

# Increasing functional diversity in a global land surface model illustrates uncertainties related to parameter simplification

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## Key Points

- **We implemented distributions of leaf economic spectrum traits in a land surface model in 15 diverse landscapes**
- **Trait variation has a substantial influence on gross primary production (GPP)**
- **Phenology plays a key role in guiding where traits fall within the global trait distribution and hence trait-GPP relationships**

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## **Abstract**

Simulations of the land surface carbon cycle typically compress functional diversity into a small set of plant functional types (PFT), with parameters defined by the average value of measurements of functional traits. In most earth system models, all wild plant life is represented by between five and fourteen plant functional types and a typical grid cell ( $\approx 100 \text{ km} \times 100 \text{ km}$ ) may contain a single PFT. Model logic applied to this coarse representation of ecological functional diversity provides a reasonable proxy for the carbon cycle, but does not capture the non-linear influence of functional traits on productivity. Here we show through simulations using the Energy Exascale Land Surface Model (ELM) in fifteen diverse terrestrial landscapes, that better accounting for functional diversity markedly alters predicted total carbon uptake. The shift in carbon uptake is as great as 30% and 10% in boreal and tropical regions, respectively, when compared to a single PFT parameterized with the trait means. The traits that best predict gross primary production vary based on vegetation phenology, which broadly determines where traits fall within the global distribution. Carbon uptake is more closely associated with specific leaf area for evergreen PFTs and the leaf carbon to nitrogen ratio in deciduous PFTs.

## **Plain Language Summary**

Plants play a critical role in the global carbon cycle, and diversity has been shown to influence vegetation productivity. However, when the land surface is simulated in a global model all wild plant life is reduced to a small number of plant functional types. Here we estimate how incorporating diversity influences ecosystem carbon uptake in fifteen globe spanning landscapes. We find that diversity has a strong influence on modeled productivity, particularly in the arctic and tropics. Further, we find that whether plants shed their leaves annually has a strong influence on where traits fall within the global distribution and thus how traits and productivity interact.

## **1 Introduction**

The representation of the land surface in an earth system model (ESM) differs from other key components of the Earth system (e.g. atmosphere, ocean) in that biological processes play an equal, or even dominant, role which interacts with physical processes to determine the functioning of the system. Early representations of the land surface (Sellers et al., 1986) primarily provided a meaningful boundary condition with appropriate physical properties for the rest of the

physical Earth System. However, as the importance of the carbon cycle in these models has grown, so too has the physiological sophistication of the biologically driven land surface, particularly photosynthesis (Albritton et al., 2001; Bonan et al., 2011; Oleson et al., 2013). Despite the increasing complexity of plant physiology in land surface models, the representation of vegetation as plant functional types (PFTs) compresses functional diversity into fewer than twenty aggregate types (Harrison et al., 2010; Oleson et al., 2013; Quillet et al., 2010; Wullschleger et al., 2014). Moreover, many grid cells (on the order of  $100 \times 100\text{km}$ ) are occupied by a single PFT, and thus have no diversity. While the quality of plant biochemistry in ESMs has provided a good first order approximation of the carbon state and fluxes of the land surface, it does not capture how plant functional diversity – known from experiments and observations (Isbell et al., 2018; Liang et al., 2016; Oehri et al., 2017; Reich, 2012; Tilman et al., 2012) to have a substantial influence on productivity – affects ESM predictions of gross primary productivity (GPP).

Representing plant life as PFTs essentially transforms diverse organisms, e.g. different plant species, each with potentially contrasting traits and growth rates, adapted to varied micro-environments, into a single aggregate organism (Sellers et al., 1986). Historically, the simplistic representation of terrestrial plants at global scale was due to a lack of available data. Now, the existence of large aggregate databases (Iversen et al., 2017; Kattge et al., 2011; Kattge et al., 2020) has allowed for the estimation of functional diversity across the global land surface (van Bodegom et al., 2014; Butler et al., 2017; Harper et al., 2016).

One of the outcomes of the simplified representation of functional diversity in PFTs is a restriction in the ways different plant life responds to both environmental variation and a directionally changing climate (Funk et al., 2017; Oehri et al., 2017; Pennekamp et al., 2018). The single PFT representation limits the phenotypic response to environmental variation to that of a single organism rather than the broader envelope of responses that a plant community will inhabit (Nicolson et al., 2010; Sakschewski et al., 2015, 2016; Scheiter et al., 2013). Ultimately, incorporating plant diversity into model analyses will enable a broader range of responses to a changing environment than the single organism response of a PFT (Sakschewski et al., 2016). Previous efforts to account for plant diversity in global vegetation models have built on community assembly theory (Pavlick et al., 2013), but had limited data to compare their results against. Other work

has produced detailed regional studies of diversity's influence on carbon and water cycles (Pappas et al., 2014). A detailed study of the Amazon rainforest (Sakschewski et al., 2015, 2016) used a large database (Kattge et al., 2011) to build tightly constrained trait distributions; however, the trait distributions were ultimately constrained by theoretical competitive dynamics, and in global scale models this region may have as few as two PFTs and is thus an incomplete test of how a broader range of landscapes will be affected by the shift to trait distributions.

Here, we use an updated selection of plant traits central to the leaf economic spectrum, i.e. to interspecific variation in traits related to carbon and nutrient uptake, processing and conservation (Wright et al., 2004), to estimate the influence of this diversity on carbon cycle simulations from the Energy Exascale Earth System Land Model (ELM) across a diverse array of regions spanning tropical to boreal ecosystems (Fig. 1, Table 1). We demonstrate that the modeled response to identical environmental fluctuations can vary dramatically for different trait combinations, even within the range of values associated with a single PFT. Further, we evaluate how modeling a PFT as a distribution of trait values, as opposed to a single mean value, changes estimates of gross primary production (GPP). This is equivalent to envisioning extant PFTs as comprising a set of representative vegetation types across a region as opposed to being a single aggregate entity. This distinguishes the analysis presented here from a sensitivity study of the model to the distribution of trait values.

**Figure 1.** Site Locations and dominant PFT. Each circle is a site in the analysis, a white ring indicates a single PFT and a black ring indicates two PFTs co-dominating (Mixed). The size of the circle scales with the number of trait observations at each site. Background colors correspond to regions dominated by the corresponding PFTs. Note that Shrub-Ar in the Southwestern United States has been jittered slightly to distinguish it from Grass-Ar.

**Table 1.** Site Summaries. This table contains detailed information for each FLUXNET tower site in the analysis according to the following categories: Name, the given name of the site in the FLUXNET Database; Country, the country that hosts the site; ID, the identification value defined by the dominant growth form (Tree, Shrub, Grass) with an asterisk (\*) indicating a mixed site, and a two letter abbreviation for one of four climate types: Tr (tropical), Te (temperate), Bo

(boreal), and Ar (arid), numerical suffixes are used to distinguish sites with repeated characteristics. Site climate was picked based on PFT, except for arid sites which are distinguished by being both hot ( $T[C]>15C$ ) and dry ( $P[mm]<500$ );  $T[C]$ : The mean annual temperature of the site in degree Celsius;  $P[mm]$ : The mean annual precipitation at the site in millimeters; PFT: The PFT(s) present at the site as defined by ELM.

Name	Country	ID	T[C]	P[mm]	PFT
Chokurdakh	Russia	Shrub-Bo <sub>1</sub>	-12.4	163	Broadleaf Deciduous Boreal Shrub
Samoylov	Russia	Shrub-Bo <sub>2</sub>	-12.1	135	Broadleaf Deciduous Boreal Shrub
Hyttiala	Finland	Tree-Bo <sub>1</sub>	3.6	507	Needleleaf Evergreen Boreal Tree
Fyodorovskoye	Russia	Tree-Bo <sub>2</sub>	4.0	488	Needleleaf Evergreen Boreal Tree
U. of Michigan Bio. Station	USA	Tree-Te <sub>1</sub>	7.1	574	Broadleaf Deciduous Temperate Tree
Tumbarumba	Australia	Tree-Te <sub>2</sub>	7.5	856	Broadleaf Evergreen Temp. Tree
Blodgett	USA	Tree-Te <sub>3</sub>	8.8	1159	Needleleaf Evergreen Temp. Tree
Park Falls	USA	Tree*-Te <sub>1</sub>	4.6	540	Bro. Deciduous Temp. Tree (50%), Nee. Evergreen Temp. Tree (50%)
Harvard Forest	USA	Tree*-Te <sub>2</sub>	5.1	980	Bro. Deciduous Temp. Tree (85%), Nee. Evergreen Temp. Tree (15%)
Puechabon	France	Tree*-Te <sub>3</sub>	13.3	901	Bro. Deciduous Temp. Tree (80%), Nee. Evergreen Temp. Tree (20%)
Kendall Grass-land	USA	Grass-Ar	17.3	256	C4 Grass
Santa Rita Mesquite	USA	Shrub-Ar	19.6	320	Broadleaf Deciduous Temperate Shrub
Kruger Park	South Africa	Grass*-Ar	22.5	490	C4 Grass (70%), Broadleaf Deciduous Tropical Tree (30%)
Guyaflox	French Guiana	Tree-Tr <sub>1</sub>	24.6	3158	Broadleaf Evergreen Tropical Tree
Santarem, km 67	Brazil	Tree-Tr <sub>2</sub>	24.7	2670	Broadleaf Evergreen Tropical Tree

