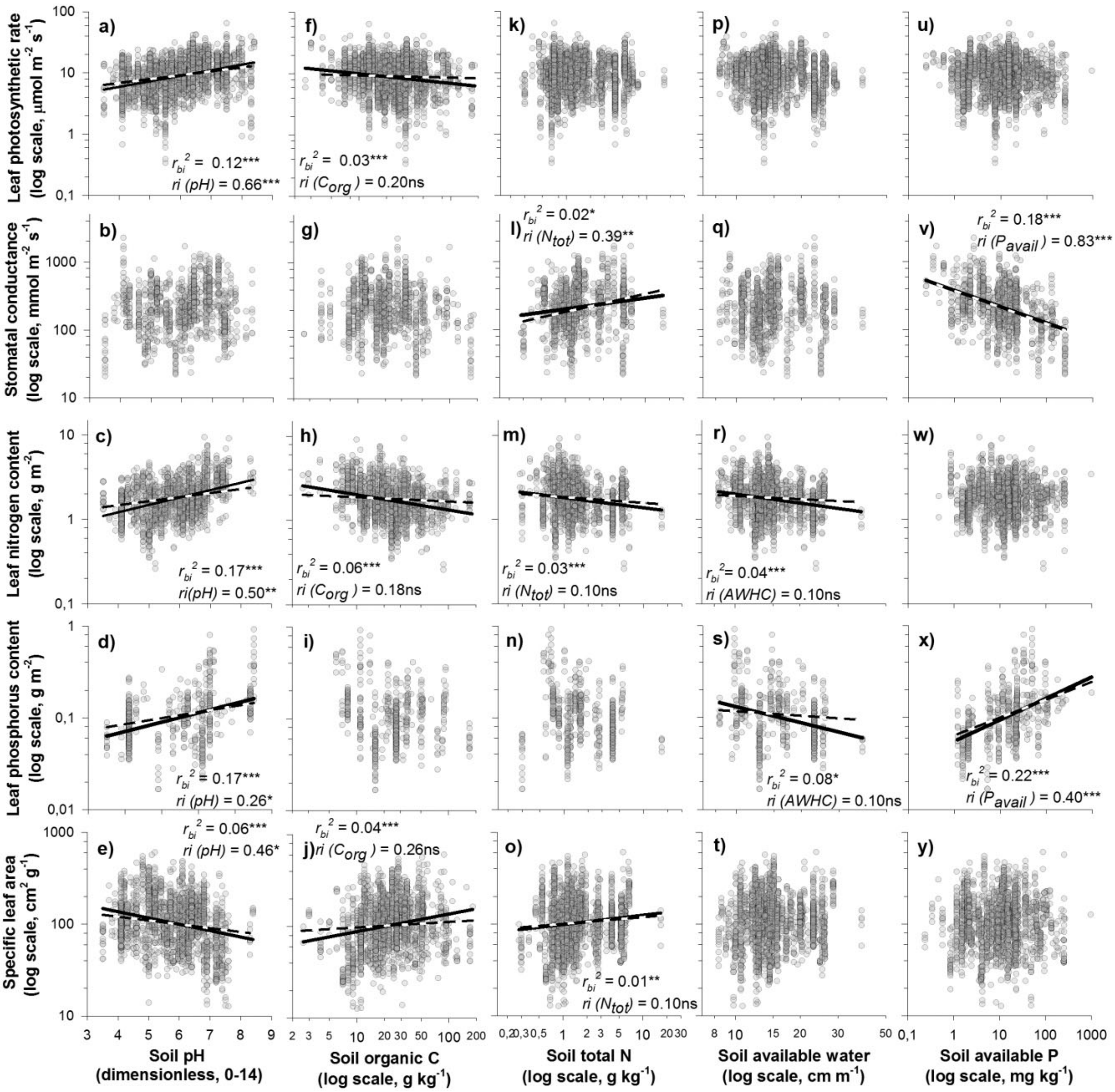

Figure 2 Relationships between area-based leaf photosynthetic traits and soil variables considered in the theoretical soil development model (Fig. 1). Leaf photosynthetic rate ($n = 2400$; a, f, k, p, u), stomatal conductance ($n = 1070$; b, g, l, q, v), leaf nitrogen content ($n = 1704$; c, h, m, r, w), leaf phosphorus content ($n = 532$; d, i, n, s, x) and specific leaf area ($n = 1964$; e, j, o, t, y) regressed on soil pH (a–e), soil organic C content (f–j), soil total nitrogen content (k–o), soil available water holding capacity (p–t) and soil available phosphate content (u–y) according to linear relationships using mixed regression models with site and species as random factors. Solid lines correspond to the significant regressions for which statistical information from mixed regression models (r_{bi}^2 and P-value) are reported on each caption. Equations are reported below. Dashed lines correspond to the impact of the soil variable in multiple mixed regression models, including two important climatic variables that can affect leaf traits (mean precipitation, PPT_{mean}, and TMP_{mean}, Wright *et al*., 2004). These conditional slopes ('*visreg*' package; R Core Team, 2013) indicated the bivariate soil–trait relationship calculated while holding constant (at their median) the two climate variables. Significance of the soil variable and its relative importance, *ri* ('*relaimpo*' package, R Core Team, 2013), in the multiple mixed regression model is reported on each caption. Statistical significance is indicated using asterisks: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Equations of bivariate relationships: (a) $\log(A_{area}) = 0.49 + (8.09 \times 10^{-2})\cdot pH$; (c) $\log(N_{area}) = -0.18 + (7.47 \times 10^{-2})\cdot pH$; (d) $\log(P_{area}) = -1.45 + (9.02 \times 10^{-2})\cdot pH$; (e) $\log(SLA) = 2.26 - (4.26 \times 10^{-2})\cdot pH$; (f) $\log(A_{area}) = 1.15 - 0.13\cdot\log(C_{org})$; (h) $\log(N_{area}) = 0.48 - 0.16\cdot\log(C_{org})$; (j) $\log(SLA) = 1.84 + 0.12\cdot\log(C_{org})$; (l) $\log(g_s) = 2.29 + 0.18\cdot\log(N_{tot})$; (m) $\log(N_{area}) = 0.28 - 0.15\cdot\log(N_{tot})$; (o) $\log(SLA) = 1.99 + 0.11\cdot\log(N_{tot})$; (q) $\log(g_s) = 2.57 - 0.24\cdot\log(P_{avail})$; (s) $\log(P_a) = -1.16 + 0.19\cdot\log(P_{avail})$; (w) $\log(N_{area}) = 0.66 - 0.34\cdot\log(AWHC)$; (x) $\log(P_a) = -0.37 - 0.47\cdot\log(AWHC)$. *AWHC*, available water holding capacity; *SLA*, specific leaf area.

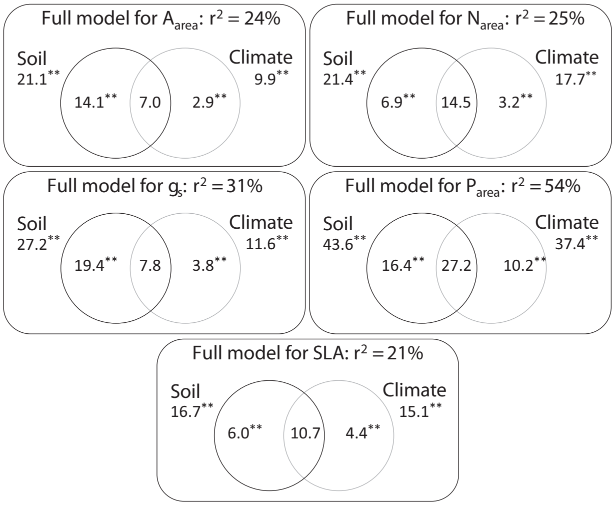

Figure 3 Partitioning of the respective variation in leaf photosynthetic rate (A_{area}), stomatal conductance (g_s), leaf nitrogen content (N_{area}), leaf phosphorus content (P_{area}) and specific leaf area (*SLA*) between the unique effect of soil, the unique effect of climate and the joint effect of soil and climate variables. Multiple mixed regressions were used to compute the adjusted r^2 of the fixed effects (climate and soil variables). Site and species were considered as random factors. The soil and climate variables used in these analyses were the ones revealed to be most relevant by a stepwise model selection procedure: MI_Q, SUN_{max}, TMP_{max}, $TMP5_{nb}$, PPT_{season}, *RH*, TMP_{range}, pH, N_{tot}, P_{avail}, *SILT*, *SAND*, *BULK*, *CECS* and *SALT*, are respectively moisture index, maximum monthly fractional sunshine duration, maximal monthly temperature, number of days with daily temperature above 5 °C, seasonality of precipitation, relative humidity, mean diurnal temperature range, soil pH, soil total nitrogen content, available soil phosphate content, soil silt and sand contents, soil bulk density, cation exchange capacity and soil salinity. Statistical significance is indicated using asterisks: $^{**}P < 0.01$.

being strongest for A_{area} and g_s. For the other traits (N_{area}, P_{area} and *SLA*), about half the total variation explained was accounted for by the common patterns of variation in climate and soils (the 'joint' effects).

Step 4. Multidimensional covariation between soils, climate and leaf traits

We used redundancy analysis to better understand how the structure in the matrix of leaf traits could be explained using the structure in the matrix of the most important soil and climate variables (selected at Step 2). Note, first, that A_{area} covaried significantly with g_s, N_{area}, P_{area} and *SLA* ($r^2 = 0.76$, 0.14, 0.07, 0.01, respectively). Thirty per cent of the variation in the four-trait matrix was explained by soils and climate (Fig. 4). Vectors representing variation in N_{area} and g_s were orthogonal and clearly associated with a number of environmental variables, while the vectors for A_{area} and *SLA* were also orthogonal to each other, and less clearly associated with environmental variables. In this analysis N_{area} was mainly explained by soil pH and by MI_Q, with high values of N_{area} found in arid sites on soils with high pH. g_s was mainly explained by P_{avail}, bulk density, sand content and growing season temperature, with high values of g_s found in warm sites on compact soils with low values of P_{avail}.

Step 5. Interdependences between key site variables and photosynthetic traits

Three environmental variables were repeatedly shown to be key for explaining variation in leaf traits: soil pH, soil available P, and *MI*. We used path analyses to explore the interdependences between these variables and the key photosynthetic traits A_{area}, N_{area} and g_s. The most parsimonious path analysis model explained 64% of the variation in A_{area} (Fig. 5). Figure 5 shows that high *MI* promotes acid soils. High *MI* and acid soils both (independently) promote low N_{area}. High P_{avail} and arid climate both (independently) promote low g_s. Both g_s and N_{area} (independently) determine A_{area}, in accord with theory (Wright *et al.*, 2003). There are also significant direct effects of *MI* and pH on A_{area} that are in the same direction as, but not accounted for by, the effects of N_{area} and g_s. Note that when *SLA* was added (considering its impact on N_{area}, g_s and A_{area}, and depending on MI_Q and pH), the models were consistently far weaker; hence they are not presented.

DISCUSSION

Climate plays a key role in soil development (Jenny, 1941); this leads to correlations among present-day soil and climate variables, and interactive effects of soils and climate on plant traits. We identified two main dimensions of environmental variation, key to understanding variation in leaf photosynthetic traits, which we discuss in relation to concepts of soil and ecosystem development.

A soil pH–aridity dimension

The first dimension was most strongly associated with soil pH (and exchangeable cations) decreasing with increasing precipitation and MI_Q. Higher values of N_{area}, P_{area} and A_{area} were found in more arid sites and on soils with a higher pH, but g_s was unrelated to this dimension.

The tendency for species to have higher N_{area} (and, less so, P_{area}) at drier sites is well known (Field *et al.*, 1983; Schulze *et al.*, 1998), and accords with theory which predicts the predominance of high-N_{area} strategies as a means to economise on water use during photosynthesis (Farquhar *et al.*, 2002; Wright *et al.*, 2003, discussed further below). By contrast, broad-scale patterning of leaf traits with soil pH has rarely been reported (but see Han *et al.*, 2011) and is correspondingly less well understood. These pH-related relationships were not simply secondary correlations flowing from the well-documented regional negative relationships between soil pH and precipitation, but probably relate to non-climatic determinants of soil pH, like parent rock and topography (Jenny, 1941). Soil pH is implicated in many soil chemical, enzymatic and microbial processes that affect the

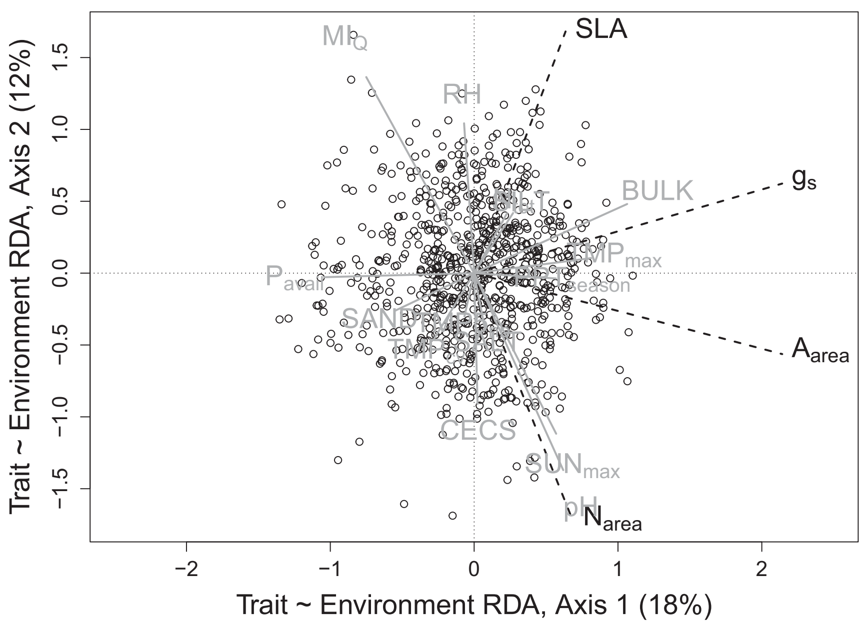

Figure 4 Redundancy analysis predicting the composition and structure of leaf photosynthetic traits (A_{area}, N_{area}, g_s and *SLA*) from the composition and structure of the most important soil and climate variables (selected by a stepwise procedure, see caption to Fig. 3). Abbreviations are defined in the caption to Fig. 3.

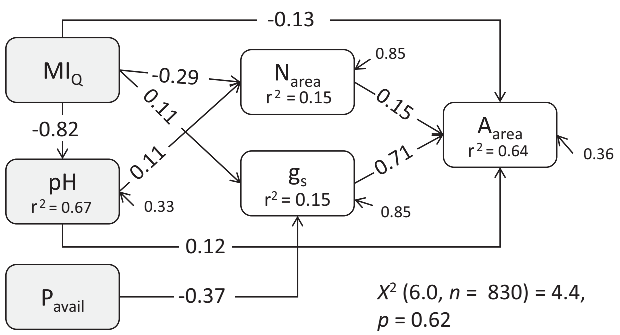

Figure 5 Path analysis depicting the direct and indirect effects of the main environmental predictors of leaf photosynthetic rate A_{area} through its covariation with stomatal conductance (g_s) and leaf nitrogen content (N_{area}). Environmental variables were selected based on the results of Fig. 4 and were soil pH (pH), moisture index (MI_Q) and soil available phosphorus content (P_{avail}). The path coefficients are the simple standardized regression coefficient. The goodness-of-fit and the unexplained variance of A_{area}, N_{area} and g_s are given. A Pearson correlation between N_{area} and g_s was tested and was not significant.

availability of micronutrients and nutrients (for a review see Sinsabaugh & Follstad Shah, 2012), and therefore so are N_{area} and P_{area}. Considered across a broad gradient of soil types, higher pH should generally equate to faster and/or higher availability of nutrients held in SOM and reduce the overall acquisition costs of N and thus the costs of achieving a given biochemical capacity for photosynthesis.