We take a three-step approach within and across 15 globally distributed grid cells, each of which includes a FLUXNET site (Falge et al., 2016), to assess whether and how increasing the functional diversity of model parameterization can lead to substantial differences in model output. Based on the trait records compiled in the TRY database (Kattge et al., 2020) we generate site-specific three-dimensional distributions of trait values for specific leaf area (leaf area per dry mass, SLA), leaf carbon-nitrogen (mass) ratio (LCN), and leaf lifespan (LLS), accounting for the well-known trait-trait covariance structure (joint distributions) (Wright et al., 2004). In the ELM

model, each of these traits has a substantial influence on model output: LCN is a major control of canopy nitrogen content, which influences photosynthesis rates (Thornton & Zimmermann, 2007); SLA determines carbon investment in leaf area; LLS controls the time over which a leaf will fix carbon. These three traits together describe the main carbon and nutrient economy, and growth strategy (from inherently “fast to slow”), of different plant species and types; and thereby for productivity (Reich, 2014). Further, SLA and LCN directly influence  $V_{\text{cmax}}$ , (the maximum velocity of carboxylation) a key parameter in photosynthesis. Using the joint distributions, we first evaluate the ranges of modeled GPP with a focus on generalizable characteristics between traits and GPP. Second, we evaluate how updating trait values changes GPP estimates relative to GPP based on FLUXNET measurements using three sets of model runs (Fig. 2): (i) default parameterization; (ii) updated mean trait parameterization, and (iii) multiple model runs using the joint trait distributions. Third, we evaluate the non-linear relationship between traits and modeled GPP and summarize this using the updated mean trait values (ii above) to the mean of GPP using the joint trait distributions (iii above). Lastly, we analyze a subset of sites to better interpret how the trait-GPP relationship influences these differences. These approaches demonstrate the many ways that trait distributions drive differences in modeled GPP relative to a single trait value.

**Figure 2.** The three types of model simulations. There are three distinct model configurations analyzed in this study: two single runs with trait means, (i) the model default based on old species trait values (black vertical dashed line); (ii) an updated mean based on the trait distributions generated here (green vertical dashed line) and (iii) the distribution of traits (green solid line). These three model runs generate corresponding output from ELM as indicated by the black arrow and the grey distributions and vertical lines, where the line-style of the trait input corresponds to the line-style of the GPP output.

## 2 Materials and Methods

The model used throughout this analysis is the Energy Land Model (ELM, v1), the land component of the U.S. Department of Energy’s Energy Exascale Earth System Model (E3SM), which may be run as a fully coupled Earth System Model with atmosphere, land, ocean, sea ice, and land ice components. ELM is based on the Community Land Model version 4.5 (CLM4.5) (Oleson et al., 2013), including canopy integrated leaf photosynthesis (Bonan et al., 2011, 2012),

dynamically coupled carbon and nitrogen in vegetation and soil (Thornton et al., 2007), soil biogeochemistry resolved across vertical layers (Koven et al., 2013), and permafrost hydrology (Swenson et al., 2012). Further, it uses temperature revised Rubisco kinetics (Bernacchi et al., 2001; Bernacchi et al., 2003) as well as a high temperature adjustment to photosynthesis (Leuning, 2002). More recently a prognostic phosphorus cycle has been added (Yang et al., 2014, 2019).

We modify the model by including a wider range of trait values based on observed functional diversity. Leveraging the global scale trait database, TRY (Kattge et al., 2011; Kattge et al., 2020), the subset used for this analysis includes 83,585 measurements from 7,489 species across the 14 PFTs in ELM. Each trait measurement from TRY was assigned to one of the 14 natural PFTs in ELM based on its species and location. We estimate trait distributions from observations associated with the extant PFTs of ELM to explore how three key traits, specific leaf area (SLA), leaf nitrogen concentration (LCN), and leaf lifespan (LLS), influence ELM's carbon cycle estimates as summarized by gross primary production (GPP). For consistency with ELM, mass based leaf nitrogen is converted to leaf carbon nitrogen ratio (LCN) and SLA is converted to units of area per carbon mass by a simplifying assumption of 50% carbon content for each leaf.

These traits were selected for the central role they play in photosynthesis within ELM. A central parameter in the photosynthesis model used in ELM is the maximum velocity of carboxylation ( $V_{cmax}$ ), which was modified in (Thornton & Zimmermann, 2007) to dynamically respond to changes in leaf SLA and LCN through the following relationship:

$$V_{cmax} = N_a F_{LNR} \frac{1}{F_{NR}} \alpha_R \quad (1),$$

In eqn. (1)  $N_a$  is area based leaf nitrogen content ( $\text{gN m}^{-2}$  one-sided leaf area),  $F_{LNR}$  is the fraction of leaf nitrogen in Rubisco (unitless),  $F_{NR}$  is the mass ratio of nitrogen in a Rubisco molecule to total molecular mass (unitless) and  $\alpha_R$  is the specific activity of Rubisco ( $\mu\text{mol CO}_2 \text{gRubisco}^{-1} \text{s}^{-1}$ ). The area based leaf nitrogen,  $N_a$ , may then be defined as:

$$N_a = \frac{1}{SLA \times LCN} \quad (2),$$

with SLA and LCN being, specific leaf area ( $\text{m}^2$  one-sided leaf area  $\text{gC}^{-1}$ ) and leaf carbon nitrogen ratio ( $\text{gC gN}^{-1}$ ). Thus, the inverse value of SLA and LCN exert a linear control on  $V_{\text{cmax}}$ , whose components have been shown to be key parameters in controlling GPP (Ricciuto et al., 2018). The relationship between the inverse trait values and GPP is roughly consistent among sites; but, however, somewhat variable (Fig. S1). For LLS, its inclusion in the model is critical due to its covariance with these traits and its importance to evergreen PFTs (Reich et al., 2014), as deciduous PFTs are governed by a separate phenology module.

To determine an appropriate size for the distributions to simulate we conducted an extensive analysis using 1000 simulations at two sites, one temperate deciduous (Tree- $\text{Te}_1$ ) and one tropical evergreen (Tree- $\text{Tr}_2$ ) to determine the requisite size of trait distribution. We expanded this pool of 1000 simulations up to 100,000 using a simulation analysis (Castruccio et al., 2014), and tested subsets of simulations including between 20 and 1000 samples in the distribution against the simulation with 100,000 samples. From this we determined that 100 samples, or subPFTs, were a sufficient balance between computational efficiency and accuracy. Please see Supplemental Text S1: Supplemental Methods and Figures S2 and S3 in the Supplemental material for a complete description of the simulation analysis conducted to reach this conclusion.

Lastly, the distributions we report in the manuscript are from a screened subset of the original 100 trait values (Fig. S4) because some trait combinations, generally with low leaf lifespan, generated no carbon uptake at some of these sites (GPP values of 0) and others, with high LLS, produced highly unrealistic model output (e.g. Leaf Area Index (LAI) values  $> 1000$ , Fig. S5), this issue has been reported in other analyses where leaf life span was modified from model defaults (Reich et al., 2014). This screening reduced the included simulations to between 45 and 99% of the original 100 draws, with a mean of 68%. This leads to a unique set of trait values for each site from a previously identical distribution for each PFT.

We estimate formal non-linear trait-GPP relationships with the following form:

$$GPP_s = \beta_0 * TR_s^{\beta_1}, (3)$$



here  $GPP_s$  is the annual average gross primary production at a site,  $s$ , for a given trait value,  $TR_s$ . All trait-GPP relationships are evaluated at each site, but generally a single trait shows a clear non-linear relationship. The  $\beta$  values are empirically fit constants using the Levenberg-Marquardt algorithm in SciPy (Virtanen et al., 2020).

### 3 Data Screening and Model Protocol

The data were screened for outliers after log transformation by removing entries greater than the 95th percentile, but only if the 95th percentile was more than three times (i.e. three orders of magnitude) the value of the 5th percentile. This criterion filtered entries that were outliers while leaving large trait values intact. Then, within each of the 14 PFTs each trait was summarized into a mean value (Table S1) and a pairwise covariance matrix was calculated across all PFTs (Table S2) (Reich, 2014; Wright et al., 2004). In other words, we assume the distribution of traits to be a multi-variate log-normal for each PFT and that each PFT is, initially, identical at every site, per the current model logic. Trait values were then screened at each site based on leaf life span and producing non-zero GPP output, as noted above. This produces a set of trait values with a higher Pearson's correlation than a pairwise estimate from the raw data, but preserves the general covariance structure. Independent of this analysis PFTs have been assigned a percentage presence at each site (Table 1) and regardless of the size of the presence each PFT is assigned a unique draw from the trait distribution for each model run.

For each simulation ELM was fully spun-up under pre-industrial conditions using a 250 year accelerated decomposition spin-up (Koven et al., 2013; Thornton & Rosenbloom, 2005) followed by a 600 year final spin-up. The spin-ups are followed by a transient simulation from 1850-present forced by historically varying  $CO_2$ , nitrogen deposition (Lamarque et al., 2010), and site based meteorological observations. The observed meteorology at each site is recycled in a loop for the spin-ups and the period preceding observation, with the exact time frame rounded up to make an even multiple of the observed meteorological forcing. Site specific data are also used to update the soil texture and PFT presence. In total, we produce 102 model simulations at each of the sites. As each of the model runs is conducted independently, the subPFT simulations do not interact with each other and there is no competition between subPFTs. Thus, the modeling protocol assumes that the estimated subPFTs are present at each site and will remain static. This is in

keeping with the logic that assigns the spatial location of PFTs across the land surface in most land surface models. This analysis is a simulation of how diversity influences the carbon cycle, not how that diversity arose in the first instance, as pioneered by community ecologists (Sakschewski et al., 2015, 2016; Scheiter et al., 2013).

Flux tower data are from the FLUXNET network, and we used mean annual GPP estimates (Falge et al., 2016). The flux towers were selected to cover a wide range of plant functional types at sites with at least ten years of data collected. We evaluated model output relative to flux tower data through a Kruskal-Wallis test in SciPy (Virtanen et al., 2020), by calculating the root mean square error and standard deviation across all sites, and the absolute difference between each model configuration and the flux tower estimated GPP.

## 4 Results and Discussion

### 4.1 Carbon cycle simulations from the distribution of traits.

The individual runs within the distribution of traits generate GPP estimates that vary up to over an order of magnitude within a site (Fig. 3). We find the greatest influence of functional trait variation on simulated productivity in the boreal zone. At one boreal shrub site in Russia (Shrub-Bo<sub>2</sub>), the extreme trait combinations for GPP range from  $\approx 100$  to  $\approx 1300$  gC m<sup>-2</sup> yr<sup>-1</sup>. There are suites of traits that produce much lower and much higher GPP in this environment than other suites, and use of a single ‘mean organism’ in the model parameterization misses this heterogeneity. Other boreal sites show a similar range of GPP values; e.g., a Finnish evergreen tree site (Tree-Bo<sub>1</sub>) varies from  $\approx 300$ -1600 gC m<sup>-2</sup> yr<sup>-1</sup>. At another climatic extreme, the magnitude of simulated GPP variation within tropical sites is also large, approximately a factor of five at both tropical evergreen sites. At both sites the least productive trait combination has a GPP of  $\approx 1,000$  gC m<sup>-2</sup> yr<sup>-1</sup> and the most productive trait combination yields  $\approx 5,000$  gC m<sup>-2</sup> yr<sup>-1</sup>.

By contrast, environmentally constrained arid sites tend to show little influence on GPP from biological variation, with one arid grassland site in the US Southwest (Grass-Ar) varying as little as  $\approx 200$ -300 gC m<sup>-2</sup> yr<sup>-1</sup>, only a factor of 1.5, across the trait distribution. Despite a comparable range of input trait values (Fig. S4) the arid sites produce a narrower GPP distribution than other

locations. In the environmentally constrained arid sites there is little room for greater productivity with the leaf economic spectrum traits selected for this analysis, but in highly productive tropical sites and environmentally variable boreal sites distinct trait combinations can yield vastly different outcomes.

These simulations are distinct from a parameter sensitivity analysis because all three traits are varied together and constrained by their trait-trait covariances (Table S2). In essence, these GPP distributions may be thought of as each representing a set of patches within the simulated grid cell. Each simulation and its estimated GPP is equivalent to the productivity of different coexisting species or individuals with varying trait values.

Most of the GPP distributions are approximately normal by both visual inspection and a D'Agostino  $K^2$  normality test ( $p < 0.05$ , at 13 sites, Fig. S6). However, the near normality of most of the GPP distributions is contrasted by net primary production (NPP, Fig. S7) which fails the test at six sites ( $p < 0.05$ ). Three sites fail the normality test for leaf maintenance respiration (Fig. S8) ( $p < 0.05$ ). Temperate and arid sites most frequently show varying distribution shapes across these different components of the carbon cycle. The variation in shape of these distributions highlights the non-linear influence of leaf economic spectrum traits on the carbon cycle, and challenges reducing the distribution down to a single value as is currently done (Oleson et al., 2013).

**Figure 3.** The distribution of GPP estimates at each site. The distribution of GPP from the joint distribution of trait values is in gray, the green arrow indicates the mean of the distribution. Sites are ordered from coldest to hottest within rows which are determined by their climatic region, border colors display the annual average temperature per the color bar in the right column. The range of GPP values displayed on the x-axis is determined by the climatic region: boreal/temperate, arid, or tropical, the three are displayed on a common axis in the lower right corner.

#### *4.2 Phenology, trait distributions, and GPP*

We focus on the divergence between deciduous and evergreen phenology in terms of the influence of traits on GPP within the model. Phenology is a convenient division between SLA and LCN

because these two groups, evergreen and deciduous, occupy markedly different components of the global trait distribution for these two traits, Fig. 4. Deciduous PFTs cluster around the mean of both groups for SLA (Fig. 4a), while evergreen PFTs occupy the low valued tail of the SLA distribution. For LCN it is the reverse, evergreen PFTs are more strongly clustered around the mean of the two groups while deciduous PFTs skew into the tail. Because of the relationship between these traits and  $V_{\text{cmax}}$  (Eqn. 1-2), and therefore GPP, we expect these traits to have variable influence on model behavior for these two groups.

**Figure 4:** Distributions of inverse traits broken down by phenology. In both panels the inverse of SLA and LCN is shown to more easily visualize the impact on  $V_{\text{cmax}}$  (Eqns. 1-2), similarly both panels are centered on the mean value of both groups combined, this emphasizes deviation from a common value. Evergreen counts are shown in green, while deciduous values are in brown. In a) the evergreen PFTs skew towards high values of  $\text{SLA}^{-1}$ , while in b) the deciduous PFTs skew towards high values of  $\text{LCN}^{-1}$ .

As expected from the position of these phenological groups within the trait distributions, the trait-GPP relationships are quite different. The deciduous sites show a close coupling between LCN and GPP while the evergreen sites show a tighter relationship between SLA and GPP; to simplify across sites, GPP and traits are normalized across sites into z-scores (Fig. 5). We focus on SLA and LCN because LLS covaries closely with SLA (Table S2) and thus the relationship between LLS and GPP is largely redundant (Fig. S9). Further, SLA and LCN are directly coupled with  $V_{\text{cmax}}$ , as noted earlier. Further, LLS is only used with evergreen species as leaf lifespan is governed by a separate phenology module for deciduous PFTs. However, the inclusion of LLS is still critical for constraining model output for evergreen PFTs. Within ELM, phenological habit sorts PFTs into different portions of trait space, which then drives which trait will have a more predictable influence on GPP. However, as discussed below, apparent phenological habit is only a guide and not fully predictive of the model relationship between traits, environment, and productivity (see section 4.4).

**Figure 5:** Relationships between traits and GPP. Panels a) and b) are for deciduous sites and panels c) and d) are for the evergreen sites. Within each 2D histogram lighter colors indicate

more site-trait combinations that fall within the GPP-trait pixel, after normalization to z-scores. At the deciduous sites the relationship between LCN and GPP is constrained while SLA is more diffuse. The evergreen sites are the opposite, with a tight relationship between SLA and GPP and a more diffuse relationship with LCN.

**4.3 Comparing model GPP against flux data.** We compare three estimates of model GPP to evaluate how the representation of functional diversity influences the prediction of GPP and how those compare to an external benchmark. The first used unmodified trait values from the prior version of the model (*default*). Second, we updated the default values to the mean of the draws from the trait distribution (*updated mean*). Third, we produced an estimate using the distribution of traits as input (*distribution mean*). Across all sites, the difference between flux tower GPP and any of the three estimates (Fig. 6) were comparable. Formally, a Kruskal-Wallis test could not distinguish between the median differences of the flux tower GPP and all three GPP model estimates ( $p < 0.05$ ). The default mean had a root mean squared error ( $\pm$  standard deviation, across sites) of  $538 \pm 928 \text{ gC m}^{-2} \text{ yr}^{-1}$  versus  $624 \pm 950 \text{ gC m}^{-2} \text{ yr}^{-1}$  using the updated mean. The mean of all runs from the trait distribution, the distribution mean, is intermediate to the default and updated mean simulations with a root mean squared error of  $609 \pm 985 \text{ gC m}^{-2} \text{ yr}^{-1}$ . As is clear from the difference at each site (Table S3), all three configurations have comparable differences (on average) relative to the flux tower data, so we consider these results to be inconclusive regarding which of these methods is the best match to a flux tower benchmark. We further note that flux tower footprints cover only a tiny proportion of any (roughly  $100 \times 100 \text{ km}$ ) grid cell, and thus the vegetation in the flux footprint and the flux data are unlikely to represent the full diversity of the grid cell, so one should not necessarily expect a close match between tower flux data and grid cell model output. Despite this, we believe that comparisons with the flux tower data serve as a useful contextual framing, but not as validation of the models.

**Figure 6.** Each site's temporal mean annual GPP estimated by four different methods. The x-axis is labeled with the site ID (Fig. 1, Table 1). The colors of each bar indicate the method used to estimate GPP as indicated in the legend. Thin black lines are the temporal standard deviation at the site. The solid blue line across all bars at each site is the flux tower estimate of GPP and the dashed lines are the temporal standard deviation.