Conversely, higher SOM concentration (indexed by C_{org} or N_{tot}) does not necessarily denote higher N availability. In acid conditions SOM becomes recalcitrant, and N availability is correspondingly low (Jenny, 1941). Hence, here and elsewhere (Santiago *et al*., 2005; Ordoñez *et al*., 2009) we found the counterintuitive result that leaf N decreased with increasing soil total N.

Interestingly, the first dimension of soil fertility partially associated with the variation of A_{area} seems to be unrelated to g_s. Thus, the tendency of plants sampled locally to be strongly co-varying in A_{area} and g_s and hydraulic properties (Reich, 2014) does not hold in the same fashion across very broad climate and soil gradients, supporting the hypothesis that trade-offs between water and nutrient use predominate at larger scales.

The soil available P dimension

The second key environmental dimension was represented by P_{avail} in the topsoil horizon, covarying with the sand content and bulk density of soil and the site temperature (Fig. 4; Tables S7-3 & 7-4 in Appendix S7). Both leaf P_{area} and g_s showed strong patterning with this dimension, with higher P_{area} but lower g_s (but not A_{area}) on soils with higher P_{avail}.

Our study sites represented a broad range of soil types and P_{avail}, from highly weathered soils where P limitation is widespread (representing 33% of our sites, e.g. Oxisols; Table S4-4 in Appendix S4), to less (low) weathered soils with typically higher P_{avail} (21% of our sites, e.g. Inceptisols). While the P_{avail} part of our soil dataset was unavoidably underpinned by fewer soil profile data than for variables such as pH and C_{org}, our confidence in these data was boosted by observing positive relationships of P_{avail} with P_{area}, altitude and latitude, and its negative relationships with clay content, soil depth and Al saturation (Table S7-4 in Appendix 7) – echoing relationships known from regional field studies (Walker & Syers, 1976; Vitousek, 2004).

We have various prospective explanations for the observation that species on soils with higher P tend to team their maximum photosynthetic rates with lower stomatal conductance, but as yet no clear way to identify the most likely explanation, nor to place them into an optimality framework as has been done for climate-related effects on g_s (e.g. Medlyn *et al.*, 2011).

Experimentally lowering soil nutrient availability is known to stimulate higher root : shoot ratios (see Poorter *et al.*, 2012, for a comprehensive analysis), which may in turn improve plant water balance and hence allow for a higher g_s. Conversely, at a given root : shoot ratio, an increase in g_s in response to nutrient deficiency has been proposed as an evolutionary mechanism to improve plant nutrition, through an increase in the transpiration rate and the mass-flow of water from the surrounding soil (Edwards *et al.*, 1998; Cramer *et al.*, 2009). This 'mass-flow' hypothesis is generally thought to apply more to soil inorganic N than to the less mobile P (Cramer *et al.*, 2009), but higher g_s has also been observed under P deficiency for some species (Raven *et al.*, 2004).

Alternatively, in 'least-cost' photosynthetic optimality theory (Wright *et al.*, 2003), water and nitrogen supplies are considered as substitutable resources to secure carbon, and the optimization of A_{area} involves minimizing the sum of costs for acquiring and using N and water in photosynthesis. At higher soil N availability, where the costs of N acquisition are lower and therefore costs of water acquisition are relatively higher, plants are expected to operate at a given A_{area} with a higher N_{area} and lower g_s. It is conceivable that soil P and leaf P also fit into this framework, for example that higher leaf P enables a higher carboxylation capacity for a given leaf N (Niinemets *et al.*, 1999; Reich *et al.*, 2009). The same prediction (a higher N_{area} and/or a lower g_s for a given A_{area}) would be made for a scenario where costs of N acquisition were lower because of higher N availability due to more alkaline soil. Perhaps all of these effects could come into play in understanding the general trade-off between V_{cmax} and water use (Farquhar *et al.*, 2002; Wright *et al.*, 2003; Prentice *et al.*, 2014).

Limitations of our analyses

Underpinning the use of gridded soils data, we made the assumption of a high signal-to-noise ratio and an overall good match between 'actual' and spatial dataset values. Our observations of geography–soil, climate–soil and trait–soil relationships, which were in agreement with many of those observed in the literature with *in situ* soil variables measured at various scales (see details in Appendix S5 and Table S7-4 in Appendix S7), supported this. Nonetheless, we stress that local-scale variation in soil properties can certainly be large (Yemefack *et al.*, 2005) and that for more detailed assessments, values measured *in situ* at the respective plant trait sites would be ideal.

While one's ability to reliably tease apart the independent roles of soil and climate is limited in various ways in any statistical analysis (and especially since climate and soils covary) we chose path analysis as the most suitable for identifying causal structures (Legendre & Legendre, 2012). In combination with and complementary to the other approaches used (see Table S6-2 in Appendix 6 for the benefits and limitations of each statistical method), we provided evidence that soils modify A_{area}, g_s and N_{area} independently of climate. That said, we must not forget the possibility that these patterns may just be (or also be) markers of longer-term and more important factors associated with soil development, like parent rock, topography, soil age and vegetation (Jenny, 1941).

Conclusion

A key result of our study is that, in a multivariate trait–environment space (Fig. 4), there are two distinguishable dimensions of soil–climate variables influencing the two leaf traits (N_{area} and g_s) that, together, largely constrain photosynthetic activity. Soil pH and available P emerged as the best soil predictors of variation along these gradients and, indeed, overall we found stronger patterning of photosynthetic traits according to unique effects of soils than to those of climate. Plant geographers have long recognized that plant traits vary in concert with soil properties (e.g. Schimper, 1903), but only rarely have such patterns been quantified at a broad spatial scale. This work represents an important step towards a better understanding of geographic variation in leaf photosynthetic strategies, and to progress towards more reliable modelling of global vegetation function.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Literature used to extend the GLOPNET database.
Appendix S2 Dataset.
Appendix S3 Details on soil and climate variables and their biogeographic representation.
Appendix S4 Details on soil available phosphorus data.
Appendix S5 Discussion on the quality of soil and climate data.
Appendix S6 Details on data analysis
Appendix S7 Details on soil-soil, climate-climate and soil-climate analyses.
Appendix S8 Details on plant traits – environment analyses.

DATA ACCESSIBILITY

Additional references to the data sources used in this study can be found in Appendices S1 & S2 at the DRYAD Digital Repository (http://datadryad.org/) with the following doi address:10.5061/dryad.j42m7.

BIOSKETCHES

This research team aims to develop a better understanding of trait–environment interactions, particularly for use in 'next-generation' vegetation models based on plant functional traits. Expertise within the team extends from plant ecology to physiology to soil science and ecological theory.

Author contributions: V.M., I.J.W. and I.C.P. conceived the ideas and drafted the article; I.J.W. assembled the dataset with help from A.O. and V.M. V.M. performed the analyses. All authors contributed to the writing.

Editor: Greg Jordan

Appendix S1 – Literature used to extend the GLOPNET database (Wright et al., 2004)

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Appendix S2 – Dataset

The "global Amax" trait-soil-climate dataset is available at the DRYAD Digital Respository (http://datadryad.org/) with the following details:
Title: Global leaf photosynthesis database
Data identifier: doi:10.5061/dryad.j42m7

Appendix S3 – Details on soil and climate variables and their biogeographic representation

Table S3-1: Description of soil and climate variables used in this study.

Variable	Description	Unit	Database
Complex driver			
ELEV	Elevation	m	OS
LAT	Latitude	°	OS
Temperature			
TMP_{mean}	Mean annual temperature	ºC	OS > CRU
TMP_{min}	Minimal monthly temperature	ºC	CRU
TMP_{max}	Maximal monthly temperature	ºC	CRU
TMP_{gs}	Cumulative daily temperature above 0˚C ($TMP0_{gs}$) or 5˚C ($TMP5_{gs}$)	ºC	Calculated
TMP_{nb}	Number of days with daily temperature above 0˚C ($TMP0_{nb}$) or 5˚C ($TMP5_{nb}$)	#	Calculated
TMP_{range}	Mean diurnal temperature range (Σ (TMP_{max} –TMP_{min}) / 12)	ºC	Calculated
TMP_{iso}	Isothermality (TMP_{range}/(TMP_{max} –TMP_{min}))*0	-	Calculated
Precipitation			
PPT_{mean}	Mean annual precipitation	mm	OS > CRU
PPT_{min}	Minimum monthly precipitation	mm	CRU
PPT_{max}	Maximum monthly precipitation	mm	CRU
PPT_{cv}	Coefficient of variation of monthly precipitation	mm	CRU
PPT_{season}	Seasonality of precipitation: seasonal concentration of precipitation over the year (PPT_{season} = 1, all the precipitation are concentrated on one month)	0-1	Calculated
Radiation			
SUN_{mean}	Mean annual fractional sunshine duration (measured sunshine hours / theoretical maximum duration of sunshine hours)	%	CRU
SUN_{min}	Mean monthly fractional sunshine duration	%	CRU
SUN_{max}	Maximum monthly fractional sunshine duration	%	CRU
SUN_{range}	Range of monthly fractional sunshine duration Σ (SUN_{max}-SUN_{min}) / 12	%	CRU
PAR	Cumulative photosynthetically active radiation with daily temperature above 0 ˚C (PAR0) or 5˚C (PAR5)	W m^{-2}	Calculated
RAD	Global radiation	W m^{-2}	Calculated
Aridity			
RH	Relative humidity	%	CRU
PET_F	Potential evapotranspiration (Penman Monteith equation)	mm $month^{-1}$	FAO 2004
PET_Q	Equilibrium evapotranspiration (Prentice equation)	mm $month^{-1}$	Calculated
MI_F	Moisture index (MI_F = PPT_{mean} / PET_F)	mm mm^{-1}	FAO 2004
MI_Q	Moisture index (MI_Q = PPT_{mean} / PET_Q)	mm mm^{-1}	Calculated
Soil structure - texture			
BULK	Bulk density	kg dm^{-3}	SoilGrids
AWHC	Available water holding capacity (-33 to -1500 kPa; USDA standard)	mm m^{-1}	ISRIC
CLAY	Clay content	%wt	SoilGrids
SILT	Silt content	%wt	SoilGrids
SAND	Sand content	%wt	SoilGrids
GRAVEL	Gravel content	%wt	SoilGrids
DEPTH	Depth to the parent rock	cm	SoilGrids
Soil ion exchange capacity			
pH	Soil pH measured in H_2O solution	0-14	SoilGrids
TBA	Total exchangeable bases	cmol kg^{-1}	HWSD > ISRIC
SBA	Base saturation as percentage of CECS	%	HWSD > ISRIC
CECS	Cation exchange capacity	$cmol_c$ kg^{-1}	SoilGrids
CECC	Cation exchange capacity of clay size fraction, corrected from contribution of organic matter	$cmol^+$ kg^{-1}	HWSD > ISRIC
SALT	Salinity measured by the electrical conductivity of the soil	dS m^{-1}	HWSD > ISRIC
SODIUM	Sodicity measured by the exchangeable sodium percentage	% of ECEC	HWSD > ISRIC
ALU	Exchangeable aluminium percentage	% of ECEC	ISRIC
CARB	Calcium carbonate content	g kg^{-1}	HWSD > ISRIC
Soil chemistry			
C_{org}	Organic carbon content	gC kg^{-1}	SoilGrids
N_{tot}	Total nitrogen content	gN kg^{-1}	ISRIC
CN	CN ratio	gC gN^{-1}	ISRIC
P_{avail}	Available soil phosphate content	mgP_2O_5 kg^{-1}	see App. S4

For the 288 sites of our study we obtained the variables from the following climate and soil international databases: Global map of monthly reference evapotranspiration (FAO, 2004); Climatic

Research Unit (CRU, New et al., 2002); Harmonised World Soil Database (HWSD, FAO et al., 2012); ISRIC-WISE database (ISRIC, Batjes, 2012); SoilGrids (ISRIC, 2013). Latitude and altitude were obtained from original sources (OS). For most of the sites, mean annual temperature and precipitation were also obtained from the original sources. Otherwise, they were obtained from the CRU dataset, with TMP_{mean} corrected where necessary assuming an altitudinal lapse rate of 0.6°C per 100m. The symbol ‘>’ indicates the order of database utilisation to obtain a full site-matrix of values. Some climatic variables were calculated (indexed ‘calculated’ in the table) using monthly values of temperature, sunshine duration and precipitation (originated from the CRU database) and formulae from Wang et al. (2014).

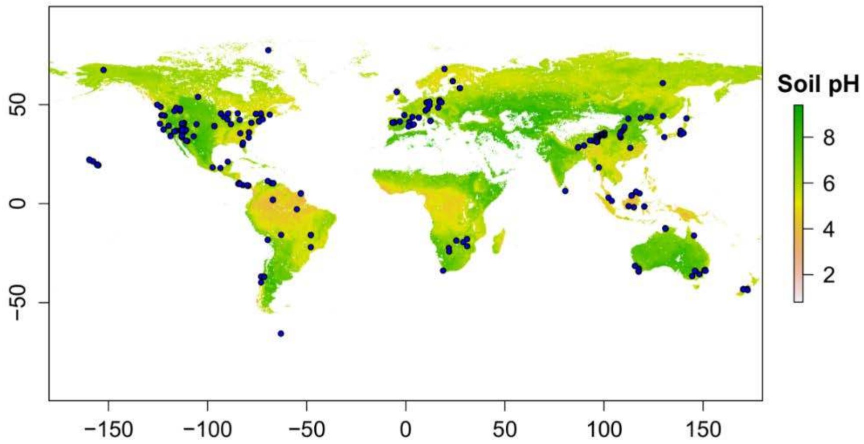

Figure S3-1: Geographical distribution of the 288 study sites on the Earth map representing the variation of soil pH at a 30’’*30’’ geographical resolution (SoilGrids, ISRIC 2013).

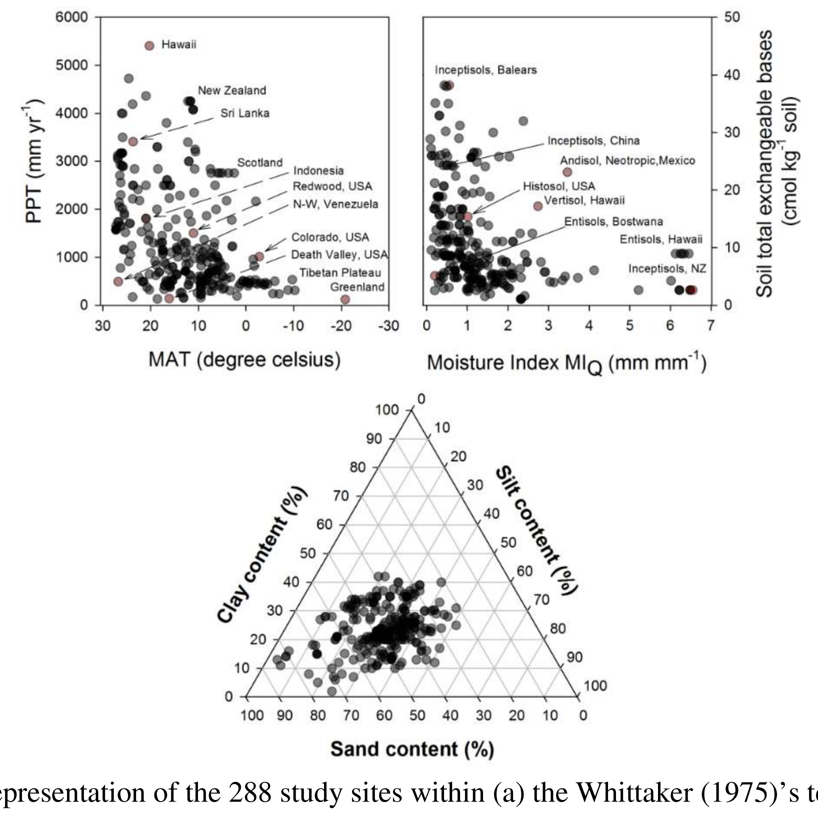

Figure S3-2: Representation of the 288 study sites within (a) the Whittaker (1975)’s temperature-precipitation diagram; (b) the Albrecht (1957 in Huston, 2012)’s conceptual model of soil development and degradation; and (c) the soil texture triangle.