*4.4 Evaluating the difference between GPP from the trait distribution and the updated mean across sites.* A particular challenge to the single PFT representation that motivated this analysis is the non-linearity of the relationships between functional traits and carbon fluxes of ecosystems (Medvigy et al., 2009; Moorcroft et al., 2001). Jensen's Inequality (Cover & Thomas, 1991; Jensen, 1905) ensures that using the mean of the trait distribution as input to a convex function will give a lesser (or equal) result than taking the mean of the output of the function, and the opposite for a concave function (Fig. S10). Here, Jensen's Inequality serves as an entry point to evaluate the magnitude of difference that a single extant PFT, the updated mean, compares to a diverse set of organisms or subPFTs, the distribution mean. To summarize the influence of the trait distribution we used the mean of the model output over the observation period at each site. This provides an estimate of the magnitude of Jensen's inequality at these sites, which we may write as:

$$f(E[x]) \leq E[f(x)], \quad (4)$$

for a convex function  $f$ . When a function is concave the less than (or equal to) relationship reverses to greater than (or equal to), so  $f(E[x]) \geq E[f(x)]$ . In this equation the function  $f$ , represents the whole set of algorithms and equations that comprise the vegetation model in ELM,  $E[]$  indicates the expected value, and  $x$  is the distribution of trait values. In the context of this analysis the left-hand side of Eqn. (4) is the updated mean while the right-hand side is the distribution mean.

As already noted, using the updated (or for that matter, the default) mean masks considerable variation in projected GPP for the individual trait runs (Figs. 2-3,5). Beyond the distribution driven variation in model output the comparison of updated and distribution mean values between these sites reveals substantial differences, varying between a 36% increase and 6% decline when comparing the distribution mean of the trait distribution to the single updated mean value (Fig. 7). Four of 15 sites show an increase of at least 9% in GPP when using the distribution, with the largest percentage increase in one boreal shrub site; whereas on an absolute basis, the largest magnitude increase occurred at the two tropical forest sites (Fig. S11).

**Figure 7.** Difference in modeled GPP between the updated mean and the distribution mean. The x-axis labels are the corresponding site IDs (Fig. 1, Table 1) ordered from coldest to warmest. The largest percentage differences are in more extreme sites, with larger GPP estimates from the distribution at one boreal shrub site and both tropical evergreen sites but negligible differences at boreal tree sites. Temperate sites are mixed but generally negative. Phenological habit and the structure of the trait-GPP relationship provide some further insight into these differences, see Figs. 4-5 and 8.

Interestingly, the contrasting results between the distribution mean and the updated mean show that incorporating the distribution of functional traits as evaluated here did not have a consistent influence on model GPP, and hence the constraint implied by Jensen's inequality is not a straightforward guide to how functional diversity will affect model behavior. In short, the set of algorithms denoted by  $f(x)$  in Eqn. 4 does not respond consistently, even non-linearly, to trait input values (Fig. 8, S9). However, there is some rough structure to the differences between the updated mean and the distribution mean. The phenological differences (Fig. 4-5) are apparent here with a sharp contrast between increases at tropical evergreen sites and decreases in most deciduous angiosperm systems. However, boreal systems show a mixed effect the output at one of the very cold deciduous shrub sites had a large increase using trait distributions whereas the other boreal shrub site and the two boreal evergreen conifer sites showed almost no effect. One explanation for the deviation between boreal and tropical evergreen systems is that the tropics are photosynthetically active year-round, but the evergreen conifers have a long dormant season.

The phenological differences noted earlier (Fig. 4-5), coupled with a sub-set of four sites sheds some further light on the basis for the widely varying differences between the estimated GPP from the distribution mean relative to the updated mean. A suite of factors including how closely coupled each trait is with GPP as well as the non-linear structure of the relationship between the trait and GPP estimate both appear to influence this result. For example, in Shrub-Bo<sub>2</sub> there is a tight convex relationship between LCN and GPP (Fig. 8a) and this site has a substantial difference between the updated and distribution mean. By contrast, Tree\*-Te<sub>3</sub> (Fig 8b) shows a much

looser relationship and the distribution and updated means show notably different results. Critically the relationship flips to concave, which - as Jensen's Inequality would predict - induces a sign change between these two sites. However, among evergreen sites the tropical site Tree-Tr<sub>2</sub> (Fig. 8c) has only a slightly tighter relationship between SLA and GPP than Tree-Te<sub>3</sub> (Fig. 8d). Because both have concave SLA-GPP relationships it is now the variation around this relationship that drives a sign change between the updated and distribution mean. The variation of GPP for a given trait value occurs because we draw trait combinations from a joint distribution, e.g., there is a range of SLA values for a given LCN and vice versa. Even modest variation around the non-linear trait-GPP relationship can drive a substantial shift in the modeled output and in this case the trait variation appears to be a more dominant factor than the concavity of the trait-GPP relationship. The phenology still serves as a guide to the trait-GPP relationship, but Jensen's Inequality alone cannot predict how the distribution mean will vary relative to the updated mean.

**Figure 8: Non-linear trait-GPP relationships at four sites.** Two deciduous sites a) Shrub-Bo<sub>2</sub> and b) Tree\*-Te<sub>3</sub> and two evergreen sites c) Tree-Tr<sub>2</sub> and d) Tree-Te<sub>3</sub> highlight how differences in the trait-GPP relationship can drive divergent responses in the updated mean and the distribution mean depending on how tight the correspondence is between GPP and the trait value as well as the nature of the non-linear relationship. Blue lines indicate a non-linear fit of the form described in Eqn. 3.

## 5. Conclusions

Our analyses show that accounting for leaf functional diversity can have a substantial influence on modeled carbon fluxes. We focused our analysis on three approaches. First, we evaluated the distribution of modeled GPP when using a distribution of traits as input and found that GPP could vary over an order of magnitude at some sites among hypothetical 'patches' differing in traits. We found that phenological habit was a guide to which trait appears to govern the GPP response within the model with a contrast between deciduous and evergreen habits driven by LCN and SLA, respectively. This contrast is likely to result from the portion of trait space occupied by the PFTs within these phenology groups where deciduous trees have values of LCN more favorable to high  $V_{\text{cmax}}$  and the same for evergreen trees and SLA. Second, we compared three different modeling schemes against flux tower data, and found that all were generally in rough agreement



with tower data (except for one site), which we note represent only one of the myriad possible trait distributions within the large grid cells the model parameters are set to describe. Third, we evaluated how using updated mean trait values as input in modeling GPP compared to evaluating the distribution mean from the output of the distribution of trait values. A boreal shrub site and both tropical tree sites showed the greatest influence when modeling the trait distribution, with a notable but less pronounced effect at temperate tree sites. However, further work is needed to refine what drives both the non-linear structure and tightness of coupling between traits and modeled GPP. Until there is a stronger theoretical basis for these differences, explicitly modeling the trait distribution is the only means to ensure how varying traits will influence productivity.

By contrast with previous efforts to incorporate functional diversity into land surface models (Pavlick et al., 2013; Sakschewski et al., 2015, 2016), we developed an empirical method to derive representative trait combinations and use them for model ensemble runs, without explicit mechanisms for community assembly. This method is closer to the current framework applied in global vegetation models and could be implemented in future global simulations. There are competing ideas for both what can and should be improved in terrestrial vegetation models (Fatichi et al., 2019). Here, we have pioneered a method to incorporate empirical distributions of plant traits into the model structure as a method to simulate the functional diversity that occurs at the scales the models simulate ( $\approx 100$  km x 100km). The impact in tropical regions was consistently substantial and, while less consistent in boreal regions, the effect was potentially much greater in a proportional sense. Accurately simulating these vulnerable and rapidly changing regions is critical to improving projections of the global carbon cycle, and the magnitude of the response in these regions suggests that improving our understanding and modeling of trait diversity impacts on carbon cycling processes is of paramount importance.

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**Data Availability:** Analysis code and model output are stored in a Zenodo repository: <https://zenodo.org/record/6127506>.

## References

- Albritton, D. L., Meira Filho, L. G., Cubasch, U., Dai, X., Ding, Y., Griggs, D. J., et al. (2001). IPCC TAR: WG I Technical summary. *Climate Change*, 21–83.
- Bernacchi, C., Singsaas, E., Pimentel, C., Portis Jr, A., & Long, S. (2001). Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell & Environment*, 24(2), 253–259.
- Bernacchi, C. J., Pimentel, C., & Long, S. P. (2003). In vivo temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant, Cell & Environment*, 26(9), 1419–1430. <https://doi.org/10.1046/j.0016-8025.2003.01050.x>
- van Bodegom, P. M., Douma, J. C., & Verheijen, L. M. (2014). A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences*, 111(38), 13733–13738. <https://doi.org/10.1073/pnas.1304551110>
- Bonan, G. B., Lawrence, P. J., Oleson, K. W., Levis, S., Jung, M., Reichstein, M., et al. (2011). Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of Geophysical Research*, 116(G2), 1–22. <https://doi.org/10.1029/2010JG001593>

Bonan, G. B., Oleson, K. W., Fisher, R. A., Lasslop, G., & Reichstein, M. (2012). Reconciling leaf physiological traits and canopy flux data: Use of the TRY and FLUXNET databases in the Community Land Model version 4. *Journal of Geophysical Research: Biogeosciences*, *117*(2), 1–19. <https://doi.org/10.1029/2011JG001913>

Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., et al. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of National Academy of Sciences*, *114*(51), E10937–E10946.

Castruccio, S., McInerney, D., Stein, M., Liu, C. F., Jacob, R., & Moyer, E. (2014). Statistical emulation of climate model projections based on precomputed GCM runs. *Journal of Climate*, *27*(5), 1829–1844.

Cover, T. M., & Thomas, J. A. (1991). *Elements of Information Theory*. New York, NY: John Wiley & Sons.

Falge, E., Aubinet, M., Bakwin, P., Baldocchi, D., Berbigier, P., Bernhofer, C., et al. (2016). FLUXNET research network site characteristics, investigators, and bibliography. *Oak Ridge Natl. Lab., Oak Ridge, TN*.

Fatichi, S., Pappas, C., Zscheischler, J., & Leuzinger, S. (2019). Modelling carbon sources and sinks in terrestrial vegetation. *New Phytologist*, *221*(2), 652–668.

<https://doi.org/10.1111/nph.15451>

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., et al. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes: Plant functional traits. *Biological Reviews*, *92*(2), 1156–1173.

<https://doi.org/10.1111/brv.12275>

- Harper, A. B., Cox, P. M., Friedlingstein, P., Wiltshire, A. J., Jones, C. D., Sitch, S., et al. (2016). Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4.2) using plant trait information. *Geoscientific Model Development*, 9(7), 2415–2440. <https://doi.org/10.5194/gmd-9-2415-2016>
- Harrison, S. P., Prentice, I. C., Barboni, D., Kohfeld, K. E., Ni, J., & Sutra, J.-P. (2010). Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, 21(2), 300–317. <https://doi.org/10.1111/j.1654-1103.2009.01144.x>
- Isbell, F., Cowles, J., Dee, L. E., Loreau, M., Reich, P. B., Gonzalez, A., et al. (2018). Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology Letters*, 21(6), 763–778. <https://doi.org/10.1111/ele.12928>
- Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., et al. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, 215(1), 15–26. <https://doi.org/10.1111/nph.14486>
- Jensen, J. (1905). Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Mathematica*, 30(1), 175–193.
- Kattge, J., & et al. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26, 119–188.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., et al. (2011). TRY—a global database of plant traits. *Global Change Biology*, 17(9), 2905–2935.
- Koven, C. D., Riley, W. J., Subin, Z. M., Tang, J. Y., Torn, M. S., Collins, W. D., et al. (2013). The effect of vertically resolved soil biogeochemistry and alternate soil C and N models

on C dynamics of CLM4. *Biogeosciences*, 10(11), 7109–7131.

<https://doi.org/10.5194/bg-10-7109-2013>

Lamarque, J.-F., Bond, T. C., Eyring, V., Granier, C., Heil, A., Klimont, Z., et al. (2010).

Historical (1850–2000) gridded anthropogenic and biomass burning emissions of reactive gases and aerosols: methodology and application. *Atmospheric Chemistry and Physics*, 10(15), 7017–7039. <https://doi.org/10.5194/acp-10-7017-2010>

Leuning, R. (2002). Temperature dependence of two parameters in a photosynthesis model.

*Plant, Cell & Environment*, 25(9), 1205–1210.

Liang, J., Lee, B., Ngugi, M. R., Rovero, F., Herault, B., Schmid, B., et al. (2016). Positive

biodiversity-productivity relationship predominant in global forests. *Science*, 354(6309), aaf8957–aaf8957. <https://doi.org/10.1126/science.aaf8957>

Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y., & Moorcroft, P. R. (2009).

Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research*, 114(G1).

<https://doi.org/10.1029/2008JG000812>

Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling vegetation

dynamics: the ecosystem demography model (ED). *Ecological Monographs*, 71(4), 557–586.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., et al.

(2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15(12), 684–692. <https://doi.org/10.1016/j.tplants.2010.09.008>

Oehri, J., Schmid, B., Schaepman-Strub, G., & Niklaus, P. A. (2017). Biodiversity promotes

primary productivity and growing season lengthening at the landscape scale. *Proceedings*

*of the National Academy of Sciences*, 114(38), 10160–10165.

<https://doi.org/10.1073/pnas.1703928114>

Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., et al. (2013). *Technical Description of version 4.5 of the Community Land Model (CLM)* (No. Climate and Global Dynamics Division) (p. 434). <https://doi.org/10.5065/D6RR1W7M>

Pappas, C., Fatichi, S., & Burlando, P. (2014). Terrestrial water and carbon fluxes across climatic gradients: does plant diversity matter? *New Phytologist*, 16(i), 3663.

<https://doi.org/10.1111/nph.13590>

Pavlick, R., Reu, B., Bohn, K., Kleidon, A., & Drewry, D. T. (2013). The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs.

*Biogeosciences*, 10(6), 4137–4177. <https://doi.org/10.5194/bg-10-4137-2013>

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., et al. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563(7729), 109–112.

<https://doi.org/10.1038/s41586-018-0627-8>

Quillet, A., Peng, C., & Garneau, M. (2010). Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews*, 18(NA), 333–353.

<https://doi.org/10.1139/A10-016>

Reich, P. B., Rich, R. L., Lu, X., Wang, Y.-P., & Oleksyn, J. (2014). Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections.

*Proceedings of the National Academy of Sciences*, 111(38), 13703–13708.

<https://doi.org/10.1073/pnas.1216054110>

Reich, Peter B. (2012). Key canopy traits drive forest productivity. *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2128–2134.

<https://doi.org/10.1098/rspb.2011.2270>

Reich, Peter B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>

Ricciuto, D., Sargsyan, K., & Thornton, P. (2018). The Impact of Parametric Uncertainties on Biogeochemistry in the E3SM Land Model. *Journal of Advances in Modeling Earth Systems*, 10(2), 297–319. <https://doi.org/10.1002/2017MS000962>

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., et al. (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, 21(7), 2711–2725.

<https://doi.org/10.1111/gcb.12870>

Sakschewski, B., von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., et al. (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*, 6(11), 1032–1036. <https://doi.org/10.1038/nclimate3109>

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist*, 198(3), 957–969.

<https://doi.org/10.1111/nph.12210>

Sellers, P. J., Mintz, Y., Sud, Y. C., & Dalcher, A. (1986). A Simple Biosphere Model (SiB) for Use within General Circulation Models. *Journal of the Atmospheric Sciences*, 43(6), 505–531.

- Swenson, S., Lawrence, D., & Lee, H. (2012). Improved simulation of the terrestrial hydrological cycle in permafrost regions by the Community Land Model. *Journal of Advances in Modeling Earth Systems*, 4(3).
- Thornton, P. E., & Rosenbloom, N. A. (2005). Ecosystem model spin-up: Estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecological Modelling*, 189(1–2), 25–48. <https://doi.org/10.1016/j.ecolmodel.2005.04.008>
- Thornton, P. E., & Zimmermann, N. E. (2007). An Improved Canopy Integration Scheme for a Land Surface Model with Prognostic Canopy Structure. *Journal of Climate*, 20(15), 3902–3923. <https://doi.org/10.1175/JCLI4222.1>
- Thornton, P. E., Lamarque, J.-F., Rosenbloom, N. A., & Mahowald, N. M. (2007). Influence of carbon-nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Global Biogeochemical Cycles*, 21(4).
- Tilman, D., Reich, P. B., & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences*, 109(26), 10394–10397. <https://doi.org/10.1073/pnas.1208240109>
- Virtanen, P., Gommers, R., Oliphant, T. E., Haberland, M., Reddy, T., Cournapeau, D., et al. (2020). SciPy 1.0: Fundamental Algorithms for Scientific Computing in Python. *Nature Methods*, 17, 261–272. <https://doi.org/10.1038/s41592-019-0686-2>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827.
- Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., et al. (2014). Plant functional types in Earth system models: Past experiences and future



directions for application of dynamic vegetation models in high-latitude ecosystems.

*Annals of Botany*, 114(1), 1–16. <https://doi.org/10.1093/aob/mcu077>

Yang, X., Thornton, P., Ricciuto, D., & Post, W. (2014). The role of phosphorus dynamics in tropical forests—a modeling study using CLM-CNP. *Biogeosciences*, 11(6), 1667–1681.

Yang, Xiaojuan, Ricciuto, D. M., Thornton, P. E., Shi, X., Xu, M., Hoffman, F., & Norby, R. J. (2019). The effects of phosphorus cycle dynamics on carbon sources and sinks in the amazon region: a modeling study using ELM v1. *Journal of Geophysical Research: Biogeosciences*, 124(12), 3686–3698.

#### References From the Supporting Information

Adler, PB, Milchunas, DG, Lauenroth, WK, Sala, OE, and Burke, IC. (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 2004 41, 653-663

Adriaenssens S. (2012). Dry deposition and canopy exchange for temperate tree species under high nitrogen deposition. PhD thesis, Ghent University, Ghent, Belgium, 209p.

Atkin, O. K., M. H. M. Westbeek, M. L. Cambridge, H. Lambers, and T. L. Pons. 1997. Leaf respiration in light and darkness - A comparison of slow- and fast-growing *Poa* species. *Plant Physiology* 113:961-965.

Atkin, O. K., M. Schortemeyer, N. McFarlane, and J. R. Evans. 1999. The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO<sub>2</sub>: an analysis of the underlying components of relative growth rate. *Oecologia* 120:544-554.

Auger, S., Shipley, B. (2012). : Interspecific and intraspecific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science*. DOI: 1111/j.1654-1103.2012.01473.x

Bahn, M., G. Wohlfahrt, E. Haubner, I. Horak, W. Michaeler, K. Rottmar, U. Tappeiner, and A. Cernusca. 1999. Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. Pages 247-255 in A.