Table S3-1: Representation of soil types encountered in the plant trait dataset. Soil information was extracted from SoilGrids (ISRIC, 2013) and corresponded to the soil taxonomy from the world reference base (WRB) and the United State Department of Agriculture (USDA)

WRB		USDA	
Soil group	site #	Soil order	site #
Acrisols	35	Alfisols	53
Alisols	7	Andisols	17
Andosols	18	Aridisols	18
Anthrosols	1	Entisols	16
Arenosols	6	Gelisols	2
Calcisols	2	Histosols	1
Cambisols	59	Inceptisols	25
Chernozems	1	Mollisols	58
Cryosols	13	Oxisols	53
Ferralsols	16	Spodosol	12
Fluvisols	2	Ultisols	32
Gleysols	3	Vertisols	1
Histosols	1		
Kastanozems	5		
Leptosols	22		
Luvisols	28		
Nitisols	3		
Phaeozems	5		
Planosols	1		
Podzols	21		
Regosols	32		
Solonchaks	3		
Umbrisols	2		
Vertisols	1		

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Appendix S4 – Details on soil available phosphorus data

1. Method

We assembled different sources of soil profile data to obtain a global representation of soil phosphorus. We first assembled geo-located soil profiles from (i) ISRIC-WISE v1.1 (South-African and South-American soils, Batjes, 2002), (ii) a large international soil P database (North American soils, Batjes, 2011a), (iii) an European topsoil survey (LUCAS, Tóth et al., 2013), (iv) a Chinese soil dataset (Shangguan et al., 2013) and (v) an Amazonian soil survey (Quesada et al., 2010).

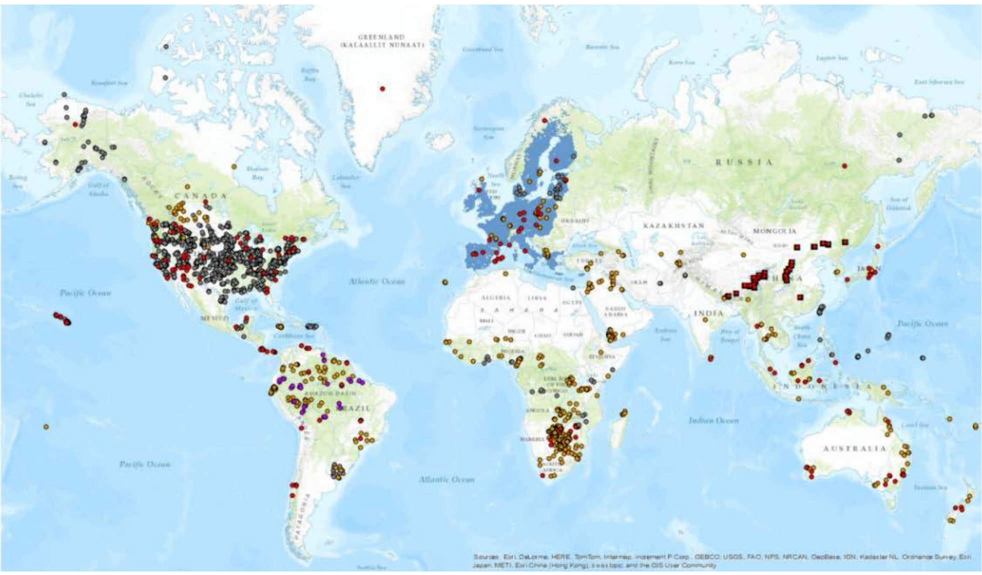

Figure S4-1: Representation of the different datasets used to get P data for our plant trait sites (red circles). ISRIC 2002 (orange); ISRIC 2011 (grey); LUCAS 2009 (blue); Quesada 2010 (purple); Shangguan 2013 (black square).

Using the 'Point Distance' tool in ArcGis 10.1, we recorded the nearest soil profiles for each site in the plant trait dataset. We did a literature survey to search for data from closer locations when the distance from the nearest profile was more than 100 km.

Table S4-1: Sources of soil available phosphorus data used in our study. In the literature survey, phosphorus data were extracted either from the original sources (OS) where the plant traits were measured or from other resources / studies (OR) that included soil available P measurements at the proximity of the site where plant traits were measured.

Row Labels	Number of sites
ISRIC11	97
ISRIC02	55
Shangguan13	35
LUCA09	43
Original Source (OS)	29
Other resource (OR)	28
Quesada10	1

Despite issues of scale, as described further in Appendix S5, this protocol yielded a relatively accurate soil phosphorus dataset (Figure S4-2).

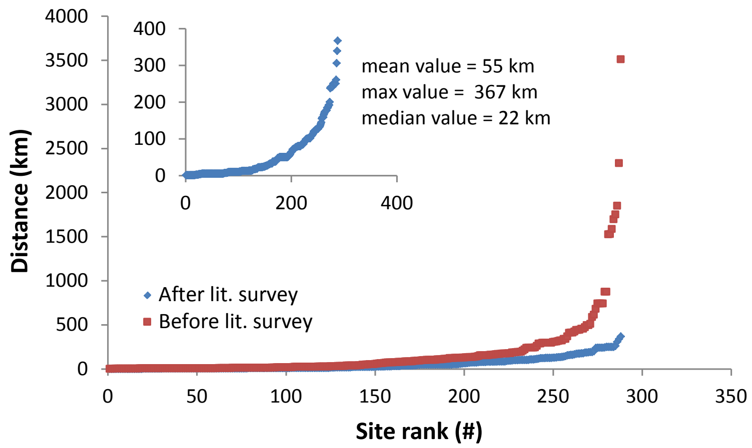

Figure S4-2: Distance between plant trait sites and soil available P sites, before and after the literature survey.

A limited availability of soil P to plants may be due to deficiency and/or severe P-retention. Therefore it is unlikely that a single extractant for measuring soil available P will suit all soils and ecosystems (Fairhurst et al., 1999). Indeed, the data for plant available soil P held in the above-mentioned databases were measured using a variety of chemical extraction methods, with methods normally chosen as most appropriate for local conditions (e.g. pH). Table S4-2 shows that five different methods were used of which the Bray I method most frequently. Soil properties (e.g. pH, soil mineralogy) affecting the selection of the appropriate P-test and recommended methods are described elsewhere (Elrashidi, 2010).

Table S4-2: Chemical extraction procedures to measure plant available soil phosphorus. Mean pH and Max pH are the average and the maximum values of soil pH observed for the respective P-analysis methods in our dataset. Abbreviation Si:St means soil to solution ratio.

Row Labels	Brief protocol of the chemical extraction	Sites #	Mean pH	Max pH
Bray I	0.03M NH_4F, 0.025M HCl, 1:10 SiSt, 5min	139	5.9	7.7
Olsen	0.5M $NaHCO_3$, pH 8.5, , 1:20 SiSt, 30min	98	6.3	8.4
Bray II	0.03M NH_4F, 0.080M HCl, 1:10 SiSt, 5min	15	5.3	6.4
Colwell	0.5 M $NaHCO_3$, pH 8.5, , 1:100 SiSt, 16h	18	5.8	7.9
Mehlich III	0.2M CH_3COOH, 0.25M NH_4NO_3, 0.015M NH_4F, 0.013M HNO_3, 0.001M EDTA, , 1:10 SiSt, 5min	18	5.9	7.7

For our study, global in scope, these data were harmonized to the Bray I method based on published conversion factors. In view of the range in chemical extraction protocols (Table S4-2), we had to harmonize the various values to a common 'standard'. Several conversion factors are available for this (e.g. Mallarino, 1995), but these are often region specific. As the Bray I method is most widely used in our dataset we selected it as the "target" method to which all P-values should be converted. Based on a literature survey and some initial analyses we opted to use a mean conversion factor. That is, we could not consider a globally consistent pH-threshold for this (see Table S4-3); there simply is no consensus for this in the literature.

Table S4-3: Conversion factors between Bray I method and other chemical extraction methods used to measure soil P values. Among studies, linear equations (Bray 1 = b*P.method + a) are used considering either the intercept *a* different of zero or not. To avoid calculation issues (negative values) linked with the value of the intercept, we calculated a new slope value (new *b*) considering no intercept (*a* = 0).

Bray I - Mehlich III	*b*	*a*	new *b*	Comment
Mallarino 1995	1.14	-6.25	1.06	North Dakota soils, pH < 7.5
Kleinman 2001	0.89	-0.84	0.88	Comparison of 9 labs and states, USA soils
Wolf 1985	2		2.00	USA soils, pH < 7.5
Alvey 2013	0.9	-8.4	0.79	North America soils, pH < 7.5
Cade-Menun 2008	0.88		0.88	Canada soils, spodosols, pH < 7.5
Ayodele 1981	1.04		1.04	African savannah soils
Mickaelson 1991	1	-4	0.95	Alaska soils
Gutierrez 2011	0.77		0.77	Argentina, pampean soils, Mollisols
Sawyer 1999	1.05	-2	1.02	America soils, pH < 7.3
Wunschler 2013	1.25		1.25	Austria, Germany soils, 6.1 < pH < 8
Sabbe 1998	0.94	-1.13	0.90	Arkansas soils
Mallarino 1997	1.03	-3.09	0.91	Iowa soils, pH < 7.5
Michaelson 1987	0.76	-1.21	0.74	Alaska soils
Matejovic 1994	1.74	-3.14	1.68	Slovakia soils
Average			**1.06**	

Bray I - Olsen	*b*	*a*	new *b*	Comment
Mallarino 1995	2.27	-7.05	2.22	North Dakota USA, pH < 7.5
Kleinman 2001	1.34	13.5	1.43	Comparison of 9 labs and states, USA
Wolf 1985	2.5		2.5	USA, pH < 7.5
Ayodele 1981	1.34		1.34	African savannah soils
Magyar 2011	1.37	10.2	1.44	Hungary soils
Sawyer 1999	1.74	-2	1.73	America soils, pH < 7.3
van Lierop 1988	2.43	1.95	2.39	British Columbia soils
da Silva 1999	1.25	2.14	1.21	Brazil soils
Average			**1.78**	

Bray I - Bray II	*b*	*a*	new *b*	Comment
Wunschler 2013	0.855		**0.86**	Austria, Germany 6.1 < pH < 8

Bray I - Colwell	*b*	*a*	new *b*	Comment
Moody 2013	0.62	1.81	0.63	Australia pH < 7.5
Moody 2013	1.27	-11.29	1.20	Australia, pH > 7.6
Average			**0.92**	

2. Evaluation of the P dataset

The broad-scale reliability of the harmonised P data was confirmed using categorical information: the global distribution of soil P retention potential (Batjes, 2011b) and the weathering stage associated with the soil orders of plant trait sites. As indicated in Appendix S5, the assumption here (as for all the soils data) is that the overall correlations between "actual" and dataset values should be robust and probably without strong systematic bias, although the accuracy of individual estimates presumably varies rather widely.

Table S4-4: Representation of soil types encountered in the plant trait dataset and their corresponding weathering stage. Soil taxonomical information was extracted from Soilgrids (ISRIC 2013) and is defined according to the soil taxonomy from the United State Department of Agriculture (USDA, Soil Survey Staff, 2010). Subsequently, the weathering stage of each soil type has been attributed following Cross & Schlesinger (1995) and Yang & Post (2011).

Soil order	Site #	Weathering stage	Soil order	Site #	Weathering stage
Alfisols	53	Intermediate	Inceptisols	25	Low
Andisols	17	Low	Mollisols	58	Intermediate
Aridisols	18	Intermediate	Oxisols	53	High
Entisols	16	Low	Spodosol	12	High
Gelisols	2	Low	Ultisols	32	High
Histosols	1	Low	Vertisols	1	Intermediate

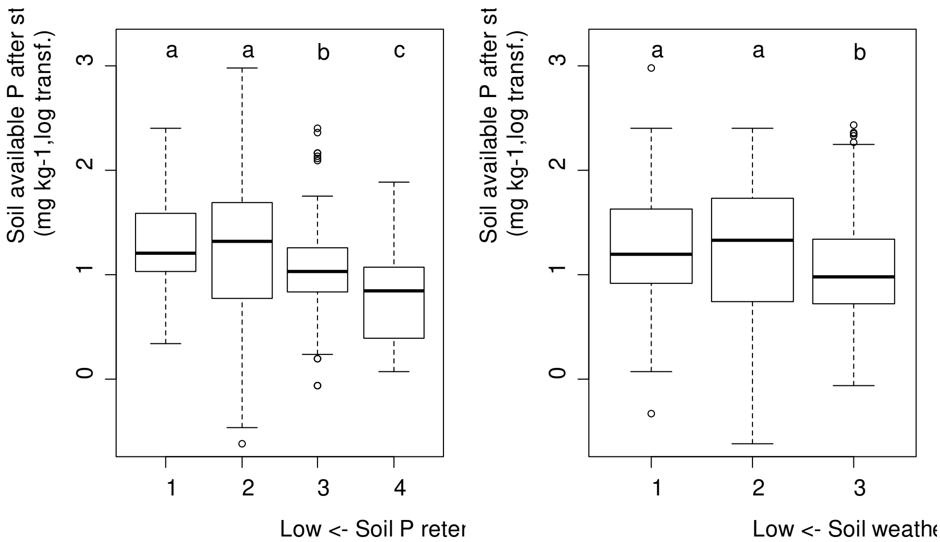

Figure S4-4: Soil available P data (after resolution improvement and method harmonization) among the 288 sites grouped according to the inferred soil P retention class (Batjes, 2011) resp. soil weathering stage (Yang et al., 2011).

Soil P and soil P retention

Recent studies based on analyses of a large soil profile database have concluded that it is not yet possible to derivate meaningful/accurate values of soil available phosphorus at the global scale (Batjes, 2010, Batjes, 2011a). Alternatively, it is possible to classify the ability of soils to retain P based on their mineralogy, pH and clay content (Batjes, 2011b). Four classes, rated from low to very high, have been proposed for this at the global scale. For the present study, we have extracted the P-retention class at the 288 trait sites to evaluate if our new soil P continuous (i.e. harmonised) data are in accordance with the categorical P retention classes. Overall, we expected lower soil available P in soils with a very high P retention and higher values for available P in low P retention soils.