Bakker, C., J. Rodenburg, and P. Bodegom. 2005. Effects of Ca- and Fe-rich seepage on P availability and plant performance in calcareous dune soils. *Plant and Soil* 275:111-122.

- Bakker, C., P. M. Van Bodegom, H. J. M. Nelissen, W. H. O. Ernst, and R. Aerts. 2006. Plant responses to rising water tables and nutrient management in calcareous dune slacks. *Plant Ecology* 185:19-28.
- Baraloto, C., C. E. T. Paine, L. Poorter, J. Beauchene, D. Bonal, A.-M. Domenach, B. Herault, S. Patino, J.-C. Roggy, and J. Chave. 2010. Decoupled leaf and stem economics in rainforest trees. *Ecology Letters* 13:1338-1347
- Beckmann, M, Hock, M, Bruelheide, H, and A Erfmeier (2012) The role of UV-B radiation in the invasion of *Hieracium pilosella* - A comparison of German and New Zealand plants. *Environmental and Experimental Botany* 75 173- 180
- Blonder, B., Buzzard, B., Sloat, L., Simova, I., Lipson, R., Boyle, B., Enquist, B. The shrinkage effect biases estimates of paleoclimate. *American Journal of Botany* (2012).
- Blonder, B., Vasseur, F., Violle, C., Shipley, B., Enquist, B.J., Vile, D. Testing models for the leaf economics spectrum with leaf and whole-plant traits in *Arabidopsis thaliana*, *AoB PLANTS*, Volume 7, 2015, plv049, <https://doi.org/10.1093/aobpla/plv049>
- Blonder, B., Violle, C. and Enquist, B.J. (2013), Assessing the causes and scales of the leaf economics spectrum using venation networks in *Populus tremuloides*. *J Ecol*, 101: 981-989. <https://doi.org/10.1111/1365-2745.12102>
- Bond-Lamberty, B., C. Wang, and S. T. Gower (2002), Leaf area dynamics of a boreal black spruce fire chronosequence, *Tree Physiol.*, 22(14), 993-1001.
- Brendan Choat, Steven Jansen, Tim J. Brodribb, Herve Cochard, Sylvain Delzon, Radika Bhaskar, Sandra J. Bucci, Taylor S. Feild, Sean M. Gleason, Uwe G. Hacke, Anna L. Jacobsen, Frederic Lens, Hafiz Maherali, Jordi Martinez-Vilalta, Stefan Mayr, Maurizio Mencuccini, Patrick J. Mitchell, Andrea Nardini, Jarmila Pittermann, R. Brandon Pratt, John S. Sperry, Mark Westoby, Ian J. Wright & Amy E. Zanne (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491:752-755 doi:10.1038/nature11688
- Brown et al. (2011) *PLoS ONE* 6(9): e24107. doi:10.1371/journal.pone.0024107
- S. Burrascano, R. Copiz, E. Del Vico, S. Fagiani, E. Giarrizzo, M. Mei, A. Mortelliti, F. M. Sabatini, and C. Blasi. Wild boar rooting intensity determines shifts in understory composition and functional traits. (2015) *Community ecology* 16, no. 2, 244-253. doi: [10.1556/168.2015.16.2.12](https://doi.org/10.1556/168.2015.16.2.12)
- Butterfield, B.J. and J.M. Briggs. 2011. Regeneration niche differentiates functional strategies of desert woody plant species. *Oecologia*, 165:477-487.

- Byun C, S de Blois, J Brisson (2012) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, doi: 10.1111/1365-2745.12016
- Campbell, C., L. Atkinson, J. Zaragoza-Castells, M. Lundmark, O. Atkin, and V. Hurry. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist* 176:375-389.
- Campetella, G; Botta-Dukát, Z; Wellstein, C; Canullo, R; Gatto, S; Chelli, S; Mucina, L; Bartha, S (2011): Patterns of plant trait-environment relationships along a forest succession chronosequence. *Agriculture, Ecosystems & Environment*, 145(1), 38-48. doi:10.1016/j.agee.2011.06.025
- Carnell, R. 2018. lhs: Latin Hypercube Samples. R.
- Carswell, F. E., Meir, P., Wandelli, E. V., Bonates, L. C. M., Kruijt, B., Barbosa, E. M., Nobre, A. D. & Jarvis, P. G. 2000 Photosynthetic capacity in a central Amazonian rain forest. *Tree physiology*. 20, 3, p. 179-186 8 p.
- Castruccio, S., D. McInerney, M. Stein, C. F. Liu, R. Jacob, and E. Moyer. 2014. Statistical emulation of climate model projections based on precomputed GCM runs. *Journal of Climate* 27:1829–1844.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:S109-S122.
- Cavender-Bares, J., L. Sack, and J. Savage. 2007. Atmospheric and soil drought reduce nocturnal conductance in live oaks. *Tree Physiology* 27:611-620.
- Cerabolini B.E.L., Brusa G., Ceriani R.M., De Andreis R., Luzzaro A. & Pierce S. 2010. Can CSR classification be generally applied outside Britain? *Plant Ecology* 210: 253-261
- Cernusca, U. Tappeiner, and N. Bayfield, editors. Land-use changes in European mountain ecosystems. ECOMONT- Concept and Results. Blackwell Wissenschaft, Berlin.
- Chen, Y, Han, W, Tang, L, Tang, Z, and Fang, J. 2011 Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography* 34, doi: 10.1111/j.1600-0587.2011.06833.x
- Coomes, D. A., S. Heathcote, E. R. Godfrey, J. J. Shepherd, and L. Sack. 2008. Scaling of xylem vessels and veins within the leaves of oak species. *Biology Letters* 4:302-306.
- Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84:573-582.
- Cornelissen, J. H. C., B. Cerabolini, P. Castro-Diez, P. Villar-Salvador, G. Montserrat-Marti, J. P. Puyravaud, M. Maestro, M. J. A. Werger, and R. Aerts. 2003. Functional traits of

woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* 14:311-322.

Cornelissen, J. H. C., H. M. Quested, D. Gwynn-Jones, R. S. P. Van Logtestijn, M. A. H. De Beus, A. Kondratchuk, T. V. Callaghan, and R. Aerts. 2004. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology* 18:779-786.

Cornelissen, J. H. C., P. C. Diez, and R. Hunt. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology* 84:755-765.

Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, N. Pérez-Harguindeguy, H. M. Quested, L. S. Santiago, D. A. Wardle, I. J. Wright, R. Aerts, S. D. Allison, P. van Bodegom, V. Brovkin, A. Chatain, T. V. Callaghan, S. Díaz, E. Garnier, D. E. Gurvich, E. Kazakou, J. A. Klein, J. Read, P. B. Reich, N. A. Soudzilovskaia, M. V. Vaieretti, and M. Westoby. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11:1065-1071.

Cornwell, W. K., R. Bhaskar, L. Sack, S. Cordell, and C. K. Lurch. 2007. Adjustment of structure and function of Hawaiian *Metrosideros polymorpha* at high vs. low precipitation. *Functional Ecology* 21:1063-1071.

Craine JM, Nippert JB, Towne EG, Tucker S, Kembel SW, Skibbe A, McLauchlan KK (2011) Functional consequences of climate-change induced plant species loss in a tallgrass prairie. *Oecologia* 165: 1109-1117

Craine JM, Towne EG, Ocheltree TW, Nippert JB (2012) Community traitscape of foliar nitrogen isotopes reveals N availability patterns in a tallgrass prairie. *Plant Soil* 356: 395-403

Craine, J. M., A. J. Elmore, M. P. M. Aida, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, M. C. Mack, K. K. McLauchlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, J. Penuelas, P. B. Reich, E. A. G. Schuur, W. D. Stock, P. H. Templer, R. A. Virginia, J. M. Welker, and I. J. Wright. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* 183:980-992.

Craine, J. M., W. G. Lee, W. J. Bond, R. J. Williams, and L. C. Johnson. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology* 86:12-19.

Craven, D., Braden, D., Ashton, M. S., Berlyn, G. P., Wishnie, M., and Dent., D. 2007. Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *Forest Ecology and Management* 238:335-346.

- Demey A, J Staelens, L Baeten, P Boeckx, M Hermy, J Kattge, K Verheyen (2013) Nutrient input from hemiparasitic litter favors plant species with a fast-growth strategy. *Plant and Soil* DOI 10.1007/s11104-013-1658-4
- Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Martí, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M. C. Pérez-Rontomé, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15:295-304.
- Domingues TF, Meir P, Feldpausch TR, et al. (2010) Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant, Cell & Environment* (33): 959-980.
- Domingues, TF, Martinelli, LA, Ehleringer, JR. (2007) Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil. *Plant Ecol* (2007) 193:101-112 DOI 10.1007/s11258-006-9251-z
- Dunbar-Co, S., M. J. Sporck, and L. Sack. 2009. Leaf Trait Diversification and Design in Seven Rare Taxa of the Hawaiian Plantago Radiation. *International Journal of Plant Sciences* 170:61-75.
- Fitter, A. H. and H. J. Peat 1994. The Ecological Flora Database. *Journal of Ecology* 82:415-425.
- Fonseca, C. R., J. M. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88:964-977.
- Frenette-Dussault, C., Shipley, B., Léger, J.F., Meziane, D. & Hingrat, Y. (2012). Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *Journal of Vegetation Science* 23: 208-222.
- Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology* 98:362-373.
- Fyllas, N. M., S. Patino, T. R. Baker, G. Bielefeld Nardoto, L. A. Martinelli, C. A. Quesada, R. Paiva, M. Schwarz, V. Horna, L. M. Mercado, A. Santos, L. Arroyo, E. M. Jimenez, F. J. Luizao, D. A. Neill, N. Silva, A. Prieto, A. Rudas, M. Silveira, I. C. G. Vieira, G. Lopez-Gonzalez, and J. Lloyd. 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate *Biogeosciences* 6:2677-2708.
- Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, E. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Lepš, T. Meier, R. Pakeman, M. Papadimitriou, V. P. Papanastasis, H. Quested, F. Quéfier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J.-P. Theau, A. Thébault, D. Vile, and M. P. Zarovali. 2007. Assessing the effects of land-use

change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* 99:967-985.