Soil P and soil weathering

Soil orders following the soil taxonomy of the United State Department of Agriculture (USDA) were extracted for our 288 sites from SoilGrids (ISRIC, 2013). This information has been be used to determine the weathering stage according to rules published by Cross & Schlesinger (1995) and Yang & Post (2011). Then, we could evaluate if our soil available P data follow the decrease in soil available P that is expected along the weathering process. As expected, Figure S4-4a shows that soils with a high inferred potential for P-retention , overall, have lower soil available P levels than soils belonging to the high and low P-retention classs ($p < 0.01$, Tukey test). Similarly, as we can expect from soil development models (Walker and Syers, 1976), Figure S4-4b shows that soil available P levels tend to increase from low to intermediately soil weathering class, while it decreases significantly in the highly weathered soil class ($p < 0.05$, Tukey test) leading to lower soil available P values compared with slightly and intermediately weathered soil class. Considering proximal and distal soil P sites from plant trait sites, results slightly changed as shown in Fig. S4-5. Overall, our selection of soil available phosphorus data is in accord with what we could expect from chemical and soil development characteristics of the soil.

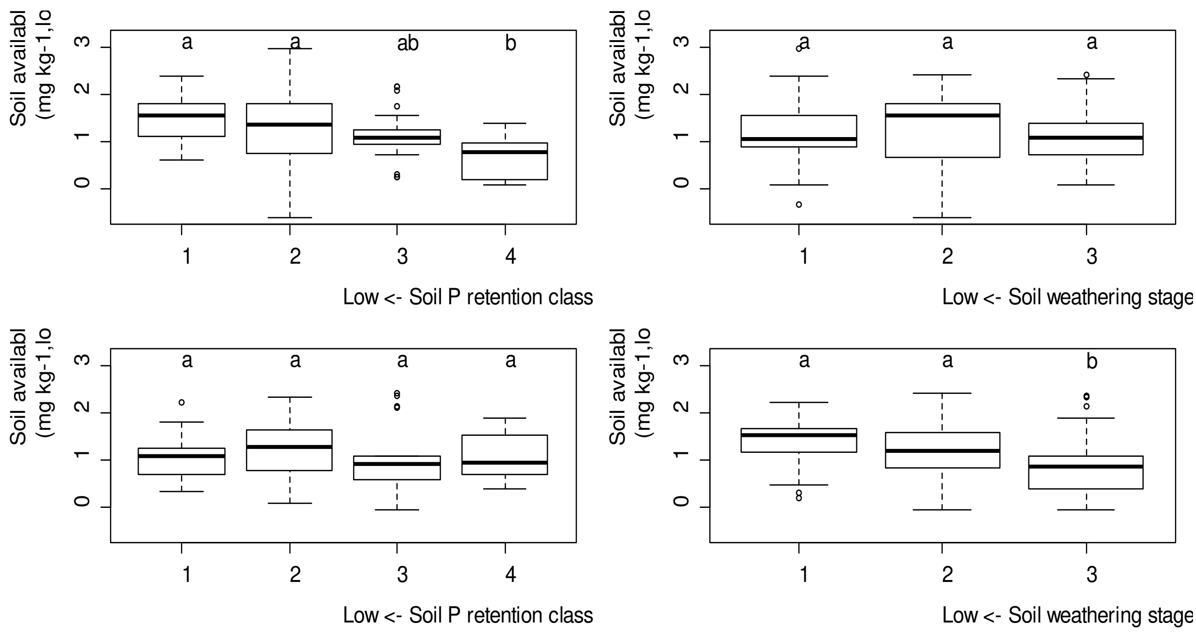

Figure S4-5: Soil harmonized available P data among the 288 sites, grouped according to soil P-retention class (Batjes, 2011) and soil weathering class (Yang et al., 2011), clustered according to proximity of plant trait sites (Upper panel: < 25 km; Lower panels:>=25 km).

3. Linking soil P with leaf photosynthetic traits

The covariation of the harmonised available soil P data with the stomatal conductance and the leaf P content is shown in Figure S4-6.

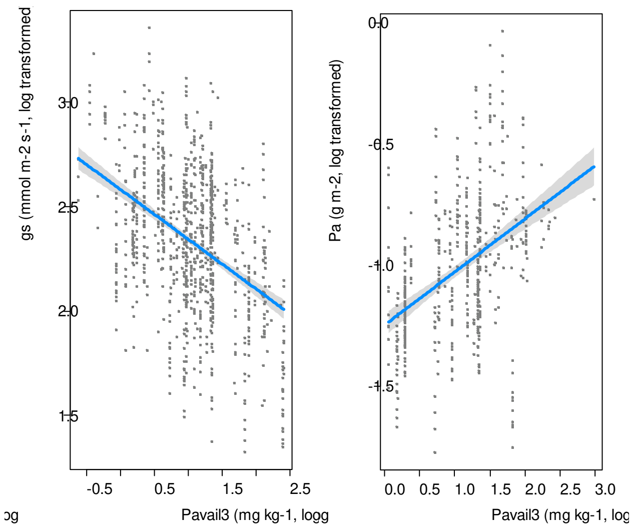

Figure S4-6: Relationship between soil harmonized available phosphorus and leaf stomatal conductance and between soil harmonized available phosphorus and leaf phosphorus content. $\log g_s = -0.24 \log P_{avail} + 2.58$, $p < 0.001$, $r^2 = 0.18$; $\log P_{area} = -0.19 \log P_{avail} -1.17$, $p < 0.001$, $r^2 = 0.18$.

The covariation of P_{avail} with the stomatal conductance and leaf P, split between the different sources the soil P values, is show in figure S4-6. Importantly, the significance of the relationships observed above are not only driven by the original sources (OS, see Table S4-1), where available soil P was measured *in-situ*.

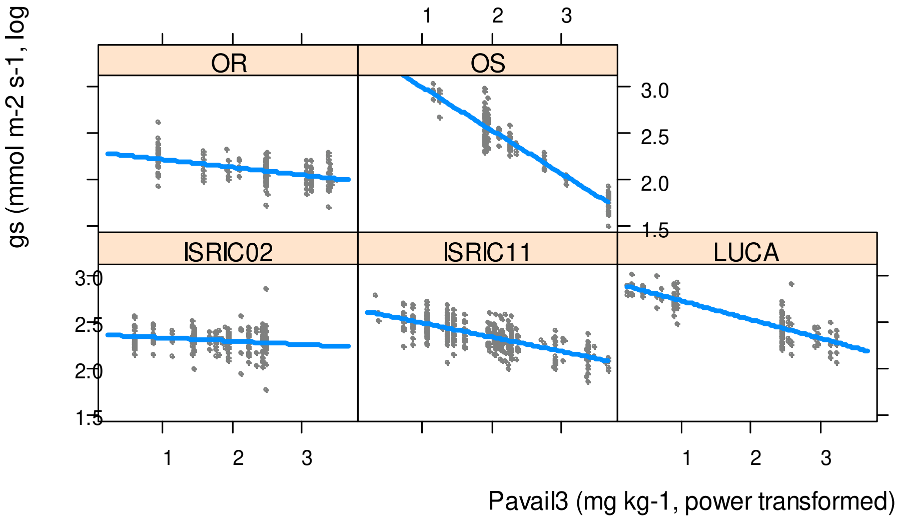

Figure S4-7: Relationship between soil harmonized available phosphorus and leaf stomatal conductance, observed for the different data sources.
LUCAS : r2 = 0.44, log Yt = -0.25 log X + 2.78, p < 0.001
OR : r2 = 0.04, log Yt = -0.14 log X + 2.29, p = ns
OS : r2 = 0.40, log Yt = -0.60 log X + 3.14, p < 0.001
ISRIC02 : r2 = 0.04, log Yt = -0.06 log X + 2.34, p = ns
ISRIC11: r2 = 0.20, log Yt = -0.19 log X + 2.53, p < 0.001

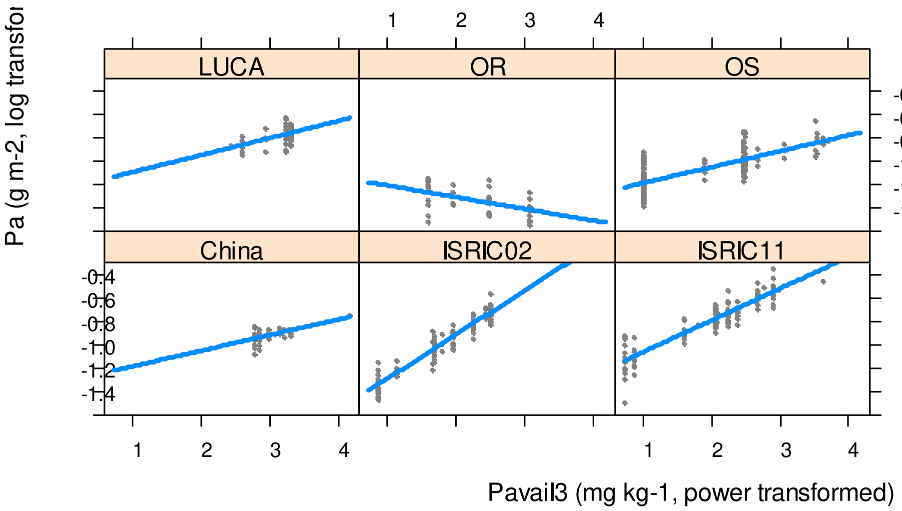

Figure S4-8: Relationship between harmonized soil available phosphorus and leaf P content, observed for the different data sources.
LUCAS : r2 = 0.07, log Yt = 0.19 log X – 1.10, p = ns
OR : r2 = 0.07, log Yt = -0.15 log X – 0.92, p = ns
OS : r2 = 0.32, log Yt = 0.18 log X -1.23, p < 0.01
China: r2 = 0.03, log Yt = 0.10 log X -1.08, p = ns
ISRIC02 : r2 = 0.44, log Yt = 0.55 log X -1.47, p < 0.05
ISRIC11: r2 = 0.32, log Yt = 0.37 log X -1.18, p < 0.001

The covariation of P_{avail} with the stomatal conductance (Fig. S4-9) and leaf P split (Fig. S4-10) between the different methods used to measure soil P is shown below.

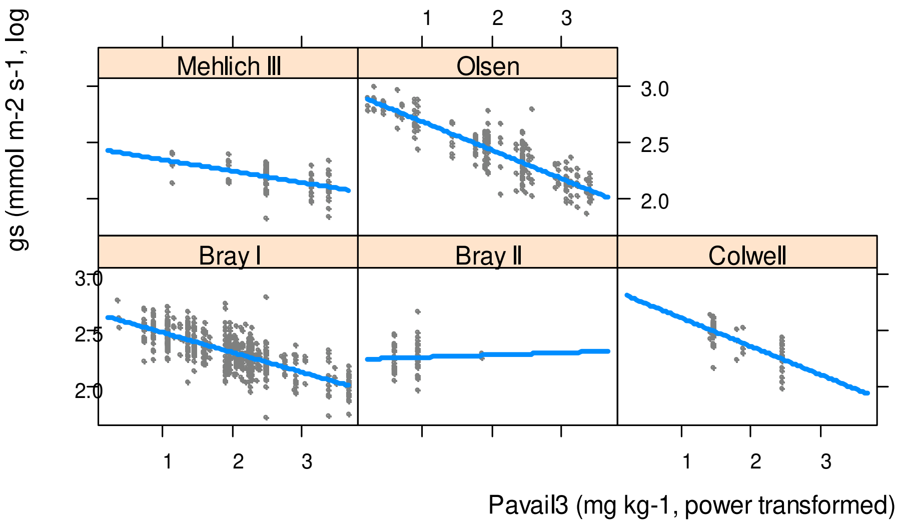

Figure S4-9: Relationship between soil harmonized available phosphorus and leaf stomatal conductance, observed for the different data sources.
Mehlich III : r2 = 0.19, log Yt = -0.18 log X + 2.43, p = ns
Olsen : r2 = 0.39, log Yt = -0.31 log X + 2.75, p < 0.001
Bray I : r2 = 0.18, log Yt = -0.22 log X + 2.54, p < 0.001
Bray II : r2 = 0.02, log Yt = 0.06 log X + 2.28, p = ns
Colwell: r2 = 0.29, log Yt = -0.34 log X + 2.71, p = ns

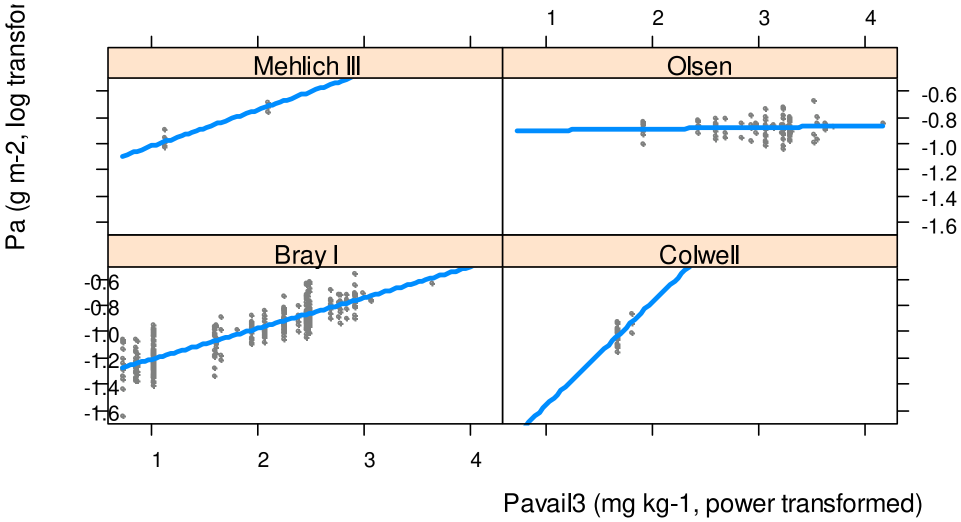

Figure S4-10: Relationship between soil harmonized available phosphorus and leaf P content, observed for the different data sources.

Mehlich III : r2 = 0.68, log Yt = 0.39 log X – 1.14, p = ns

Olsen : r2 = 0.00, log Yt = 0.03 log X – 0.92, p = ns

Bray I : r2 = 0.27, log Yt = 0.31 log X -1.29, p < 0.001

Colwell: r2 = 0.05, log Yt = 1.11 log X -1.90, p = ns

Figures S4-11 and S4-12 present the covariation of soil harmonized available P (P_{avail}) with the stomatal conductance and leaf P content for different distances proximity classes between the sites where soil P information has been measured and the plant trait sites. Irrespective of site proximity, the figures show that P_{avail} is negatively related with stomatal conductance and positively related with leaf phosphorus.

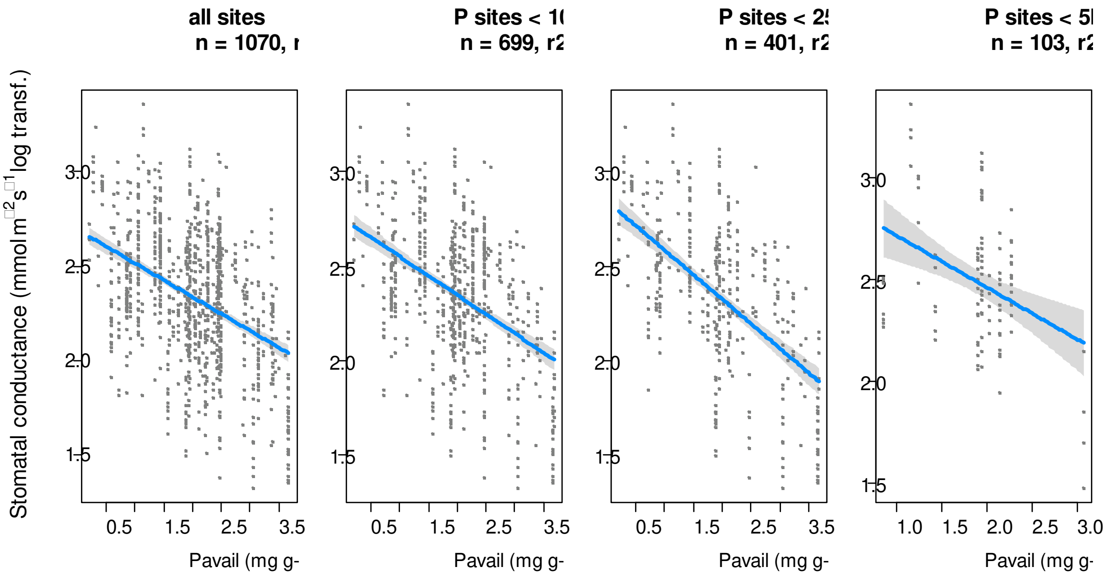

Figure S4-11: Relationship between soil harmonized available phosphorus and leaf stomatal conductance, considering different selection of soil data based on the distance between plant trait sites and soil P sites.

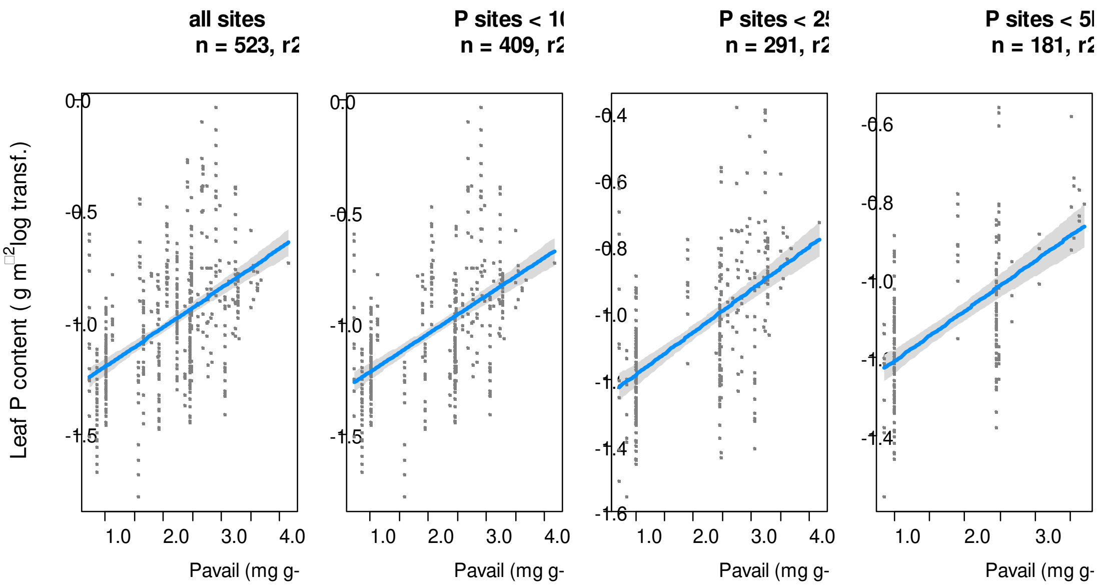

Figure S4-12: Relationship between soil harmonized available phosphorus and leaf P content, considering different selection of soil data based on the distance between plant trait sites and soil P sites.

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Appendix S5 - Quality of soil data

Underpinning the use of gridded soils data in soil-trait analyses is the assumption that, while the various individual estimates of “actual” site properties must surely vary widely in accuracy, the overall correlations between “actual” and gridded values should be robust and without strong systematic bias – especially when considering sites that vary so broadly in soil properties. Of course, the same assumption is made when using climate data from gridded datasets. Soil data were extracted from global soils datasets for each location where trait data had been measured. These soil datasets vary in spatial resolution (SoilGrids and HWSD: 30 arc-second; ISRIC-WISE v1.2: 5 arc-minute) but have in common that they are interpolated GIS surfaces underpinned by analyses of large soil profile datasets. Despite the relatively high spatial resolution datasets of this kind inherently imply some level of generalisation; further, their reliability and accuracy are determined by the availability and quality of the underlying spatial and attribute data, which itself may vary from region to region, as well as the adopted mapping approach (Cambardella & Karlen, 1999; Sanchez et al., 2009; Omuto et al., 2012; Hengl et al., 2014).

Different relationships can be considered to evaluate the reliability and quality of our soil data. The relationship observed between soil variables and geographical coordinates of the plant trait sites can be considered as a first test in regards to the theoretical models of soil / ecosystem development (e.g. Peltzer et al., 2010; Huston, 2012). We observed that lower latitude and altitude soils tend to be more acidic and have lower P_{avail} (Table S7-4). This is in agreement with the geographic history of the Earth locating, on average, younger and thinner soils with higher soil pH and higher soil P content at high latitude and altitude (Sanchez, 1976; Huston, 2012).

Relationships observed between soil and climate variables that were extracted from independent datasets can provide a second way to evaluate the suitability of our soil data for the present analyses. Following well-known regional or global relationships (e.g. Jenny, 1941; Post et al., 1982; Jobbagy & Jackson, 2000), soil pH was strongly, negatively related with precipitation and moisture index, while accumulation of soil organic C was positively related with precipitation and negatively related with temperature (Table S7-4).

Third, some relationships between soil variables and leaf traits observed in our study were in line with previous studies, where soil variables were measured *in-situ*. As such, several regional studies in Africa and South America show that TBA (and soil pH) increase N_{area} and P_{area} (Mantlana et al., 2008; Patino et al., 2012). Moreover, it has been already observed that soil total nitrogen content negatively covaries with N_{area} (Santiago et al., 2005; Ordoñez et al., 2009). The highest accumulation of soil OM is observed in soils where precipitation is high, temperature is low and soil pH is acidic, and where water-saturated, low oxygen environments are unfavourable to microbial activity and organic matter decomposition, such as in Histosols.

Finally, despite the soil P data being at lower spatial resolution than other variables, and only representing available inorganic P (not, e.g. organic fractions), P_{avail} was positively related with P_{area} and with absolute latitude and altitude (Table S7-4; Kitayama et al., 2002; Buendia et al., 2010), suggesting the data were of sufficient quality to encompass the main geological difference found at the global scale that can impact leaf traits. Appendix 4 deals with soil P data in more details.

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Appendix S6 Details on data analysis

This appendix includes details on the data analyses section of the main text. First, we detail the power transformation that had been applied to each of the soil and climate variable before statistical analysis. Second, we present in details the methods, their benefits and limitations to answer the different questions tackled by our study.

1. Power transformation of environmental variables

Environmental variables were subjected to the Yeo-Johnson transformation using the '*car*' package (R core team, 2013):

$$Y_t = [(Y+1)^{\lambda} - 1]/\lambda \qquad \text{[Eq. 1]}$$

The transformation provides a powerful way of reducing skewness and can be applied to variables that include negative values (e.g. temperature). Values of λ for each variable are given in Table S6-1.

Table S6-1: Value of lambda λ for the transformation of the environmental variables. See table S3-1 for abbreviations.

Climate	Lambda	Soil	lambda
MI_F	-0.833	ALU	0.500
MI_Q	-0.717	AWHC	-1.000
PAR0	1.588	BULK	6.467
PAR5	1.472	CARB	0.330
PET_F	1.000	CECC	0.771
PPT_{cv}	-1.343	CECS	0.330
PET_Q	1.184	CLAY	0.894
PPT_{max}	0.140	CN	0.000
PPT_{mean}	0.067	C_{org}	-0.153
PPT_{min}	0.082	DEPTH	0.274
PPT_{season}	-1.546	GRAV	0.093
RAD	2.831	N_{tot}	-1.281
RH	2.492	P_{avail}	-0.160
SUN_{max}	1.000	pH	1.000
SUN_{mean}	1.000	SALT	-2.097
SUN_{min}	1.232	SAND	0.500
SUN_{range}	0.000	SBA	1.000
$TMP0_{gs}$	0.640	SILT	1.000
$TMP5_{gs}$	0.500	SODIUM	-0.767
TMP_{iso}	-0.205	TBA	0.122
TMP_{max}	2.138	ALU	0.500
TMP_{mean}	1.073		
TMP_{min}	1.000		
$TMP0_{nb}$	7.556		
$TMP5_{nb}$	4.417		
TMP_{range}	0.500		

2. Step-by-step statistical approach

Our study asks the following questions: (1) How do leaf traits vary together with facets of soil fertility? (2) What are the most important soil and climate variables to explain the variation of leaf traits? (3) How is leaf trait variation shared between soil and climate? As climate and soil covary, the joined effect of soil-climate may dominate the pure effects of climate and soil (Reich & Oleksyn 2004). As different soils are encountered in a given climatic envelop, a significant pure effect of soils may be expected. (4) Photosynthetic rates depends both on leaf N and gs, two strategic independent dimensions. Are these two dimensions promoted by independent climate and soil dimensions? (5) Finally, what is the minimal set of environmental and trait variables to represent the hypothesis structure for photosynthetic rate and associated traits? To answer each question, a step-by-step statistical approach has been followed and is presented in Table S6-2 with the ultimate aim to disentangle soil and climate effects on leaf traits and photosynthetic rates. Teasing apart the independent role of soil from the one of climate is certainly limited by the causality linking soil to climate in such broad scale investigation. The use of path analysis is appropriate in that exercise, while multiple mixed regressions were not but allowed accounting for the unbalanced structure of the dataset (Table S6-2). Together, our overall approach showed that an independent role of soil on leaf traits can be fairly considered.

Table S6-2 Step-by-step summary of statistical methods including the form of the underlying statistical models, and the benefits and limitations of each analysis type.

Aim: Determine and quantify the role of key environmental variables on leaf photosynthetic traits and rates			
Step	**Model**	**Benefit**	**Limitation**
1. Defining key dimensions of soil fertility and quantifying their relationships with leaf traits (using mixed regression models)			
	Y = X	- Accounts for the hierarchical structure of the data	- Does not account for collinearity between explanatory variables
2. Selecting the most important climatic and soil variables for explaining leaf trait variation (stepwise procedure using multiple mixed regression models)			
	Y = [X1, X2, …, Xn]	- Accounts for the hierarchical structure of the data	- Does not account for causality between explanatory variables
3. Quantifying unique and joint effects of soils and climate in explaining variation in each leaf trait (using variation partitioning with the most important environmental variables selected at step 2)			
	Y = [X1, X2, …, Xn]	- Accounts for the hierarchical structure of the data	- Does not account for causality between explanatory variables
4. Quantifying the explanatory power of soils and climate (selected at step 2) for the matrix of leaf traits (using redundancy analysis)			
	[Y1, Y2, …, Yn] = [X1, X2, …, Xn]	- With no *a-priori*, allows one to explain covariance structure in a trait matrix with covariance structure of soil and climate matrices	- Does not account for causality between explanatory variables - Does not account for the hierarchical structure of the data
5. Disentangling direct and indirect effects of leaf traits, soil and climate (selected at step 4) on photosynthetic rate 'A_{area}' (using path analysis)			
	[Y1, Y2, …, Yn] = [X1, X2, …, Xn]	- Accounts for the causality between Y1 and Yn, between X1 and Xn and between Yn and Xn.	- An *a-priori* approach, i.e. one linked with the knowledge limits of the scientist. - Does not account for the hierarchical structure of the data

Appendix S7 Ordination analyses of climatic and edaphic variable

This appendix includes the different analyses between environmental variables. Principal component analyses identified the principal dimensions among climate variables, and those among soil variables. The matrices of correlation between environmental variables are also given.

1. Correlations between environmental variables

a. Principal component analyses of climatic and edaphic variables

Table S7-1: Principal component analyses of climate variables and soil variables. Each PCA included 20 variables that were power-transformed (Table S6-1) and was based on the correlation matrix and considered a Varimax rotation. PCA has been computed with the '*psych*' R package (R core team, 2013). The proportion of the variation explained by each axis and its corresponding eigenvalues are given. For each variable, bold text denotes its highest contribution among the PCA axes. Note that PET_F, MI_F, $TMP0_{gs}$, $TMP0_{nb}$, PAR0, PPT_{cv} as being highly redundant with PET_Q, MI_Q, $TMP5_{gs}$, $TMP5_{nb}$, PAR5, PPT_{season}, respectively (Table S7-3). See table S3-1 for abbreviations.

PCA of climatic variables

Variable	Axis 1	Axis 2	Axis 3
	40 %	*32 %*	*8 %*
	8.0	*6.8*	*1.3*
TMP_{mean}	**0.91**	0.16	-0.05
TMP_{min}	**0.93**	0.29	0.02
TMP_{max}	**0.82**	-0.12	-0.21
TMP_{range}	-0.09	**-0.76**	0.17
TMP_{ISO}	**0.81**	0.20	0.20
$TMP5_{gs}$	**0.95**	0.15	-0.
$TMP5_{nb}$	**0.88**	0.16	-0.
PPT_{mean}	0.43	**0.80**	0.00
PPT_{min}	0.18	**0.70**	-0.55
PPT_{max}	0.48	**0.75**	0.28
PPT_{season}	-0.07	-0.26	**0.91**
RH	0.15	**0.88**	-0.18
PET_Q	**0.90**	-0.26	0.18
MI_Q	0.07	**0.91**	-0.09
SUN_{mean}	0.41	**-0.84**	0.17
SUN_{min}	0.48	**-0.72**	0.01
SUN_{max}	0.29	**-0.83**	0.26
SUN_{range}	-0.30	0.25	-0.24
PAR5	**0.95**	-0.18	-0.03
RAD	**0.74**	-0.47	0.28

PCA of soil variables

Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
	21%	*18%*	*13%*	*11%*	*9%*
	4.7	*3.3*	*2.4*	*1.6*	*1.2*
ALU	0.15	-0.20	-0.14	**-0.69**	-0.02
AWHC	**0.83**	0.04	0.12	0.03	-0.01
BULK	-0.46	0.27	0.04	0.05	**-0.68**
CARB	-0.17	**0.53**	-0.23	-0.28	0.51
CECC	0.40	**0.66**	-0.13	0.19	-0.07
CECS	0.29	**0.69**	0.34	-0.07	0.11
CLAY	-0.50	-0.31	**0.52**	-0.28	0.02
CN	**0.71**	-0.25	-0.19	-0.16	-0.03
C_{org}	**0.84**	-0.12	0.11	0.00	0.26
DEPTH	0.01	-0.13	0.34	**-0.56**	0.08
GRAV	0.05	-0.05	0.11	0.20	**0.62**
N_{tot}	**0.81**	0.06	0.06	0.00	0.01
P_{avail}	0.12	0.01	-0.13	**0.71**	0.37
pH	-0.42	**0.77**	-0.11	0.14	-0.1
SALT	-0.32	-0.04	0.11	0.00	**0.33**
SAND	0.06	-0.03	**-0.96**	0.13	-0.04
SBA	-0.45	**0.70**	0.15	0.34	-0.16
SILT	0.34	0.33	**0.74**	0.07	0.05
SODIUM	**-0.43**	0.23	-0.17	0.32	0.16
TBA	-0.21	**0.76**	0.17	0.34	-0.17

b. Correlation matrix between climatic variables

Table S7-2: Pearson correlation matrix between the 26 climate variables (n = 288). All variables were power-transformed (see Table S6-1). Latitude and altitude are also considered here. See table S3-1 for abbreviations. *, p < 0.05; **, p < 0.01; ***, p < 0.001; ns, not significant.