- Givnish T.J., Montgomery, R.A., and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany* 91: 228-246
- Gutiérrez AG, & Huth A (2012) Successional stages of primary temperate rainforests of Chiloé Island, Chile. *Perspectives in plant ecology, systematics and evolution*. 14: 243- 256
- Guy, A. L., Mischkolz, J. M., and E. G. Lamb. 2013. Limited effects of simulated acidic deposition on seedling survivorship and root morphology of endemic plant taxa of the Athabasca Sand Dunes in well watered greenhouse trials. *Botany* 91:176-181.  
<http://dx.doi.org/10.1139/cjb-2012-0162>
- Han, W. X., J. Y. Fang, D. L. Guo, and Y. Zhang. 2005. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist* 168:377-385.
- Hao, G. Y., L. Sack, A. Y. Wang, K. F. Cao, and G. Goldstein. 2010. Differentiation of leaf water flux and drought tolerance traits in hemiepiphytic and non-hemiepiphytic *Ficus* tree species. *Functional Ecology* 24:731-740.
- Hickler, T. 1999. Plant functional types and community characteristics along environmental gradients on Öland's Great Alvar (Sweden) Masters Thesis, University of Lund, Sweden.
- Hoof, J., L. Sack, D. T. Webb, and E. T. Nilsen. 2008. Contrasting structure and function of pubescent and glabrous varieties of Hawaiian *Metrosideros polymorpha* (Myrtaceae) at high elevation. *Biotropica* 40:113-118.
- Kattge, J., W. Knorr, T. Raddatz, and C. Wirth. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* 15:976-991.
- Kazakou, E., D. Vile, B. Shipley, C. Gallet, and E. Garnier. 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* 20:21-30.
- Kennedy, M., and A. O'Hagan. 2001. Bayesian calibration of computer models. *Journal of the Royal Statistical Society Series B (Statistical Methodology)* 63:425-464.
- Kerkhoff, A. J., W. F. Fagan, J. J. Elser, and B. J. Enquist. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist* 168:E103-E122.
- Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W. and Freschet, G.T. (2013), Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along

an environmental gradient. *Funct Ecol*, 27: 1254-1261. <https://doi.org/10.1111/1365-2435.12116>

- Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschod, J. M. van Groenendael, L. Klimes, J. Klimesova, S. Klotz, G. M. Rusch, Hermy, M., D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-K. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96:1266-1274.
- Kraft, N. J. B., R. Valencia, and D. Ackerly. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322:580-582.
- Kurokawa, H. and T. Nakashizuka. 2008. Leaf herbivory and decomposability in a Malaysian tropical rain forest. *Ecology* 89:2645-2656.
- Laughlin, D. C., J. J. Leppert, M. M. Moore, and C. H. Sieg. 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24:493-501.
- Laughlin, D.C., P.Z. Fulé, D.W. Huffman, J. Crouse, and E. Laliberte. 2011. Climatic constraints on trait-based forest assembly. *Journal of Ecology* 99:1489-1499.
- Louault, F., V. D. Pillar, J. Aufrere, E. Garnier, and J. F. Soussana. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* 16:151-160.
- Loveys, B. R., L. J. Atkinson, D. J. Sherlock, R. L. Roberts, A. H. Fitter, and O. K. Atkin. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology* 9:895-910.
- Martin, R. E., G. P. Asner, and L. Sack. 2007. Genetic variation in leaf pigment, optical and photosynthetic function among diverse phenotypes of *Metrosideros polymorpha* grown in a common garden. *Oecologia* 151:387-400.
- Medlyn, B. E., F.-W. Badeck, D. G. G. De Pury, C. V. M. Barton, M. Broadmeadow, R. Ceulemans, P. De Angelis, M. Forstreuter, M. E. Jach, S. Kellomäki, E. Laitat, M. Marek, S. Philippot, A. Rey, J. Strassmeyer, K. Laitinen, R. Liozon, B. Portier, P. Roberntz, K. Wang, and P. G. Jarvis. 1999. Effects of elevated CO<sub>2</sub> on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell and Environment* 22:1475-1495.
- Meir, P. & Levy, P. E. 2007 Photosynthetic parameters from two contrasting woody vegetation types in West Africa. *Plant Ecology*. 192, 2, p. 277-287 11 p.

- Meir, P., Kruijt, B., Broadmeadow, M., Kull, O., Carswell, F. & Nobre, A. 2002 Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. *Plant, Cell and Environment*. 25, 3, p. 343-357 15 p.
- Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13:838-848.
- Meziane, D. and B. Shipley. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant Cell and Environment* 22:447-459.
- Milla & Reich 2011 *Annals of Botany* 107: 455-465, 2011.
- Minden, V, Andratschke, S, Spalke, J, Timmermann, H, Kleyer, M. (2012): Plant trait-environment relationships in salt marshes: Deviations from predictions by ecological concepts. *Perspectives in Plant Ecology, Evolution and Systematics*, 14: 183-192
- Minden, V, Kleyer, M. (2011): Testing the effect-response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science* 22: 387-401
- Nakahashi, C. D., K. Frole, and L. Sack. 2005. Bacterial leaf nodule symbiosis in *Ardisia* (Myrsinaceae): Does it contribute to seedling growth capacity? *Plant Biology* 7:495-500.
- Niinemets, U. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology* 82:453-469.
- Ogaya, R. and J. Penuelas. 2003. Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany* 50:137-148.
- Onoda, Y., M. Westoby, P. B. Adler, A. M. F. Choong, F. J. Clissold, J. H. C. Cornelissen, S. Diaz, N. J. Dominy, A. Elgart, L. Enrico, P. V. A. Fine, J. J. Howard, A. Jalili, K. Kitajima, H. Kurokawa, C. McArthur, P. W. Lucas, L. Markesteijn, N. Perez-Harguindeguy, L. Poorter, L. Richards, L. S. Santiago, Jr. E. Sosinski, S. Van Bael, D. I. Warton, I. J. Wright, S. J. Wright, and N. Yamashita. 2011 . Global patterns of leaf mechanical properties. *Ecology Letters* 14:301-312.
- Ordóñez, J. C., P. M. van Bodegom, J. P. M. Witte, R. P. Bartholomeus, J. R. van Hal, and R. Aerts. 2010. Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments: Does Theory Mirror Nature? *American Naturalist* 175:225-239.
- Pahl, A.T., Kollmann, J., Mayer, A. & Haider, S. (2013): No evidence for local adaptation in an invasive alien plant: field and greenhouse experiments tracing a colonization sequence. *Annals of Botany* 112 (9): 1921-1930. DOI: 10.1093/aob/mct246



- Peco B., de Pablos I., Traba J. , & Levassor C. (2005) The effect of grazing abandonment on species composition and functional traits: the case of dehesa *Basic and Applied Ecology*, 6(2): 175-183
- Penuelas, J., J. Sardans, J. Llusia, S. Owen, J. Carnicer, T. W. Giambelluca, E. L. Rezende, M. Waite, and Ü. Niinemets. 2010. Faster returns on "leaf economics" and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology* 16:2171-2185.
- Pierce S., Brusa G., Sartori M. & Cerabolini B.E.L. 2012. Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. *Annals of Botany* 109(5): 1047-1053
- Pierce S., Brusa G., Vagge I. & Cerabolini B.E.L. 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology* (in press) DOI: 10.1111/1365-2435.12095.
- Pierce S., Ceriani R.M., De Andreis R., Luzzaro A. & Cerabolini B. 2007. The leaf economics spectrum of Poaceae reflects variation in survival strategies. *Plant Biosystems* 141(3): 337-343.
- Pierce S., Luzzaro A., Caccianiga M., Ceriani R.M. & Cerabolini B. 2007. Disturbance is the principal  $\alpha$ -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology* 95: 698-706.
- Pillar, V. D. and E. E. Sosinski. 2003. An improved method for searching plant functional types by numerical analysis. *Journal of Vegetation Science* 14:323-332.
- Poorter, H., U. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182:565-588.
- Powers, JS and Tiffin, P. 2012 Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology* 2010, 24, 927-936 doi: 10.1111/j.1365-2435.2010.01701.x
- Prentice, I.C., Meng, T., Wang, H., Harrison, S.P., Ni, J., Wang, G., 2011. Evidence for a universal scaling relationship of leaf CO<sub>2</sub> drawdown along a moisture gradient. *New Phytologist* 190: 169-180
- Preston, K. A., W. K. Cornwell, and J. L. DeNoyer. 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist* 170:807-818.
- Price, C.A. and B.J. Enquist. Scaling of mass and morphology in Dicotyledonous leaves: an extension of the WBE model. (2007) *Ecology* 88(5): 1132-1141.
- Pyankov, V. I., A. V. Kondratchuk, and B. Shipley. 1999. Leaf structure and specific leaf mass: the alpine desert plants of the Eastern Pamirs, Tadjikistan. *New Phytologist* 143:131-142.