	TMP_{mean}	TMP_{min}	TMP_{max}	TMP_{range}	TMP_{iso}	$TMP0_{gs}$	$TMP5_{gs}$	$TMP0_{nb}$	$TMP5_{nb}$	PPT_{mean}	PPT_{min}	PPT_{max}	PPT_{cv}	PPT_{season}	SUN_{mean}	SUN_{min}	SUN_{max}	SUN_{range}	RAD	PAR0	PAR5	RH	PET_F	PET_Q	MI_F	MI_Q	ELEV	LAT
TMP_{mean}																												
TMP_{min}	0.91***																											
TMP_{max}	0.81***	0.69***																										
TMP_{range}	-0.23***	-0.32***	-0.07																									
TMP_{iso}	0.72***	0.86***	0.42***	-0.06																								
$TMP0_{gs}$	0.94***	0.94***	0.86***	-0.27***	0.74***																							
$TMP5_{gs}$	0.93***	0.92***	0.88***	-0.27***	0.70***	1.00***																						
$TMP0_{nb}$	0.74***	0.82***	0.55***	-0.26***	0.62***	0.76***	0.73***																					
$TMP5_{nb}$	0.84***	0.88***	0.67***	-0.27***	0.68***	0.88***	0.86***	0.88***																				
PPT_{mean}	0.47***	0.59***	0.22***	-0.55***	0.49***	0.50***	0.48***	0.45***	0.45***																			
PPT_{min}	0.23***	0.34***	0.06	-0.53***	0.26***	0.27***	0.27***	0.32***	0.26***	0.71***																		
PPT_{max}	0.50***	0.62***	0.22***	-0.50***	0.56***	0.52***	0.50***	0.42***	0.44***	0.86***	0.52***																	
PPT_{cv}	-0.08	-0.10	-0.06	0.33***	0.03	-0.10	-0.11	-0.19**	-0.13*	-0.33***	-0.78***	-0.01																
PPT_{season}	-0.10	-0.13*	-0.11	0.31***	0.00	-0.13*	-0.14*	-0.21***	-0.16**	-0.30***	-0.77***	0.01	0.97***															
SUN_{mean}	0.19**	0.11	0.36***	0.67***	0.22***	0.20***	0.20***	0.09	0.17**	-0.40***	-0.55***	-0.34***	0.38***	0.32***														
SUN_{min}	0.22***	0.18**	0.39***	0.54***	0.28***	0.26***	0.26***	0.17**	0.26***	-0.29***	-0.36***	-0.25***	0.23***	0.15*	0.88***													
SUN_{max}	0.13*	0.03	0.31***	0.64***	0.10	0.12*	0.12*	0.04	0.11	-0.48***	-0.67***	-0.39***	0.46***	0.42***	0.91***	0.69***												
SUN_{range}	-0.14*	-0.25***	-0.11	0.13*	-0.28***	-0.23***	-0.22***	-0.21***	-0.25***	-0.31***	-0.45***	-0.27***	0.31***	0.35***	0.05	-0.36***	0.40***											
RAD	0.55***	0.54***	0.56***	0.30***	0.58***	0.57***	0.56***	0.41***	0.53***	-0.03	-0.33***	0.10	0.38***	0.31***	0.75***	0.74***	0.66***	-0.09										
PAR0	0.74***	0.76***	0.75***	0.17**	0.68***	0.81***	0.80***	0.69***	0.75***	0.14*	-0.08	0.18**	0.11	0.05	0.65***	0.64***	0.56***	-0.12*	0.81***									
PAR5	0.82***	0.83***	0.79***	0.02	0.69***	0.89***	0.89***	0.76***	0.86***	0.23***	0.02	0.27***	0.04	-0.02	0.52***	0.53***	0.44***	-0.15*	0.75***	0.97***								
RH	0.32***	0.39***	0.08	-0.74***	0.23***	0.33***	0.32***	0.34***	0.31***	0.68***	0.68***	0.63***	-0.41***	-0.36***	-0.75***	-0.61***	-0.73***	-0.19**	-0.38***	-0.14*	0.01							
PET_F	0.73***	0.68***	0.79***	0.23***	0.63***	0.77***	0.77***	0.52***	0.63***	0.05	-0.14*	0.11	0.14*	0.08	0.70***	0.67***	0.60***	-0.10	0.83***	0.92***	0.88***	-0.29***						
PET_Q	0.72***	0.77***	0.73***	0.14*	0.77***	0.80***	0.79***	0.52***	0.65***	0.20***	-0.09	0.30***	0.21***	0.15*	0.62***	0.62***	0.50***	-0.17**	0.84***	0.92***	0.88***	-0.14*	0.91***					
MI_F	0.15*	0.28***	-0.08	-0.63***	0.20***	0.17**	0.15*	0.23***	0.17**	0.91***	0.73***	0.75***	-0.39***	-0.34***	-0.67***	-0.55***	-0.71***	-0.26***	-0.37***	-0.23***	-0.12*	0.77***	-0.34***	-0.18**				
MI_Q	0.17**	0.28***	-0.06	-0.63***	0.17**	0.18**	0.16**	0.25***	0.19**	0.90***	0.75***	0.72***	-0.44***	-0.39***	-0.67***	-0.55***	-0.71***	-0.25***	-0.37***	-0.22***	-0.11	0.76***	-0.31***	-0.20***	0.99***			
ELEV	-0.55***	-0.37***	-0.49***	0.42***	0.00	-0.49***	-0.51***	-0.47***	-0.48***	-0.31***	-0.35***	-0.21***	0.40***	0.36***	0.27***	0.25***	0.22***	-0.02	0.09	-0.17**	-0.31***	-0.52***	-0.12*	0.05	-0.27***	-0.35***		
LAT	-0.47***	-0.51***	-0.19**	0.00	-0.56***	-0.45***	-0.42***	-0.50***	-0.58***	-0.32***	-0.18**	-0.35***	0.03	0.02	-0.11	-0.18**	-0.01	0.26***	-0.42***	-0.38***	-0.44***	-0.12*	-0.36***	-0.36***	-0.16**	-0.17**	0.19**	
alat	-0.74***	-0.80***	-0.59***	0.08	-0.86***	-0.78***	-0.77***	-0.45***	-0.60***	-0.45***	-0.15*	-0.56***	-0.15*	-0.11	-0.27***	-0.32***	-0.16**	0.25***	-0.64***	-0.68***	-0.69***	-0.16**	-0.68***	-0.86***	-0.14*	-0.09	-0.03	0.43***

c. Correlation matrix between soil variables

Table S7-3: Pearson correlation matrix between the 20 soil variables (n = 288). All variables were power-transformed (see Table S6-1). See table S3-1 for abbreviations. *, p < 0.05; **, p < 0.01; ***, p < 0.001; ns, not significant.

	ALU	AWHC	BULK	CARB	CECC	CECS	CLAY	CN	C_{org}	DEPTH	GRAV	N_{tot}	P_{avail}	pH	SALT	SAND	SILT	SODIUM
ALU																		
AWHC	0.11^{ns}																	
BULK	-0.12*	-0.33***																
CARB	0.01^{ns}	-0.18**	0.02^{ns}															
CECC	-0.14*	0.31***	0.01^{ns}	0.13*														
CECS	0.09^{ns}	0.31***	0.04^{ns}	0.24***	0.42***													
CLAY	0.10^{ns}	-0.31***	0.05^{ns}	0.05^{ns}	-0.50***	0.06^{ns}												
CN	0.21***	0.52***	-0.36***	0.11^{ns}	0.08^{ns}	0.00^{ns}	-0.25***											
C_{org}	0.17**	0.62***	-0.55***	0.05^{ns}	0.18**	0.27***	-0.27***	0.53***										
DEPTH	0.29***	0.03^{ns}	0.07^{ns}	0.06^{ns}	-0.17**	0.03^{ns}	0.23***	0.04^{ns}	0.04^{ns}									
GRAV	0.10^{ns}	0.05^{ns}	-0.32***	0.09^{ns}	0.05^{ns}	0.02^{ns}	0.09^{ns}	0.05^{ns}	0.19**	0.02^{ns}								
N_{tot}	0.05^{ns}	0.74***	-0.34***	0.08^{ns}	0.34***	0.24***	-0.28***	0.54***	0.61***	0.09^{ns}	0.01^{ns}							
P_{avail}	-0.31***	0.03^{ns}	0.10^{ns}	0.10^{ns}	0.12*	0.03^{ns}	-0.26***	0.00^{ns}	0.15**	-0.20***	0.19***	0.04^{ns}						
pH	-0.31***	-0.29***	0.42***	0.31***	0.31***	0.35***	-0.15*	-0.41***	-0.57***	-0.14*	0.06^{ns}	-0.28***	0.06^{ns}					
SALT	0.06^{ns}	0.09^{ns}	0.02^{ns}	0.08^{ns}	0.04^{ns}	-0.13*	0.20***	-0.21***	-0.26***	0.10^{ns}	0.10^{ns}	0.05^{ns}	0.05^{ns}	0.05^{ns}				
SAND	0.01^{ns}	0.05^{ns}	-0.04	0.06^{ns}	0.13*	-0.32***	-0.61***	0.17**	0.09^{ns}	-0.30***	0.07^{ns}	0.02^{ns}	0.15*	0.09^{ns}	0.10^{ns}			
SILT	0.09^{ns}	0.32***	0.02^{ns}	0.01^{ns}	0.25***	0.47***	0.08^{ns}	0.02^{ns}	0.35***	0.19**	0.17**	0.26***	0.05^{ns}	0.03^{ns}	0.05^{ns}	-0.74***		
SODIUM	-0.25***	-0.22***	0.15*	0.16**	0.05^{ns}	0.01^{ns}	0.07^{ns}	-0.31***	-0.35***	-0.27***	0.04^{ns}	-0.25***	0.14*	0.38***	0.10^{ns}	0.10^{ns}	-0.17**	
TBA	-0.44***	0.11^{ns}	0.35***	0.21***	0.39***	0.39***	0.11^{ns}	-0.38***	-0.28***	-0.25***	0.06^{ns}	0.11^{ns}	0.07^{ns}	0.70***	0.02^{ns}	-0.12*	0.24***	0.21***

d. Correlation matrix between key climate and key soil variables

Table S7-4: Pearson correlation between key soil and climate variables across sites (n = 288). The correlation between soil and absolute latitude (aLAT) and altitude are also presented. For explanation of variable abbreviations, see Table S3-1. *, p < 0.05; **, p < 0.01; ***, p < 0.001; ns, not significant.

	pH	C_{org}	SAND	BULK	P_{avail}
$TMP5_{gs}$	-0.30***	-0.27***	-0.12*	0.14*	-0.45***
MI_Q	-0.74***	0.59***	-0.15*	0.48***	-0.02^{ns}
PPT_{season}	0.29***	-0.20***	0.03^{ns}	0.03^{ns}	-0.07^{ns}
aLAT	0.37***	0.20***	0.15*	0.05^{ns}	0.31***
ELEV	0.20***	0.05^{ns}	0.00^{ns}	-0.13*	0.24***

Appendix S8: Details on plant trait – environment analyses

In this appendix we present the various regressions of leaf photosynthetic rate (A_{area}), leaf nitrogen and phosphorus content (N_{area} and P_{area}, respectively), stomatal conductance (g_s) and specific leaf area (SLA) on the soil and climate variables analysed in this study. First, bivariate relationships between each functional trait and each environmental variable are presented. We used mixed regression models (see main text) and test alternatively linear and quadratic effect of the environmental variable on the plant trait.

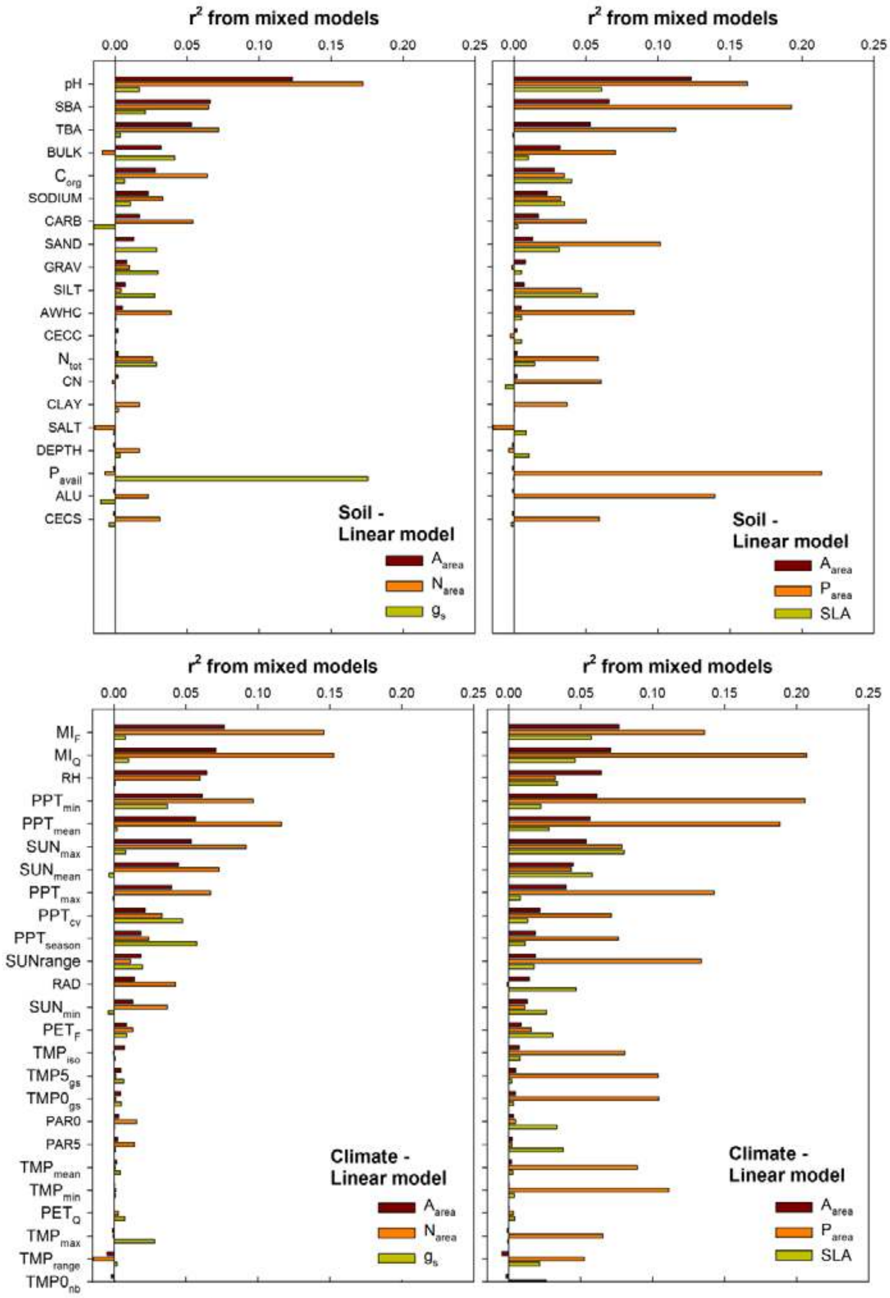

Figure S8-1: Bivariate models of linear mixed regression of A_{area}, N_{area} and g_s, and A_{area}, P_{area} and SLA with each of the climatic and environmental variables. Variables are ranked from the highest to the lowest coefficient of determination (r^2) in the regression model explaining $A_{area.}$. Details on model equations are given in Table S8-1. See table S3-1 for abbreviations.