- Quero, J. L., R. Villar, T. Maranon, R. Zamora, D. Vega, and L. Sack. 2008. Relating leaf photosynthetic rate to whole-plant growth: drought and shade effects on seedlings of four *Quercus* species. *Functional Plant Biology* 35:725-737.
- Quested, H. M., J. H. C. Cornelissen, M. C. Press, T. V. Callaghan, R. Aerts, F. Trosien, P. Riemann, D. Gwynn-Jones, A. Kondratchuk, and S. E. Jonasson. 2003. Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. *Ecology* 84:3209-3221.
- Reich, P. B., J. Oleksyn, and I. J. Wright. 2009. Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. *Oecologia* 160:207-212.
- Reich, P. B., M. G. Tjoelker, K. S. Pregitzer, I. J. Wright, J. Oleksyn, and J. L. Machado. 2008. Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters* 11:793-801.
- Rougier, J., D. Sexton, J. Murphy, and D. Stainforth. 2009. Analyzing the climate sensitivity of HadSM3 climate model using ensembles from different but related experiments. *Journal of Climate* 22:3540–3557.
- Roustant, O., D. Ginsbourger, and Y. Deville. 2012. DiceKriging, DiceOptim: Two R packages for the analysis of computer experiments by kriging-based metamodeling and optimization.
- Sacks, J., W. Welch, T. Mitchell, and H. Wynn. 1989. Design and analysis of computer experiments. *Statistical Science* 1:409–423.
- Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* 107:110-127.
- Sack, L., M. T. Tyree, and N. M. Holbrook. 2005. Leaf hydraulic architecture correlates with regeneration irradiance in tropical rainforest trees. *New Phytologist* 167:403-413.
- Sack, L., P. D. Cowan, N. Jaikumar, and N. M. Holbrook. 2003. The 'hydrology' of leaves: coordination of structure and function in temperate woody species. *Plant Cell and Environment* 26:1343-1356.
- Sack, L., P. J. Melcher, W. H. Liu, E. Middleton, and T. Pardee. 2006. How strong is intracopy leaf plasticity in temperate deciduous trees? *American Journal of Botany* 93:829-839.
- Sandel, D., Corbin, J. D., and Krupa, M. 2011. Using plant functional traits to guide restoration: A case study in California coastal grassland. *Ecosphere* 2:art23. <http://dx.doi.org/10.1890/2153-3703.2011.02.art23>
- Scherer-Lorenzen, M., Schulze, E.-D., Don, A., Schumacher, J. & Weller, E. (2007) Exploring the functional significance of forest diversity: A new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 53-70.

Scoffoni, C., A. Pou, K. Aasamaa, and L. Sack. 2008. The rapid light response of leaf hydraulic conductance: new evidence from two experimental methods. *Plant Cell and Environment* 31:1803-1812.

Shiodera, S., J. S. Rahajoe, and T. Kohyama. 2008. Variation in longevity and traits of leaves among co-occurring understorey plants in a tropical montane forest. *Journal of Tropical Ecology* 24:121-133.

Shiple B., 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance, *Functional Ecology*(16) 682-689

Shiple, B. 1995. Structured Interspecific Determinants of Specific Leaf-Area in 34 Species of Herbaceous Angiosperms. *Functional Ecology* 9:312-319.

Shiple, B. and M. J. Lechowicz. 2000. The functional co-ordination of leaf morphology, nitrogen concentration, and gas exchange in 40 wetland species. *Ecoscience* 7:183-194.

Shiple, B. and T. T. Vu. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist* 153:359-364.

Spasojevic, M. J. and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100:652-661.

Stein, M. 1987. Large sample properties of simulations using Latin hypercube sampling. *Technometrics* 29:143-151.

Swaine, E. K. 2007. Ecological and evolutionary drivers of plant community assembly in a Bornean rain forest. PhD Thesis, University of Aberdeen, Aberdeen.

Tucker SS, Craine JM, Nippert JB (2011) Physiological drought tolerance and the structuring of tallgrass assemblages. *Ecosphere* 2(4): 48

unpub.

van Bodegom, P. M., B. K. Sorrell, A. Oosthoek, C. Bakke, and R. Aerts. 2008. Separating the effects of partial submergence and soil oxygen demand on plant physiology. *Ecology* 89:193-204.

Vergutz, L., S. Manzoni, A. Porporato, R.F. Novais, and R.B. Jackson. 2012. A Global Database of Carbon and Nutrient Concentrations of Green and Senesced Leaves. Data set. Available on-line [<http://daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. <http://dx.doi.org/10.3334/ORNLDAAC/1106>

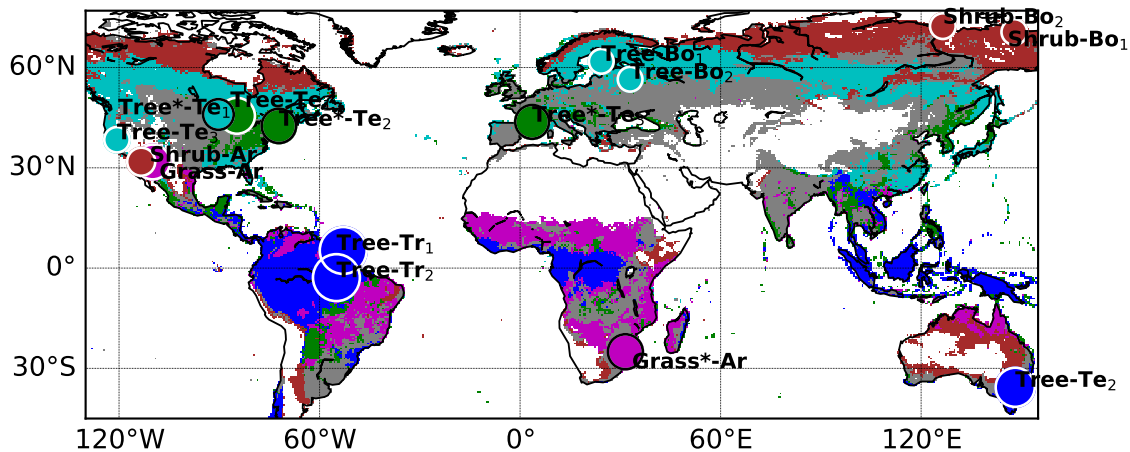
Vile, D. 2005. Significations fonctionnelle et ecologique des traits des especes vegetales: exemple dans une succession post-cultural mediterraneenne et generalisations, PHD Thesis.

- Waite, M. and L. Sack. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytologist* 185:156-172.
- Wenxuan Han, Yahan Chen, Fang-Jie Zhao, Luying Tang, Rongfeng Jiang and Fusuo Zhang, 2011, Floral, climatic and soil pH controls on leaf ash content in China's terrestrial plants. *Global Ecology and Biogeography*, DOI: 10.1111/j.1466-8238.2011.00677.x
- Williams, M., Shimabokuro, Y.E. and E.B. Rastetter. 2012. LBA-ECO CD-09 Soil and Vegetation Characteristics, Tapajos National Forest, Brazil. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. <http://dx.doi.org/10.3334/ORNLDAAAC/1104>
- Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography* 33:565-577.
- Wilson K, Baldocchi, D, Hanson, P. (2000) Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology* 20, 565-578
- Wirth, C. and J. W. Lichstein. 2009. The Imprint of Species Turnover on Old-Growth Forest Carbon Balances - Insights From a Trait-Based Model of Forest Dynamics. Pages 81-113 in C. Wirth, G. Gleixner, and M. Heimann, editors. *Old-Growth Forests: Function, Fate and Value*. Springer, New York, Berlin, Heidelberg.
- Wright JP, Sutton-Grier A (2012) Does the leaf economic spectrum hold within local species pools across varying environmental conditions? *Functional Ecology* 2012 doi: 10.1111/1365-2435.12001
- Wright, I. J., D. D. Ackerly, F. Bongers, K. E. Harms, G. Ibarra-Manriquez, M. Martinez-Ramos, S. J. Mazer, H. C. Muller-Landau, H. Paz, N. C. A. Pitman, L. Poorter, M. R. Silman, C. F. Vriesendorp, C. O. Webb, M. Westoby, and S. J. Wright. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99:1003-1015.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821-827.
- Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Díaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2011. Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology* 91:3664-3674.

Xu, L. K. and D. D. Baldocchi. 2003. Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology* 23:865-877.

Yguel B., Bailey R., Tosh N.D., Vialatte A., Vasseur C., Vitrac X., Jean F. & Prinzing A. (2011). Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives. *Ecol. Lett.*, 14, 1117-1124.

## Site Locations and Dominant PFT



- |  |   |
|--|---|
| <span style="color: green;">●</span> Broadleaf Deciduous | <span style="color: magenta;">●</span> C4 Grass |
| <span style="color: blue;">●</span> Broadleaf Evergreen  | ○ Mixed   |
| <span style="color: cyan;">●</span> Needleleaf Evergreen | ● Crop/C3 Grass                                 |
| <span style="color: red;">●</span> Shrub                 | ● Desert/Unvegetated                            |