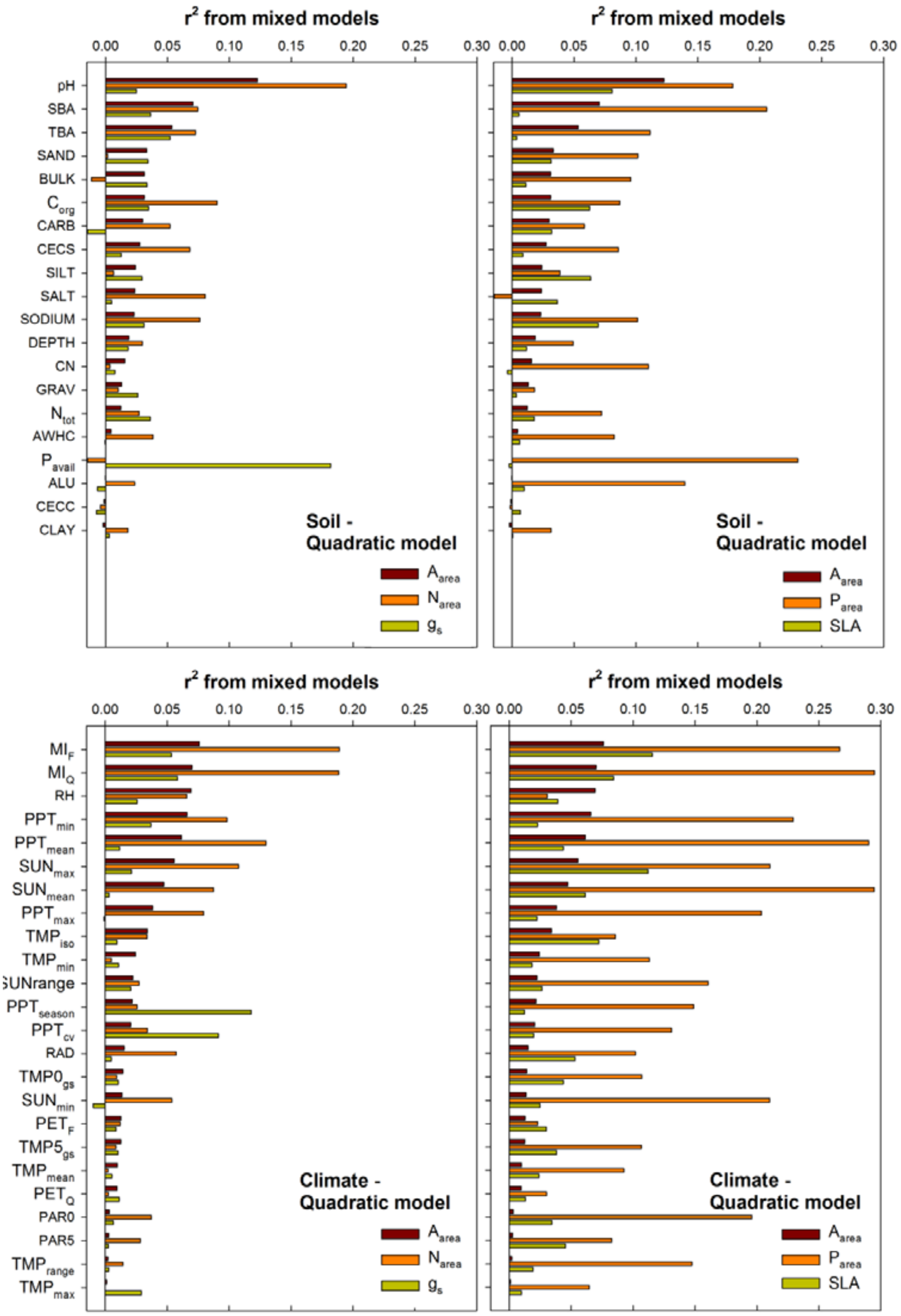

Figure S8-2: Bivariate models of quadratic mixed regression of A_{area}, N_{area} and g_s, and A_{area}, P_{area} and SLA with each of the climatic and environmental variables. Variables are ranked from the highest to the lowest coefficient of determination (r^2) in the regression model explaining $A_{area.}$ Details on model equations are given in Table S8-2. See table S3-1 for abbreviations.

Table S8-1: Details on the bivariate linear models presented in Fig S8-1.

	A_{area}			g_s			N_{area}			P_{area}			SLA		
	r2	**Slope**	**Interc.**	**r2**	**Slope**	**Interc.**	**r2**	**Slope**	**Interc.**	**r2**	**Slope**	**Interc.**	**r2**	**Slope**	**Interc.**
Climate															
MI_F	0.077	-3.75E-01	1.16	0.008	-2.02E-01	2.41	0.146	-3.54E-01	0.46	0.136	-2.59E-01	-0.76	0.057	2.23E-01	1.89
MI_Q	0.071	-3.41E-01	1.16	0.010	-2.02E-01	2.42	0.153	-3.20E-01	0.46	0.207	-2.99E-01	-0.73	0.046	1.83E-01	1.90
RH	0.064	-9.51E-06	1.14	0.001	3.10E-06	2.27	0.060	-1.37E-05	0.39	0.032	-3.04E-05	-0.84	0.034	1.01E-05	1.92
PPT_{min}	0.061	-3.82E-02	1.11	0.037	-4.15E-02	2.46	0.097	-2.57E-02	0.37	0.206	-1.96E-02	-0.79	0.022	1.39E-02	1.95
PPT_{mean}	0.057	-5.56E-02	1.46	0.002	-1.71E-02	2.50	0.116	-4.25E-02	0.68	0.189	-1.03E-02	-0.62	0.028	1.85E-02	1.82
SUN_{max}	0.054	4.41E-03	0.68	0.008	1.16E-04	2.25	0.092	1.34E-02	-0.13	0.079	3.02E-01	-2.17	0.080	-4.20E-02	2.61
SUN_{mean}	0.045	4.33E-03	0.74	-0.004	-1.75E-04	2.36	0.073	4.98E-03	-0.01	0.043	2.27E-01	-1.82	0.058	-5.45E-03	2.31
PPT_{max}	0.040	-3.48E-02	1.23	-0.001	-6.75E-03	2.37	0.067	-4.80E-02	0.57	0.143	-8.74E-03	-0.69	0.008	1.65E-02	1.90
PPT_{cv}	0.022	3.85E-01	0.86	0.048	4.16E-01	2.18	0.033	2.08E-01	0.20	0.071	1.17E+00	-1.17	0.013	-1.60E-01	2.06
PPT_{season}	0.019	4.28E-01	0.89	0.058	6.26E-01	2.19	0.024	2.21E-01	0.22	0.076	1.32E+00	-1.12	0.011	-1.89E-01	2.05
SUN_{range}	0.019	9.49E-02	0.68	0.020	4.88E-02	2.05	0.012	2.96E-02	0.17	0.134	5.17E-01	-1.91	0.018	-5.29E-02	2.17
RAD	0.014	1.31E-07	0.90	0.000	-1.05E-09	2.33	0.043	1.94E-07	0.16	0.001	-2.14E-08	-0.9	0.047	-3.40E-07	2.13
SUN_{min}	0.013	8.32E-04	0.90	-0.004	-1.10E-03	2.41	0.037	1.24E-03	0.14	0.011	4.80E-04	-0.97	0.026	-1.50E-03	2.13
PET_F	0.009	6.64E-05	0.90	0.009	7.58E-07	2.26	0.013	6.91E-05	0.19	0.016	-4.67E-06	-0.85	0.031	-1.11E-04	2.14
TMP_{iso}	0.007	-1.96E-01	1.49	0.001	-4.20E-03	2.35	0.000	1.83E-02	0.23	0.081	-2.46E-02	-0.61	0.008	-9.54E-02	2.29
$TMP5_{gs}$	0.005	-1.34E-03	1.02	0.007	1.01E-03	2.23	0.001	-1.95E-04	0.28	0.104	-8.71E-04	-0.81	0.002	-7.26E-04	2.05
$TMP0_{gs}$	0.005	-6.82E-04	1.02	0.005	2.76E-04	2.24	0.001	-8.65E-05	0.28	0.104	-2.64E-04	-0.8	0.003	-3.57E-04	2.06
PAR0	0.003	7.09E-07	0.94	0.000	6.97E-09	2.31	0.016	1.27E-07	0.19	0.005	4.67E-09	-0.96	0.034	-2.26E-07	2.15
PAR5	0.002	1.16E-06	0.95	0.001	5.10E-08	2.29	0.014	3.11E-07	0.21	0.002	-3.01E-08	-0.9	0.038	-1.84E-07	2.11
TMP_{mean}	0.002	-7.41E-04	0.99	0.004	1.93E-03	2.27	0.001	-3.89E-04	0.27	0.090	-3.85E-03	-0.84	0.003	-1.83E-03	2.04
TMP_{min}	0.000	-1.85E-03	0.99	0.001	1.36E-03	2.30	0.001	-3.70E-04	0.27	0.111	-4.35E-03	-0.87	0.004	-1.62E-03	2.02
PET_Q	0.000	4.99E-07	0.97	0.008	5.98E-07	2.26	0.003	1.50E-05	0.20	0.003	-1.97E-08	-0.9	0.004	-1.26E-05	2.07
TMP_{max}	-0.001	3.75E-05	0.96	0.028	2.60E-04	2.17	-0.001	8.63E-06	0.26	0.066	-8.35E-05	-0.84	-0.001	-2.98E-05	2.03
TMP_{range}	-0.005	1.06E-02	0.77	0.002	-1.01E-02	2.51	-0.015	1.43E-02	-0.01	0.052	4.31E-03	-1.42	0.022	-3.48E-02	2.40
$TMP0_{nb}$	-0.002	-4.00E-08	1.01	0.008	-2.78E-12	2.38	0.000	1.19E-10	0.25	0.026	-1.40E-07	-0.86	0.045	-3.04E-07	2.13
$TMP5_{nb}$	-0.001	-4.00E-05	0.98	-0.002	1.99E-08	2.30	0.002	3.05E-06	0.26	0.083	-3.67E-04	-0.79	0.049	-2.82E-04	2.11
Soil															
pH	0.123	8.10E-02	0.49	0.017	5.49E-03	2.18	0.172	4.00E-02	-0.10	0.162	5.66E-01	-1.99	0.061	-1.75E-02	2.20
SBA	0.066	2.00E-03	0.82	0.021	1.06E-03	2.25	0.065	3.00E-03	0.14	0.193	1.45E-01	-1.49	0.000	8.64E-05	2.01
TBA	0.053	5.20E-02	0.83	0.004	1.65E-02	2.28	0.072	4.80E-02	0.14	0.112	8.64E-02	-1.09	-0.001	2.60E-03	2.00
BULK	0.032	3.00E-03	0.85	0.041	2.13E-03	2.21	-0.009	2.00E-03	0.20	0.070	7.78E-03	-1.10	0.010	4.63E-04	1.99
C_{org}	0.028	-1.00E-01	1.22	0.006	-1.07E-01	2.52	0.064	-1.14E-01	0.56	0.035	-1.47E-01	-0.56	0.040	8.78E-02	1.78
SODIUM	0.023	2.80E-01	0.78	0.011	2.53E-01	2.16	0.033	2.75E-01	0.06	0.033	3.21E-01	-1.19	0.035	-2.12E-01	2.16
CARB	0.017	1.00E-02	0.90	-0.027	1.34E-02	2.26	0.054	1.30E-02	0.20	0.050	2.26E-02	-1.00	0.003	-1.55E-03	2.02
SAND	0.013	1.50E-02	0.79	0.029	-1.98E-02	2.56	0.000	0.00E+00	0.26	0.102	-1.43E-04	-0.72	0.032	-2.40E-02	2.29
GRAV	0.008	-3.30E-02	1.06	0.030	-4.84E-02	2.46	0.010	3.40E-02	0.18	-0.001	2.90E-02	-1.05	0.005	-2.86E-02	2.08
SILT	0.007	-1.00E-03	1.01	0.028	4.29E-03	2.20	0.004	-2.00E-03	0.30	0.047	6.34E-01	-2.18	0.058	5.86E-03	1.84
AWHC	0.005	-1.11E+00	2.01	0.000	8.99E-01	1.48	0.039	-2.60E+00	2.69	0.084	-2.17E-01	-0.31	0.005	1.32E+00	0.78
CECC	0.002	2.00E-03	0.93	0.001	-3.75E-04	2.33	0.000	0.00E+00	0.27	-0.002	8.93E-04	-0.94	0.005	-8.41E-04	2.03
N_{tot}	0.002	5.20E-02	0.94	0.029	3.87E-01	2.10	0.026	-3.76E-01	0.46	0.059	-2.28E-01	-0.75	0.014	3.00E-01	1.85
CN	0.002	-2.01E-01	1.18	0.000	4.02E+00	0.32	-0.002	-4.16E-01	0.70	0.061	-7.00E+01	33.87	-0.006	3.79E+00	-0.24
CLAY	0.000	-3.00E-03	1.02	0.002	6.46E-04	2.30	0.017	2.00E-03	0.21	0.037	5.42E-03	-1.04	0.000	-2.17E-04	2.01
SALT	0.000	4.00E-02	0.96	-0.001	4.58E-02	2.31	-0.014	1.99E-01	0.23	-0.112	1.96E-01	-0.96	0.008	-1.98E-01	2.04
DEPTH	-0.001	-4.00E-03	1.01	0.003	3.95E-02	2.03	0.017	-2.00E-02	0.44	-0.004	-1.13E-01	-0.64	0.010	1.50E-02	1.87
P_{avail}	-0.001	4.00E-03	0.96	0.176	-1.78E-01	2.70	-0.007	1.90E-02	0.22	0.214	8.82E-02	-1.19	0.000	-3.04E-03	2.02
ALU	-0.001	-4.00E-03	0.99	-0.010	1.00E-02	2.23	0.023	-7.00E-03	0.33	0.139	-1.70E-02	-0.76	0.000	3.69E-04	2.01
CECS	-0.001	-6.00E-03	1.00	-0.004	-5.44E-02	2.47	0.031	4.60E-02	0.13	0.059	3.57E-01	-1.45	-0.002	4.45E-03	1.99

Table S8-2: Details on the bivariate quadratic models presented in Fig S8-2

	A_{area}				g_s				N_{area}				P_{area}				SLA			
Variable	**r2**	**Slope X^2**	**Slope X**	**Inter.**	**r2**	**Slope X^2**	**Slope X**	**Inter.**	**r2**	**Slope X^2**	**Slope X**	**Inter.**	**r2**	**Slope X^2**	**Slope X**	**Inter.**	**r2**	**Slope X^2**	**Slope X**	**Inter.**
Clinate																				
MI_F	0.076	8.00E-02	-4.60E-01	1.18	0.054	-1.30E+00	1.00E+00	2.18	0.189	7.10E-01	-1.10E+00	0.64	0.116	-8.27E-01	1.15E+00	1.66	0.267	1.20E+00	-2.02E+00	-0.24
MI_Q	0.074	7.60E-02	-4.30E-01	1.18	0.058	-1.10E+00	9.10E-01	2.18	0.188	4.90E-01	-9.20E-01	0.61	0.084	-5.72E-01	8.65E-01	1.73	0.295	1.22E+00	-2.03E+00	-0.24
RH	0.069	-3.20E-10	1.20E-06	1.06	0.026	-8.50E-10	2.80E-05	2.12	0.066	1.10E-09	-3.30E-05	0.46	0.039	-5.95E-10	2.09E-05	1.87	0.031	1.26E-08	-9.38E-05	-0.77
PPT_{min}	0.066	-2.10E-03	-2.30E-02	1.09	0.037	3.60E-04	-4.40E-02	2.47	0.098	-8.20E-04	-1.90E-02	0.36	0.023	1.95E-03	-2.70E-03	1.98	0.229	2.26E-03	-5.50E-02	-0.71
PPT_{mean}	0.061	-5.10E-03	3.50E-02	1.07	0.012	-3.60E-03	5.90E-02	2.11	0.13	7.40E-03	-1.90E-01	1.38	0.044	-6.26E-03	1.48E-01	1.17	0.290	1.56E-03	-1.05E-01	0.66
SUN_{max}	0.056	3.50E-05	-1.60E-04	0.82	0.021	-9.20E-07	1.10E-03	2	0.108	1.20E-03	-5.40E-02	0.82	0.112	-1.50E-02	3.78E-01	-0.29	0.211	1.81E+00	-1.45E+01	27.96
SUN_{mean}	0.047	5.60E-05	-1.60E-03	0.89	0.003	-1.90E-06	7.60E-04	2.25	0.087	1.40E-04	-1.00E-02	0.39	0.061	-1.04E-04	5.76E-03	2.02	0.295	1.99E+00	-1.54E+01	28.78
PPT_{max}	0.038	4.70E-03	-1.00E-01	1.46	-0.001	2.60E-04	-1.10E-02	2.38	0.079	1.40E-02	-2.20E-01	1.08	0.023	-1.30E-02	1.84E-01	1.38	0.204	1.02E-03	-6.34E-02	-0.06
TMP_{iso}	0.034	-7.60E-01	3.80E+00	-3.77	0.01	3.60E-02	-5.70E-01	4.54	0.034	-2.30E+00	9.90E+00	-0.4	0.072	1.11E+00	-6.61E+00	11.75	0.086	-2.57E-03	4.10E-02	-1.02
TMP_{min}	0.024	-1.10E-04	-8.80E-04	1.01	0.011	1.80E-04	-3.30E-03	2.29	0.005	-8.40E-05	4.00E-04	0.28	0.019	1.92E-04	-3.65E-03	1.99	0.113	-7.22E-05	-2.87E-03	-0.86
SUN_{range}	0.022	2.50E-02	-6.10E-02	0.91	0.021	2.10E-03	2.50E-02	2.11	0.027	8.50E-02	-5.00E-01	0.97	0.027	-1.49E-01	8.62E-01	0.80	0.161	1.66E+00	-5.71E+00	3.88
PPT_{season}	0.022	-9.30E-01	8.20E-01	0.85	0.118	-7.50E+00	3.90E+00	1.91	0.026	8.10E-01	-1.20E-01	0.25	0.012	3.73E-01	-3.31E-01	2.06	0.149	1.24E+01	-2.28E+00	-0.90
PPT_{cv}	0.021	4.40E-01	1.20E-01	0.89	0.091	-3.40E+00	2.80E+00	1.82	0.034	3.10E-01	7.40E-03	0.23	0.020	1.38E+00	-9.77E-01	2.16	0.131	9.25E+00	-2.71E+00	-0.80
RAD	0.015	1.90E-13	7.20E-08	0.92	0.005	7.20E-13	5.20E-07	0.92	0.057	3.10E-13	-1.30E-07	0.23	0.053	-6.86E-13	1.61E-07	2.06	0.102	2.42E-12	-1.78E-06	-0.63
$TMP0_{gs}$	0.014	-2.90E-05	3.50E-03	0.9	0.011	2.30E-06	-1.10E-03	2.4	0.009	-6.60E-06	1.50E-03	0.2	0.044	1.80E-05	-4.89E-03	2.29	0.107	-3.13E-07	7.78E-06	-0.84
SUN_{min}	0.013	2.40E-06	4.20E-04	0.92	-0.01	1.20E-05	-3.10E-03	2.48	0.054	1.80E-05	-2.30E-03	0.29	0.025	-1.07E-05	2.29E-04	2.07	0.210	6.24E-05	-1.42E-02	-0.23
PET_F	0.013	1.00E-07	-1.70E-04	1.02	0.009	-6.40E-12	1.80E-06	2.22	0.012	-1.60E-08	1.10E-04	0.16	0.030	8.67E-08	-3.20E-04	2.25	0.023	1.62E-10	-9.41E-06	-0.82
$TMP5_{gs}$	0.013	-1.30E-04	6.50E-03	0.92	0.01	1.70E-05	-1.80E-03	2.34	0.009	-2.90E-05	2.60E-03	0.22	0.038	8.51E-05	-9.28E-03	2.21	0.107	-3.41E-06	-4.34E-05	-0.84
TMP_{mean}	0.012	4.20E-04	-1.30E-02	1.03	0.001	2.00E-03	-1.40E-02	2.33	0.012	1.60E-03	-2.00E-02	0.31	0.024	3.41E-04	-1.28E-02	2.09	0.093	-6.66E-05	-1.11E-03	-0.85
PET_Q	0.01	-1.40E-04	3.40E-03	0.97	0.005	8.20E-05	-2.50E-03	2.31	0.002	-1.10E-04	3.00E-03	0.26	0.013	5.14E-09	-6.25E-05	2.18	0.030	1.87E-13	-3.00E-07	-0.82
PAR0	0.01	-1.80E-08	1.20E-04	0.79	0.011	-1.00E-11	2.60E-06	2.17	0.003	-3.20E-09	4.10E-05	0.16	0.034	1.47E-13	-3.97E-07	2.19	0.196	2.44E-15	-5.48E-08	-0.72
PAR5	0.003	2.60E-12	5.00E-07	0.95	0.007	-2.70E-13	3.50E-07	2.22	0.037	4.00E-13	-3.40E-07	0.3	0.045	3.55E-13	-5.57E-07	2.18	0.083	5.17E-13	-5.52E-07	-0.82
TMP_{range}	0.003	6.40E-11	-1.00E-06	0.97	0.002	-1.30E-13	2.10E-07	2.25	0.028	3.10E-12	-6.30E-07	0.27	0.019	-7.72E-03	1.39E-01	1.43	0.148	1.14E-04	-2.27E-02	0.10
TMP_{max}	0.002	2.10E-03	-6.80E-02	1.51	0.003	-5.70E-04	1.20E-02	2.3	0.014	5.50E-03	-2.00E-01	1.96	0.010	2.42E-07	-3.34E-04	2.10	0.065	-4.42E-08	4.26E-06	-0.86
Soil																				
pH	0.123	1.26E-03	6.60E-02	0.531	0.025	-3.21E-04	2.17E-02	1.998	0.194	7.64E-03	-9.84E-02	0.5	0.081	-3.62E-03	6.32E-02	1.78	0.081	-3.62E-03	6.32E-02	1.78
SBA	0.071	4.71E-05	-3.45E-03	0.964	0.036	-5.63E-05	8.10E-03	2.073	0.075	1.80E-04	-9.18E-03	0.32	0.005	-1.03E-04	7.12E-03	1.90	0.005	-1.03E-04	7.12E-03	1.90
TBA	0.053	1.82E-02	-4.83E-02	0.953	0.052	1.59E-01	-7.14E-01	3.048	0.073	-2.98E-03	6.32E-02	0.124	0.004	8.41E-03	-4.07E-02	2.05	0.004	8.41E-03	-4.07E-02	2.05
SAND	0.033	-5.30E-03	1.41E-01	0.058	0.034	6.35E-03	-1.75E-01	3.478	0.002	-4.68E-03	1.12E-01	-0.4	0.031	7.81E-04	-4.28E-02	2.40	0.031	7.81E-04	-4.28E-02	2.40
BUILK	0.031	-1.25E-05	4.01E-03	0.838	0.034	-6.03E-05	8.46E-03	2.07	-0.011	1.38E-05	4.96E-04	0.219	0.011	6.53E-06	-1.71E-04	2.00	0.011	6.53E-06	-1.71E-04	2.00
C_{org}	0.031	3.82E-02	-2.90E-01	1.448	0.035	-4.35E-01	1.52E+00	1.04	0.090	8.05E-02	-5.29E-01	1.074	0.063	-7.01E-02	4.47E-01	1.34	0.063	-7.01E-02	4.47E-01	1.34
CARB	0.030	1.16E-03	-3.41E-03	0.933	-0.043	-2.21E-03	3.23E-02	2.231	0.052	1.24E-03	1.30E-03	0.214	0.032	3.93E-03	-3.56E-02	2.07	0.032	3.93E-03	-3.56E-02	2.07
CECS	0.028	-2.26E-02	2.13E-01	0.489	0.013	1.76E-01	-1.05E+00	3.864	0.068	-2.18E-01	1.27E+00	-1.56	0.009	3.39E-02	-2.40E-01	2.42	0.009	3.39E-02	-2.40E-01	2.42
SILT	0.024	-1.13E-04	4.87E-03	0.933	0.030	1.12E-04	-1.36E-03	2.262	0.006	-1.94E-04	4.14E-03	0.251	0.064	-1.84E-04	1.59E-02	1.72	0.064	-1.84E-04	1.59E-02	1.72
SALT	0.024	-2.81E+00	1.53E+00	0.844	0.005	1.14E+00	-5.95E-01	2.364	0.080	-3.18E+00	1.96E+00	0.087	0.037	1.95E+00	-1.18E+00	2.11	0.037	1.95E+00	-1.18E+00	2.11
SODIUM	0.023	2.07E-01	3.84E-03	0.866	0.031	-1.72E+00	2.35E+00	1.551	0.076	8.31E-01	-9.28E-01	0.474	0.070	-8.26E-01	9.73E-01	1.76	0.070	-8.26E-01	9.73E-01	1.76
DEPTH	0.019	3.85E-03	-8.39E-02	1.408	0.018	9.92E-03	-1.04E-01	2.536	0.030	4.23E-03	-9.11E-02	0.723	0.012	-3.69E-03	8.59E-02	1.54	0.012	-3.69E-03	8.59E-02	1.54
CN	0.016	7.32E-01	-1.83E+00	2.1	0.008	-3.96E+00	8.65E+00	-2.4	0.003	3.03E+00	-7.10E+00	4.4	0.091	5.23E+00	-1.24E+01	6.33	-0.003	-7.35E-01	1.72E+00	1.72
GRAV	0.013	1.13E-02	-9.50E-02	1.138	0.026	-1.30E-02	2.40E-02	2.364	0.010	1.59E-03	2.60E-02	0.187	0.003	-1.57E-02	4.48E-02	2.00	0.003	-1.57E-02	4.48E-02	2.00
N_{tot}	0.012	-9.58E-01	1.05E+00	0.694	0.036	-6.68E-01	1.18E+00	1.878	0.027	-1.05E-01	-2.65E-01	0.428	0.018	-1.16E+00	1.59E+00	1.51	0.018	-1.16E+00	1.59E+00	1.51
AWHC	0.004	2.78E+00	-6.32E+00	4.441	0.000	1.57E+01	-2.85E+01	15.19	0.038	5.36E+00	-1.26E+01	7.37	0.006	-4.06E+01	7.73E+01	-34.70	0.006	-4.06E+01	7.73E+01	-34.70
P_{avail}	0.000	-1.20E-02	5.33E-02	0.917	0.182	-1.17E-02	-1.29E-01	2.655	-0.015	-1.17E-02	7.23E-02	0.163	-0.002	3.73E-03	-1.90E-02	2.03	-0.002	3.73E-03	-1.90E-02	2.03
ALU	0.000	-3.39E-04	-1.95E-04	0.983	-0.007	-6.36E-04	2.22E-02	2.179	0.024	6.23E-04	-1.93E-02	0.377	0.010	-1.33E-03	2.50E-02	1.91	0.010	-1.33E-03	2.50E-02	1.91
CECC	-0.001	-9.91E-05	6.32E-03	0.883	-0.007	-5.86E-04	2.22E-02	2.139	-0.004	-1.01E-04	5.01E-03	0.207	0.007	1.25E-04	-6.30E-03	2.08	0.007	1.25E-04	-6.30E-03	2.08
CLAY	-0.002	-5.04E-04	1.55E-02	0.871	0.003	-1.69E-04	8.74E-03	2.218	0.018	1.72E-05	1.13E-03	0.222	0.001	-2.22E-05	8.40E-04	2.00	0.001	-2.22E-05	8.40E-04	2.00

Details of multiple regression models

Table S8-4: Estimate, standard error, t-ratio and significance of the multiple regression models between leaf functional traits (A_{area}, g_s, N_{area}, P_{area} and SLA) and, climate variables (following a stepwise procedure selecting among the 26 climate variables), which are presented in table 1.

log A_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	1.28E+00	1.45E-01	8.8	<0.001
MI_F	-3.70E-01	8.11E-02	-4.6	<0.001
TMP_{range}	-1.43E-02	6.03E-03	-2.6	<0.05
SUN_{max}	2.32E-03	1.24E-03	1.9	<0.1

log g_s

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	2.15E+00	9.80E-02	22.0	<0.001
TMP_{max}	4.93E-04	1.67E-04	3.0	<0.001
$TMP0_{nb}$	-4.43E-07	1.90E-07	-2.3	<0.05
PPT_{season}	7.88E-01	2.80E-01	2.8	<0.001

log N_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	5.64E-01	5.01E-02	11.3	<0.001
MI_Q	-4.37E-01	5.95E-02	-7.4	<0.001
TMP_{range}	-1.05E-02	4.46E-03	-2.4	<0.05

log P_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	-7.09E-01	6.57E-02	-10.8	<0.001
MI_Q	-1.13	2.14E-01	-5.3	<0.001
RH	2.63E-05	6.51E-06	4.0	<0.001

log *SLA*

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	2.44	6.23E-03	39.2	<0.001
SUN_{max}	-5.81E-03	9.05E-04	-6.4	<0.001
TMP_{max}	2.98E-04	8.07E-05	3.6	<0.001
$TMP0_{nb}$	-4.48E-07	8.07E-08	-5.6	<0.001

Table S8-5: Estimate, standard error, t-ratio and significance of the multiple regression models between leaf functional traits (A_{area}, g_s, N_{area}, P_{area} and SLA) and, soil variables (following a stepwise procedure selecting among the 20 soil variables), which are presented in table 1.

log A_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	3.54E-01	9.39E-02	3.8	<0.001
pH	1.18E-01	1.25E-02	9.5	<0.001
N_{tot}	4.69E-01	1.07E-01	4.4	<0.001
CECS	-6.96E-02	1.38E-02	-5.1	<0.001

log g_s

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	2.06	1.70E-01	12.1	<0.001
pH	1.10E-01	2.08E-02	5.3	<0.001
N_{tot}	9.10E-01	1.83E-01	5.0	<0.001
CECS	-1.04E-01	2.37E-02	-4.4	<0.001
P_{avail}	-1.83E-01	2.24E-02	-8.2	<0.001

log N_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	-5.96E-02	9.41E-02	-0.6	ns
pH	6.87E-02	1.11E-02	6.2	<0.001
N_{tot}	-2.31E-01	7.56E-02	-2.3	<0.05
SALT	2.29E-01	7.57E-02	3.0	<0.01

log P_{area}

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	-1.26	2.67E-01	-4.7	<0.001
pH	8.15E-02	2.47E-02	3.3	<0.01
P_{avail}	1.38E-01	3.13E-02	4.4	<0.001
SAND	-4.41E-02	1.64E-02	-2.7	<0.01
SALT	4.50E-01	1.73E-01	2.6	<0.05

log *SLA*

Term	**Estimate**	**Std Error**	***t* Ratio**	**Prob > |*t*|**
Intercept	1.97	1.03E-01	19.5	<0.001
pH	-5.01E-02	1.28E-02	-3.9	<0.001
Ntot	2.08E-01	1.15E-01	1.8	<0.001
SILT	5.20E-03	1.37E-03	3.8	<0.05
BULK	2.01E-03	9.02E-04	2.2	<0.1